Ocelot Population Status in Protected Brazilian Atlantic Forest

Rodrigo Lima Massara1,2*, Ana Maria de Oliveira Paschoal1,2, Paul Francis Doherty, Jr.3, André Hirsch4, Adriano Garcia Chiarello5

1 Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil, 2 Instituto SerraDiCal de Pesquisa e Conservação, Belo Horizonte, Minas Gerais, Brazil, 3 Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, United States of America, 4 Programa Institucional de Bioengenharia, Universidade Federal de São João Del Rei, Sete Lagoas, Minas Gerais, Brazil, 5 Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, São Paulo, Brazil

* rmassara@gmail.com

Abstract

Forest fragmentation and habitat loss are detrimental to top carnivores, such as jaguars (Panthera onca) and pumas (Puma concolor), but effects on mesocarnivores, such as ocelots (Leopardus pardalis), are less clear. Ocelots need native forests, but also might benefit from the local extirpation of larger cats such as pumas and jaguars through mesopredator release. We used a standardized camera trap protocol to assess ocelot populations in six protected areas of the Atlantic forest in southeastern Brazil where over 80% of forest remnants are < 50 ha. We tested whether variation in ocelot abundance could be explained by reserve size, forest cover, number of free-ranging domestic dogs and presence of top predators. Ocelot abundance was positively correlated with reserve size and the presence of top predators (jaguar and pumas) and negatively correlated with the number of dogs. We also found higher detection probabilities in less forested areas as compared to larger, intact forests. We suspect that smaller home ranges and higher movement rates in smaller, more degraded areas increased detection. Our data do not support the hypothesis of mesopredator release. Rather, our findings indicate that ocelots respond negatively to habitat loss, and thrive in large protected areas inhabited by top predators.

Introduction

Fragmentation and habitat loss are serious threats to tropical forest biodiversity [1, 2] and the Atlantic Forest is no exception [3–5]. The vast majority of remnants (> 80%) in this biome are smaller than 50 ha and 61% of these are more than 25 km from protected areas (PAs), which protect only 9% of the remaining forest and 1% of the biomes’ original area [4]. This biome scenario is inadequate for the long-term conservation of top predators such as jaguars (Panthera onca) and mountain lions (Puma concolor) [6, 7].

While impacts of forest loss and fragmentation are well documented for large predators [8, 9], the effects on mesocarnivores are less clear. Mesocarnivores are species belonging to the
order Carnivora that are neither large nor top predators [10]. They are small or medium-sized species (less than 15 kg); may be solitary to highly social, frugivorous to strictly carnivorous, and have high phenotypic plasticity [10]. These life-history characteristics might allow some species of mesocarnivores to “replace” top predators when such species are absent or declining, altering the food chain (mesopredator release theory; [11]).

The ocelot (Leopardus pardalis) is a mesocarnivore in neotropical forests that may thrive in forest patches where top predators are absent or rare [12]. In these circumstances, ocelot might expand its trophic niche in response to a competitive release [12]. Normally, ocelot diets are composed of small mammals (<2.0 kg; [13]), but recent studies suggest that in the absence of top predators, especially jaguars, ocelots take larger prey [14–16]. Ocelots can also prey on other mesocarnivores [17–19] and hunt or harass smaller felines, such as jaguarondi (Puma yagouaroundi), margay (Leopardus wiedii) and oncilla (Leopardus tigrinus) [20, 21]. Together, these findings suggest that ocelots are opportunistic, ecologically plastic and may thrive in fragmented landscapes [22, 23].

However, ocelots may be more sensitive to fragmentation than other mesocarnivores because the species may have high affinity for closed canopy forests [24, 25]. The species is considered vulnerable in fragmented areas outside the Brazilian Amazon, such as the Atlantic Forest [26]. Thus, two opposing forces may be affecting ocelot populations in fragmented landscapes. The abundance of ocelots may be increasing due to mesopredator release or, abundance may be decreasing due to fragmentation and habitat loss. To test these two main hypotheses, and to understand the ecological process driving ocelot population dynamics and conservation status, we estimated ocelot abundance in a range of Atlantic Forest PAs. Specifically we assessed the effects of the amount of habitat (percent of forest cover and reserve size), impact of an invasive domestic species (relative abundance of free-ranging domestic dogs) and presence of top predators (mountain lions and jaguars) on ocelot abundance. We hypothesize a positive relationship between ocelot abundance and reserve size because larger forested areas could support more ocelots [6, 7, 27]. We expect a negative relationship between ocelot abundance and domestic dogs and top predators, because these species are considered potential competitors to ocelots [28, 29].

Camera traps are a common tool used to assess ocelot density [29–33], but few studies have accounted for potential variation in detection probability (p). To prevent potential biases caused by such variation, we tested several hypotheses involving factors that may influence detection. We expected that detection probability may vary among the sexes: females may have a higher detection probability than males because they have smaller home ranges that they use more intensively [13]. Alternatively, males travel larger distances [34], and they may be exposed to more cameras than females and thus have a higher detection probability. We expected a trap shy behavioral response in which recapture probability (c) of ocelots would be lower than the initial detection probability (p) because of the camera flash [35, 36]. We also expected ocelots to be more elusive and restrict their movements in areas with a higher abundance of top-predators or dogs [28, 29]. The number of unpaved roads within a reserve could also influence detection because ocelots often use trails or unpaved roads to move around the landscape [37–39]. We hypothesized that detection probability would be negatively correlated with density of travel routes because we could not survey many routes with our few cameras. Further, detection may be influenced by the location of cameras. Given the known affinity of ocelots for unpaved roads, we expected a positive relationship between detection and proportion of cameras installed on unpaved roads. We also expected a low detection probability in large densely, forested areas (the preferential habitat of the species; [24, 40]), because individuals have more area to explore and may have larger home ranges. Finally, we expected a higher
detection probability in dry seasons because ocelots may be more active in the dry season due to resource scarcity [41].

In summary, our main objective is to estimate ocelot abundance and density in six Atlantic Forest reserves in southeastern Brazil, while correcting for factors that may influence detection. We also assess the ability of reserve and individual ocelot variables to explain variation in ocelot abundance and detection. Finally, we compare our estimates with other estimates to assess the current ocelot population status in Atlantic Forest remnants.

Materials and Methods

Ethics statement

Sampling was performed under licenses obtained from the State Forest Institute (Instituto Estadual de Florestas—IEF) of the State Parks (UC: 080/10, 081/10 and 082/10) and under permission from the responsible (the owner of the land) of the private reserves. Data collection used non-invasive, remotely activated camera traps and did not involve direct contact or interaction with animals.

Study areas

We sampled six protected areas in the Atlantic Forest located in the State of Minas Gerais, southeastern Brazil (Fig 1). These include one large (> 20,000 ha) and two medium-sized (10,000–20,000 ha) state parks, respectively: Rio Doce (RD), Serra do Brigadeiro (SB) and Sete Salões (SS), and three small (< 10,000 ha) private reserves: Feliciano Miguel Abdala (FMA), Mata do Sossego (MS), and Fazenda Macedônia (FM). Vegetation in all areas is classified as semi-deciduous seasonal forest [42]. Elevation in these areas ranges from 150 m (RD) to 2,075 m (SB) [43] and the climate is classified as humid tropical in SB and semi-humid in the other PAs [44]. We considered RD as a reference area since it is one of the largest PAs remaining in the Atlantic Forest of southeastern Brazil, with a diverse mammal community, including jaguars, mountain lions, tapirs (Tapirus terrestris) and giant armadillos (Priodontes maximus) [45, 46]. Although jaguars, tapirs and giant armadillos are absent in the other PAs, mountain lions can be detected in SB, SS, FMA and FM (Paschoal et al., in prep.).

Sampling design

We used a standardized camera trap protocol to detect ocelots in the six reserves. Cameras were set to operate for 24 hours with an interval of five minutes between photos. Reserves were sampled for 80 consecutive days in each season (dry: April-September; wet: October-March).

In each study area, we selected 20 random sampling points (camera locations) from satellite images using ArcGIS 9.2 [49]. We distributed camera locations to ensure that at least one trapping station was located in a circular area equivalent to the smallest known home range of ocelots (76 ha; [50]). Any two adjacent trapping stations were up to 1 km apart, thus maximizing the probability of recording every individual present in the area. In the field, camera locations were placed as close as possible to the predetermined coordinates, usually within 50 m or 100 m, but preferentially placed along game trails, human paths, or unpaved roads because ocelots use these as travel routes [37–39]. We recorded the actual camera location using a GPS unit.

We installed camera traps in pairs to obtain simultaneous recording of the right and left sides of ocelots, allowing for individual identification. Because we only had ten cameras, we randomly moved pairs of cameras among sampling locations. We left cameras in place for 20 consecutive days before moving them to another five random points in the reserve, until all 20 points were sampled (total of 80 days). When we moved cameras, we also changed film and
batteries. The total sampling effort, considering the pair of cameras at each location as a single sampling unit, was 800 camera trap-days in each reserve (400 camera trap-days /season).

Estimating abundance, density and detection probability

We individually identified ocelots by stripe patterns on flanks, which are unique among individuals. Sex was determined by observation of genitals and the presence or absence of testes were used to distinguish between males and females. From these observations, we developed encounter histories for the 80 days of sampling in each season in each reserve depending on whether each individual was detected (1) or not (0). We collapsed our 80 days into groups of ten days (i.e., each individual encounter history contained eight occasions) in order to increase detection probabilities and improve estimates, as suggested by previous studies with elusive carnivores [51, 52]. We included sex as an individual covariate and used the Huggins closed capture model [53, 54] in Program MARK [55] to estimate abundance.
We mapped the land cover types by interpreting and classifying Landsat 5 images of each sampled area, using the technique of supervised classification and a maximum similarity algorithm in program ERDAS Image 8.4 [56]. We calculated the minimum convex polygon (MCP) formed by the outer sampling points in each reserve, which covered on average 910.6 ha (range 433.8 to 1,334.5 ha; Table 1). We added an additional buffer of about 3 km based on the mean maximum distance movement (MMDM; [57]) by ocelots detected in all reserves (Table 1). Inside this area (MCP + MMDM buffer) we calculated the proportion of forest and road network coverage (composed mainly by unpaved roads) in each reserve. To check if the proportion of forest inside the MPC + MMDM buffer accurately represented the amount of forest available in the larger landscape around the sampled areas, we mapped the proportion of forest inside an area of 10,000 ha centered around the MCP centroid of each reserve. This fixed area was large enough to accommodate the MPC + MMDM buffer. After that we performed a Pearson Correlation test between the proportion of forest mapped inside the MPC + MMDM buffer and inside the 10,000 ha area and found that both were highly correlated (r = 0.99). From this, we assumed that the proportion of forest inside the MPC + MMDM buffer accurately represented the amount of forest in the surrounding landscape. We used these predictor variables (i.e., covariates) for the analyses.

We also considered the size of each reserve for the analyses as well as the number of free-ranging domestic dogs photographed in each reserve (i.e., the number of individuals that could be uniquely identified). We identified dogs based on their specific phenotypic differences and pelage coloration [29]. Finally, we considered the presence of both top predators (jaguar and mountain lion), which were detected only in the largest reserve (RD). Before using these covariates in our analysis, we tested for correlation among them using a Pearson Correlation Matrix, which indicated that none of the variables were highly correlated (|r| ≤ 0.50 in all cases).

We used four variables (percent of forest area, reserve size, number of free-ranging domestic dogs, and presence of both top predators; Table 2) in a variance components analyses in Program MARK [55]. We used a variance components analyses to focus on explaining the biological process variance (δ²), which should not be confused with the sampling variance of ocelot abundance estimates [58, 59]. We estimated the percent of ocelot abundance variation explained by each variable. However, models from this analysis could not be compared using a model selection approach (e.g., AIC) because abundance (N) is not in the likelihood in Huggins models. Therefore, we ran a mean model (intercept only) to obtain an overall estimate of process variance for each season. We then constructed additional models including each of these four variables alone for each season. We interpreted the resulting difference between the

| Reserve                      | MCP (ha) | Buffer Area (ha) | Total Area (MMDM) | Total Area (½MMDM) | Forest Area (MMDM) | Forest Area (½MMDM) |
|------------------------------|----------|------------------|-------------------|--------------------|--------------------|--------------------|
|                              | MMDM     | ½MMDM | MMDM | ½MMDM | MMDM | ½MMDM | MMDM | ½MMDM | MMDM | ½MMDM | MMDM | ½MMDM |
| Fazenda Macedônia Reserve    | 1,073.32 | 5,910.70 | 2,374.68 | 6,984.02 | 3,448.00 | 429.48 | 429.48 |
| Feliciano Miguel Abdala Reserve | 754.05 | 5,545.87 | 2,192.08 | 6,299.92 | 2,946.13 | 1,359.31 | 1,450.65 |
| Mata do Sossego Reserve      | 433.83 | 4,785.97 | 1,812.05 | 5,219.80 | 2,245.88 | 2,461.71 | 1,454.59 |
| Serra do Brigadeiro State Park | 1,334.51 | 6,309.67 | 2,574.25 | 7,644.18 | 3,908.76 | 3,974.50 | 2,343.11 |
| Sete Salões State Park       | 980.41 | 6,119.87 | 2,479.44 | 7,100.28 | 3,459.85 | 3,781.25 | 2,193.14 |
| Rio Doce State Park          | 830.97 | 5,481.00 | 2,159.95 | 6,311.97 | 2,990.92 | 3,544.83 | 2,074.27 |

doi:10.1371/journal.pone.0141333.t001
overall process variance (intercept only) and the process variance of a particular variable model as the amount of process variance explained by the variable. We also calculated the proportion of the biological variation explained as the difference divided by the overall process variance for each variable in each season.

We calculated ocelot density by dividing \( \hat{N} \) by the effective trapping area (ETA) in each reserve (Table 1). However, the estimated abundance of ocelots (\( \hat{N} \)) in one small reserve (FMA) was not reliable because we only recorded a single ocelot in each season and detection probabilities were very low (see Results). When the detection probability for rare and elusive carnivores is low (\( \leq 0.10 \)) and each individual in the population is detected less than 2.5 times, the Huggins model has difficulty estimating abundance accurately [60]. Therefore, we used the observed abundance of ocelot to estimate density in FMA. We considered four different levels of ETA to estimate ocelot density (Table 1): MMDM buffer + MCP; ½ MMDM + MCP, and actual forest area within each of these previous levels of ETA. We considered forest area in calculating ocelot density because ocelots are considered a forest dependent species [24,40, 61]. Although MMDM has been considered a more accurate approach than ½ MMDM for estimating the area effectively sampled by cameras [34,62, 63], we also used the latter for two reasons. First, to make comparisons with other studies. Second, given the size of our MCPs, we judge the ½ MMDM may portray more faithfully the area of influence around the camera traps [62]. In one small reserve (MS), for example, the MMDM was almost ten times larger than the area sampled by cameras (MPC; Table 1) and, therefore, the MMDM may underestimate the ocelot density for this reserve. We calculate the polygons, buffers, and ETA using ArcGIS 9.2 [49].

Additionally, we modelled detection (\( p \)) and recapture (\( c \)) probabilities to estimate abundance (\( \hat{N} \)) for each season in each reserve. We considered detection structures with the effects of behavior (trap shy), sex (male vs female), season (dry vs wet), presence of both top predators (reserve with both predators -largest reserve; RD- vs other reserves; Table 2), landscape features (percent of forest area, percent of road network coverage and reserve size), PAs (or reserves), number of free-ranging domestic dogs and percent of cameras installed on unpaved roads (Table 2).

### Model selection and assumptions

We considered detection probabilities structures with all possible additive combinations of reserve (or covariates associated with each reserve), trap effect, season, and sex. We used

| Reserve                        | Road Network Coverage (%) | Cameras Installed on Unpaved Roads (%) | Forested Area (%) | Number of Free-Ranging Domestic Dogs | Reserve Size (ha) | Presence of both Top Predators |
|--------------------------------|--------------------------|---------------------------------------|-------------------|-------------------------------------|-------------------|-------------------------------|
| Fazenda Macedônia Reserve      | 2.64                     | 55.00                                 | 6.15              | 18                                  | 560               | No                            |
| Feliciano Miguel Abdala Reserve| 1.27                     | 59.09                                 | 35.5              | 47                                  | 958               | No                            |
| Mata do Sossego Reserve        | 0.14                     | 0.00                                  | 47.14             | 9                                   | 134               | No                            |
| Serra do Brigadeiro State Park | 0.62                     | 0.00                                  | 51.98             | 6                                   | 14,985            | No                            |
| Sete Salões State Park         | 0.00                     | 3.85                                  | 53.21             | 16                                  | 12,520            | No                            |
| Rio Doce State Park            | 0.65                     | 35.00                                 | 56.12             | 0                                   | 35,970            | Yes                           |

doi:10.1371/journal.pone.0141333.t002
Akaike's Information Criterion adjusted for small sample size (AICc), the relative AICc difference among models (ΔAICc), and associated model weights (AICc weights) to assess strength of candidate models [64]. This strategy resulted in a balanced model set and allowed us to calculate the cumulative AICc weights for each predictor variable [65]. Because of model selection uncertainty, we calculated model-averaged estimates of detection probability and abundance [64].

We examined violations of assumptions for closed population capture-recapture models [66]. We used the median \( c \) goodness-of-fit approach in Program MARK [67], which indicates no overdispersion (or independence among the sampled ocelots) when the \( c \) value is close to “1”. Our models assume that the population is closed geographically—no movement on or off the study area—and demographically—no births or deaths [66]. We tested for closure using the POPAN model in Program MARK, which allowed us to analyze the survival (\( \phi \)) or egress (\( 1-\phi \)) and ingress rates (\( pent \)) among capture occasions [68]. Using ΔAICc we compared models in which \( \phi \) and \( pent \) parameters were fixed as “1” and “0” respectively (i.e., no egress or ingress) to models that allowed egress and ingress to vary to assess whether closure was achieved.

**Results**

We did not detect overdispersion (\( c = 1.06 \) with 95% CI = 0.90–1.23) and our closure test revealed no violation (ΔAICc of the model without closure = 3.00).

The largest State Park (RD) and one small private reserve (FM) had the highest abundance and density estimates of ocelots (Table 3). Another small private reserve (FMA) had the lowest abundance and density estimates of ocelots among all reserves (Table 3) and one medium-sized reserve (SS) had the lowest abundance and density estimates of ocelots among the State Parks; no ocelots were detected there during the wet season (Table 3). When we look at the confidence intervals, however, we noticed that abundances and densities were similar among all areas, except for RD (Table 3).

Reserve size, presence of both top predators and number of free-ranging domestic dogs all contributed to explaining variance of ocelot abundance (Table 4); ocelot abundance responded positively to reserve size and to presence of both top predators and negatively to abundance of

### Table 3. Abundance and density estimates for ocelots derived from camera-trap studies conducted in six Atlantic forest reserves, southeastern Brazil.

| Reserve                     | Season | Abundance (±95% CI) | Density (ocelots/km²± 95% CI) |
|-----------------------------|--------|--------------------|--------------------------------|
|                             |        | MMDM               | MMDM                           |
|                             |        | ½ MMDM             | Forest MMDM                    |
|                             |        | ½ Forest MMDM      |                                |
| Fazenda Macedônia Reserve   | Dry    | 5.04 (4.65–5.42)   | 0.07 (0.07–0.08)               |
|                             |        |                    | 0.15 (0.14–0.16)               |
|                             |        |                    | 1.17 (1.08–1.26)               |
|                             |        |                    | 1.17 (1.08–1.26)               |
|                             | Wet    | 4.04 (3.62–4.46)   | 0.06 (0.05–0.06)               |
|                             |        |                    | 0.12 (0.11–0.13)               |
|                             |        |                    | 0.94 (0.84–1.04)               |
|                             |        |                    | 0.94 (0.84–1.04)               |
| Feliciano Miguel Abdala     | Dry    | 1                  | 0.02                            |
|                             |        |                    | 0.03                            |
|                             |        |                    | 0.05                            |
|                             |        |                    | 0.07                            |
|                             | Wet    | 1                  | 0.02                            |
|                             |        |                    | 0.03                            |
|                             |        |                    | 0.05                            |
|                             |        |                    | 0.07                            |
| Mata do Sossego Reserve     | Dry    | 3.20 (2.18–4.22)   | 0.06 (0.04–0.08)               |
|                             |        |                    | 0.14 (0.10–0.19)               |
|                             |        |                    | 0.13 (0.09–0.17)               |
|                             |        |                    | 0.22 (0.15–0.29)               |
|                             | Wet    | 1.07 (0.48–1.67)   | 0.02 (0.01–0.03)               |
|                             |        |                    | 0.05 (0.02–0.07)               |
|                             |        |                    | 0.04 (0.02–0.07)               |
|                             |        |                    | 0.07 (0.03–0.12)               |
| Serra do Brigadeiro State   | Dry    | 3.49 (1.79–5.19)   | 0.05 (0.02–0.07)               |
|                             |        |                    | 0.09 (0.05–0.13)               |
|                             |        |                    | 0.09 (0.05–0.13)               |
|                             |        |                    | 0.15 (0.08–0.22)               |
|                             | Wet    | 4.70 (2.50–6.82)   | 0.06 (0.03–0.09)               |
|                             |        |                    | 0.12 (0.07–0.17)               |
|                             |        |                    | 0.12 (0.07–0.17)               |
|                             |        |                    | 0.20 (0.11–0.29)               |
| Sete Salões State Park      | Dry    | 2.21 (1.16–3.26)   | 0.03 (0.02–0.05)               |
|                             |        |                    | 0.06 (0.03–0.09)               |
|                             |        |                    | 0.06 (0.03–0.09)               |
|                             |        |                    | 0.10 (0.05–0.15)               |
|                             | Wet    | 0                  | 0                               |
|                             |        |                    | 0                               |
|                             |        |                    | 0                               |
| Rio Doce State Park         | Dry    | 8.39 (5.28–11.51)  | 0.13 (0.08–0.18)               |
|                             |        |                    | 0.28 (0.18–0.39)               |
|                             |        |                    | 0.24 (0.15–0.33)               |
|                             |        |                    | 0.41 (0.26–0.56)               |
|                             | Wet    | 8.51 (5.26–11.76)  | 0.14 (0.08–0.19)               |
|                             |        |                    | 0.29 (0.18–0.39)               |
|                             |        |                    | 0.24 (0.15–0.33)               |
|                             |        |                    | 0.41 (0.25–0.57)               |
free-ranging domestic dogs (Table 4). Further, the amount of variance explained by each of these variables varied seasonally (Table 4). The precision of these variance estimates were low (e.g., overlapping confidence intervals), suggesting that the differences in variance explained, both among variables and between seasons, should be considered with care.

Overall, the most parsimonious model in our candidate set indicated that the detection probability of ocelots varied among reserves (Table 5). Based on this model, detection probability of ocelots was higher in two small reserves (FM and MS), and lower in one small reserve (FMA) and in the largest reserve (RD; Fig 2). Of the reserve covariates used to model detection, the percent of forest was the only covariate that had more influence (cumulative AICc weights = 39.37%) on ocelot detection; the percent of forest had a negative relationship ($\beta = -0.02 \pm SE 0.01$) with ocelot detection (Table 6). As expected, detection probability of ocelots was lower in more forested reserves, such as RD (Table 2; Fig 2), and higher in reserves with a lower proportion of forest cover, such as FM and MS (Table 2; Fig 2). The detection probability of ocelots in FM, for example, was more than two times higher than in RD (Fig 2), which has the highest forested area among all reserves (Table 2), but precision was low (large confidence intervals) due to small sample sizes (Fig 2). Although behavior, seasonality and sex had some influence on ocelot detection, they had low cumulative AICc weights (< 35%; Table 6). Road network coverage, reserve size, presence of both top predators, percent of cameras installed on unpaved roads and number of free-ranging domestic dogs had, respectively, the lowest cumulative AICc weights (< 6%) among the variables tested (Table 6).

**Discussion**

Contrary to our expectations, we did not find higher abundance and density in fragments where the top predators were absent or rare. Rather, the presence of both top predators (jaguar and mountain lion) in the largest reserve (RD) correlated positively with an increased abundance of ocelots, especially during the dry season. Top predators may increase the area of forest by controlling the herbivory rates [69, 70], which might increase ocelot abundance because this species is dependent to canopy cover [24, 25]. In addition, high abundance and densities of territorial carnivores may positively correlate to prey density [71]. Jaguars, for example, were found only in RD and their presence may be related to a higher diversity of prey for this species, especially those of large body size, such as deer (*Mazama americana*) and collared peccary.*

---

Table 4. The percent of biological process variation in ocelot abundance explained by four reserve variables among six Atlantic Forest reserves in southeastern Brazil. Negative process variances were considered zero. See Methods for details.

| Variables               | Dry Season | Wet Season |
|-------------------------|------------|------------|
|                         | $\delta^2$ Variance (±95% CI) | Beta Values (±95% CI) | % of Variation Explained | $\delta^2$ Variance (±95% CI) | Beta Values (±95% CI) | % of Variation Explained |
| Intercept only model    | 4.96 (1.62–32.87) | 3.61 (1.75–5.47) | - | 7.33 (2.03–68.25) | 3.53 (1.04–6.01) | - |
| Reserve Size            | 3.05 (1.02–26.19) | 0.1x10^-3 (-0.3x10^-8 – 0.3x10^-8) | 38.59 | 1.34 (0.39–19.46) | 0.2x10^-3 (0.8x10^-4 – 0.3x10^-3) | 81.73 |
| Presence of both Top Predators | 2.11 (0.73–17.76) | 4.81 (1.08–8.53) | 57.47 | 3.19 (0.87–47.81) | 5.34 (0.65–10.04) | 56.50 |
| Number of Domestic Dogs | 3.33 (0.95–30.86) | -0.09 (-0.19–0.01) | 32.90 | 5.74 (1.46–88.41) | -0.09 (-0.23–0.04) | 21.63 |
| Percent of Forest       | 5.57 (1.91–56.89) | -0.4x10^-2 (-0.12–0.11) | 0 | 8.38 (2.53–143.52) | 0.03 (-0.11–0.18) | 0 |

*doi:10.1371/journal.pone.0141333.t004*
Table 5. Model selection results for variables expected to influence ocelot detection probability in six Atlantic Forest reserves in southeastern Brazil. Only models with an AICc weights ≥ 0.01 are presented here.

| Model                                      | AICc   | ΔAICc | AICc Weights | Parameters | Deviance |
|--------------------------------------------|--------|-------|--------------|------------|----------|
| p(Reserve) = c(Reserve)                    | 353.86 | 0.00  | 0.17         | 6          | 341.58   |
| p(Reserve) c(Reserve)                      | 354.63 | 0.77  | 0.11         | 7          | 340.25   |
| p(Forest) = c(Forest)                      | 354.77 | 0.91  | 0.11         | 2          | 350.73   |
| p(Forest+Sex) = c(Forest+Sex)              | 355.66 | 1.80  | 0.07         | 3          | 349.58   |
| p(Forest+Season) = c(Forest+Season)        | 355.92 | 2.06  | 0.06         | 3          | 349.84   |
| p(Reserve+Season) = c(Reserve+Season)      | 355.97 | 2.11  | 0.06         | 7          | 341.59   |
| p(Forest) c(Forest)                        | 356.16 | 2.30  | 0.05         | 3          | 350.08   |
| p(Reserve+Sex) = c(Reserve+Sex)            | 356.25 | 2.39  | 0.05         | 7          | 341.87   |
| p(Reserve+Season) c(Reserve+Season)        | 356.51 | 2.65  | 0.04         | 8          | 340.03   |
| p(Forest+Sex) c(Forest+Sex)                | 356.78 | 2.92  | 0.04         | 4          | 348.64   |
| p(Forest+Season+Sex) = c(Forest+Season+Sex)| 356.78 | 2.92  | 0.04         | 4          | 348.65   |
| p(Reserve+Sex) c(Reserve+Sex)              | 357.23 | 3.37  | 0.03         | 8          | 340.75   |
| p(Forest+Season) c(Forest+Season)          | 357.33 | 3.47  | 0.03         | 4          | 349.20   |
| p(Reserve+Season+Sex) c(Reserve+Season+Sex)| 357.55 | 3.69  | 0.03         | 8          | 341.06   |
| p(Reserve size) c(Reserve size)            | 358.72 | 4.86  | 0.01         | 2          | 354.68   |

* The detection (p) and recapture (c) probability of ocelots modeled as function of: each reserve (Reserve); proportion of forest in each reserve (Forest); reserve size in ha (Reserve size); males and females (Sex) and; Season (Dry vs Wet). The equal signal (=) indicates that p and c have the same values for detection probability. The plus signal (+) means an additive effect between two or more tested variables.

doi:10.1371/journal.pone.0141333.t005
Our other study areas have less forest area and prey densities may not allow for ocelot, jaguar and mountain lion coexistence. In other words, the positive relationship between jaguars and ocelots might result from the fact that jaguar presence means better habitat for ocelots [28, 73] and for other carnivores. Jaguar abundance was positively related with mountain lion occupancy in the Cerrado of Central Brazil [74], and another study indicated that coexistence of both top predators are mediated mainly by food resources [75]. The presence of top predators, especially the jaguar in the Atlantic Forest, may be key in controlling the food chain and maintain prey availability in an ecosystem [9, 76].

Alternatively, jaguar occurrence may be positively correlated with ocelot abundance or density through the predation and/or harassment of potential ocelot competitors. We found a negative influence of dogs on ocelot abundance; the highest ocelot abundance was found in the largest reserve (RD) where we did not detect dogs. Therefore, the presence of jaguars may reduce the abundance of domestic dogs in a reserve via predation or interference competition [77]. Although domestic dogs did not exhibit a direct influence on the detection probability of ocelots, this exotic species may decrease prey availability [78] especially in small reserves, such as in FMA.

In a recent study, Paschoal et al. [29] found approximately 40 domestic dogs in FMA at a density about six times higher than that of ocelots, suggesting potential deleterious effects on ocelots. The current estimate of dog abundance in FMA seems to be almost two times higher (Paschoal et al., in prep.) than the abundances considered here (Table 2), which suggest that the influence of domestic dogs on the ocelot ecology could be stronger. For example, domestic dogs were also responsible for negatively affecting ocelot use (or distribution) in the same reserves of Atlantic Forest (Massara et al., in prep.) as well as the distribution of other felids in this biome, such as the margay (Leopardus wiedii) and the oncilla (Leopardus tigrinus) [79].

However, we do not know exactly the ecological mechanisms behind domestic dog occurrence that resulted in a decreasing on ocelot abundance in the studied reserves. These dogs are classified as rural free-ranging domestic dogs, which are owned or peripherally associated with human settlements but are not confined in a restrict area [80]. Although considered weak competitors, they may become important competitors and predators of wildlife because high densities of these dogs are subsidized by humans that live near natural habitats [78, 80]. Additionally, these dogs cause a variety of impacts apart from direct predation on wildlife, including the spread of disease [81]. At the same time, domestic dogs can exert more intrusive edge effects in more fragmented and smaller reserves, which are surrounded by a high density of human settlements and human-modified habitats, such as agricultural lands [80, 82].
these reserves, these dogs can even form packs and explore natural areas, which make their
impacts even higher upon medium- to large- sized mammals [29]. It may explain, for example,
the high dog abundance and low ocelot abundance in smaller reserves, such as in FMA, which
is dominated and surrounded by agriculture and human habitations. However, little is known
about the variables that may indeed facilitate dog entrance in Brazilian natural areas or their
direct effects on different species [29, 79, 83]. As domestic dogs are one of the most commonly
recorded mammal species in the Atlantic Forest [29, 79, 84], managers of protected areas
should start acting to mitigate or eliminate this hazard.

Reserve size also correlated positively with abundance of ocelots. Though it is difficult to
compare densities among studies due to the lack of a standard sampling protocols and the
inconsistency in quantifying the effective trapping area [62, 85], we found that larger areas usu-
ally have higher ocelot abundances and densities in the Atlantic Forest remnants (Table 7).
Further, reserve size was negatively correlated (r = -0.92) with the edge ratio of each reserve,
which suggests that our largest reserve (RD) may provide better quality of habitat for wildlife
and suffer less edge effects, such as those exerted by the exotic species (e.g., domestic dogs). The
proportion of forested area, however, did not positively correlate with ocelot abundance in the
reserves. We suspect that it might be a reflection of one sampled reserve (i.e., Fazenda Macedô-
nia; FM).

Fazenda Macedônia had a relatively small size (560 ha), a high abundance and density of
ocelots, and no jaguars (Tables 2 and 3). We believed that due to the proximity (15 km) of this
reserve to the largest reserve (RD) and the existence of several smaller fragments connecting
these two areas, the flow of ocelots among these fragments may be facilitated, making RD act
as possible source of ocelots to FM. Young male ocelots (two or three years old), can disperse
more than 10 km [13]. Further, FM has had potential prey species reintroduced, especially Gal-
liformes and Tinamiformes birds [86], which may also attract predators, such as ocelots, to the
area. However, longer-term studies and radio-tracking approaches are needed to test this
hypothesis. At the same time, the high estimates of ocelot density in FM obtained using some
buffers (i.e., Forest MMDM and ½ Forest MMDM; Table 3) relies on the fact that this area has

Table 7. Abundance and density estimates for ocelots derived from camera-trap studies conducted in Atlantic forest sites. Estimates are provided for two levels of buffers (MMDM, ½MMDM) according to their availability in each study. Ninety-five percent confidence intervals (95% CI) are presented, unless not included in a study.

| Reserve                        | Country | Season | Sampling Effort (Trap—days) | Area (ha) | Abundance (± 95% CI) | Density (ocelots/km²) |
|-------------------------------|---------|--------|-----------------------------|-----------|----------------------|-----------------------|
| Yabotí Biosphere Reserve      | Argentina | Wet    | 1,871                       | 274,200   | 39 (35–54)           | 0.05 (MMDM) 0.09 (½MMDM) |
| Iguazú National Park / San Jorge Forest Reserve | Argentina / Brazil | Wet | 2,059                      | 259,400   | 86 (75–111)        | 0.10 (MMDM) 0.17 (½MMDM) |
| Iguazú National Park          | Argentina | Both   | 1,631                       | 170,000   | 55 (42–87)           | 0.13 (MMDM) 0.20 (½MMDM) |
| Uruguai Private Reserve       | Argentina | Both   | 1,409                       | 113,243   | 20 (18–35)          | 0.08 (MMDM) 0.13 (½MMDM) |
| Ilha do Cardoso State Park    | Brazil   | Dry    | 585                         | 15,100    | 6                    | 0.21 (MMDM) - (½MMDM) |
| Caraguatá Ecological Reserve  | Brazil   | Both   | 4,250                       | 4,300     | 3.07                 | - (MMDM) 0.04 (½MMDM)  |
| Feliciano Miguel Abdala Reserve | Brazil    | Dry    | 450                         | 957       | 2                    | 0.16 (MMDM) 0.35 (½MMDM) |

1 [30]  
2 [31]  
3 [32]  
4 [33]  
5 [29]  

doi:10.1371/journal.pone.0141333.t007
the smallest proportion of forest among all reserves (Table 2), which may inflate the ocelot den-
sity through a mathematical artifact.

Although we did not detect closure violations, detecting such violations is difficult with
small data sets. If the ocelot population is open then we are technically estimating a super-pop-
ulation (i.e., all individuals that use the sampled area during sampling; [68]). A super-popula-
tion definition also aligns with potentially high turnover of ocelots among occasions and
seasons, especially inside small or medium-sized fragments. In one small reserve (FMA) for
example, we detect just one different individual in each season and no ocelots were recorded in
one medium-sized reserve (SS) during the wet season. Further, in FMA the ocelots were only
detected in a single occasion. The super-population concept may imply the existence of a meta-
population dynamic among fragments [87], reinforcing our suggestion of a flow of ocelot indi-
viduals between the largest reserve (RD) and one small reserve (FM).

Ocelots of different sex may have different home ranges [22,31,34], and ranges may vary by
season [34, 88]. Ocelots may use large trails or unpaved roads to move around the landscape
[37–39]. However, we did not find strong support for these variables affecting detection proba-
ability of ocelots. Although the proportion of forest had just some influence (AICc
weights = 39.37%) on ocelot detection, it was the reserve variable that best explained the varia-
tion in ocelot detection. Low detectability in more forested areas may relate to large ocelot
home ranges in these areas, where individuals have a larger amount of forested area to use.
Conversely, in areas poorly covered by forests, ocelots may have smaller home ranges (i.e.
Bolivia; [62]) and concentrate travel (about 3 to 7 km per night) in a smaller area to attain their
daily energy requirements [22, 24, 89], which can increase their detection probabilities. This
reasoning however does not explain our results in one small reserve (FMA), which has the sec-
ond lowest proportion of forest among all sampled areas (Table 2) but the lowest detection
probability (Fig 2). We believe that some other variables that we did not measure in this present
study may better explain the variation in ocelot detection probability among reserves and
should be investigated in future studies. Some obvious possibilities that are known to affect
mammal populations includes degree of surveillance or poaching pressure [3, 90]. We refrain
to speculate about these, given that an accurate assessment of such effects are lacking for our
six reserves.

We do have data on the immediate surrounding landscapes of our reserves. One of our
small and least forested reserve (i.e., FM) for example, is surrounded by eucalyptus, which may
be used constantly by ocelots as travel routes to move between native habitats within or outside
the reserve [91]. Because ocelot is a forest dependent species [25,61, 92], it may uses eucalyptus
more often than open habitats (e.g., pasture or croplands) to find native habitats (e.g., native
forest). Therefore, reserves surrounded by more permeable matrices may have higher ocelot
detection than areas surrounded by more inhospitable habitats (e.g., pasture around FMA).

Overall, our findings suggest that top predators, especially the jaguar, seem to act as an
umbrella species for ocelots and other sympatric mesocarnivores [73] and that ecological pro-
cesses that are detrimental to top predators may also be detrimental to ocelots. By protecting
top predators we may also protect other species, such as ocelots. Indeed, top predators have
been target by conservation initiatives to protect entire communities in different ecosystems
[76]. Although our data show that the ocelot is able to inhabit smaller reserves, the lower densi-
ties (except for FM) indicate that these reserves might represent poor habitats. These results
corroborates other authors working on the effects of forest fragmentation in the Atlantic forest,
which show that only large fragments in the range of 20,000 ha or more can sustain viable pop-
ulations of medium to large sized mammal species [6, 7, 27].

Low densities in small fragments translates to small populations with low viability. In the
USA, for example, only two known isolated ocelot populations occur in southern Texas. For
these isolated populations, conservation concerns include loss of dense forest habitat, mortality from vehicle-collisions, and genetic drift [93]. A habitat-based population strategy was adopted for the recovery efforts of these populations [92, 93]. The long-term recovery strategy included the restoration of ocelot habitat and the establishment of a dispersal corridor between ocelot breeding populations [92]. Whether increased connectivity will be able to overcome genetic drift or the reduction in the genetic diversity is unknown [94–96]. Unfortunately, a similar situation may be occurring among the remnant ocelot populations in the Atlantic Forest. A recent study found the first report of a unilateral cryptorchidism (i.e., the absence of one testis from the scrotum) in an wild adult ocelot, an inherited condition linked to low genetic variability in inbred wild cats [97]. This finding is especially concerning because it comes from the largest of our study areas (RD, with 36,000 ha). Therefore, without increased connectivity, the outlook for ocelots in the Atlantic Forest may be pessimistic, a view also backed by others [30, 31].

Conclusion and Recommendations

Our findings do not support the hypothesis of mesopredator release. Rather, our analyses indicate that presence of top predators and reserve size correlated positively with an increased abundance of ocelots in the Atlantic Forest reserves. The implementation of biodiversity corridors could protect and increase the current ocelot population in small Atlantic Forest fragments, reducing the isolation of small populations and augmenting structural and functional connectivity among forest patches. However, a better alternative might be based on improving connections via native vegetation and protection through the Brazilian Forest code (Federal Law number 12,651 from May 25, 2012). Preliminary data of an ongoing project carried out in São Paulo state show, for example, that ocelots do inhabit areas of permanent protection (Áreas de Proteção Permanente—APPs), even when these are immersed in sugar cane or eucalyptus matrices [98]. According to the Brazilian forest code, these APPs protect mainly watercourses. Therefore, the possibility that these areas act like true corridors might indeed be real. We note that one small reserve (FM) and the largest reserve (RD) are linked by the Rio Doce River. Implementing the Forest Code law would therefore translate to increasing structural connectivity between these two protected areas via restoration of riparian forests along the Rio Doce River. Future studies should investigate more closely these areas and their surrounding matrices in order to assess their use by ocelots.

Acknowledgments

Volunteers assisted with fieldwork. Dr. Larissa Bailey, the Wagar 113 super-population, Dr. Bailey’s laboratory and three anonymous reviewers kindly reviewed and helped to improve the manuscript. Dr. Adriano Paglia, Dr. Flávio Rodrigues and Dr. José Eugênio Figueira for suggestions in a previous version of the manuscript.

Author Contributions

Conceived and designed the experiments: RLM AMOP AGC. Performed the experiments: RLM AMOP. Analyzed the data: RLM PFDJ. Contributed reagents/materials/analysis tools: PFDJ AH. Wrote the paper: RLM AMOP PFDJ AGC.

References

1. Fahrig L. Effects of habitat fragmentation on biodiversity. Annu Rev Ecol, Evol Syst. 2003; 34: 487–515.
2. Gascon C, Williamson GB, Fonseca GABd. Ecology: Receding forest edges and vanishing reserves. Science. 2000; 288: 1356–1358. doi: 10.1126/science.288.5470.1356 PMID: 10847849
3. Galetti M, Giacomini HC, Bueno RS, Bernardo CSS, Marques RM, Bovendorp RS, et al. Priority areas for the conservation of atlantic forest large mammals. Biol Conserv. 2009; 142: 1229–1241.

4. Ribeiro MC, Metzger JP, Martensen AC, Ponzone FJ, Hirota MM. The brazilian atlantic forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv. 2009; 142: 1141–1153.

5. Tabarelli M, Aguiar AV, Ribeiro MC, Metzger JP, Peres CA. Prospects for biodiversity conservation in the atlantic forest: Lessons from aging human-modified landscapes. Biol Conserv. 2010; 143: 2328–2340.

6. Canale GR, Peres CA, Guidorizzi CE, Gatto CAF, Kierulf MCM. Pervasive defaunation of forest remnants in a tropical biodiversity hotspot. PloS one. 2012; 7: 1–8.

7. Jorge MLSP, Galetti M, Ribeiro MC, Ferraz KMPMB. Mammal defaunation as surrogate of trophic cascades in a biodiversity hotspot. Biol Conserv. 2013; 163: 49–57. doi: 10.1016/j.biocon.2013.04.018

8. Crooks KR. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conserv Biol. 2002; 16: 488–502.

9. Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, et al. Trophic downgrading of planet earth. Science. 2011; 333: 301–306. doi: 10.1126/science.1205106 PMID: 21764740

10. Roemer GW, Gompper ME, Valkenburgh BV. The ecological role of the mammalian mesocarnivore. Bioscience. 2008; 58: 165–173.

11. Crooks KR, Soulé ME. Mesopredator release and avifaunal extinctions in a fragmented system. Nature. 1999; 400: 563–566.

12. Moreno RS, Kays RW, Samudio RJ. Competitive release in diets of ocelot (Leopardus pardalis) and puma (Puma concolor) after jaguar (Panthera onca) decline. J Mammal. 2006; 87: 808–816.

13. Sunquist ME, Sunquist F. Wild cats of the world. 1st ed. Chicago: University of Chicago Press; 2002.

14. Bianchi RdC, Mendes SL, Júnior PDM. Food habits of the ocelot, Leopardus pardalis, in two areas in southeast Brazil. Stud Neotrop Fauna Environ. 2010; 45: 111–119. doi: 10.1080/01650521.2010.514791

15. Bianchi RdC, Mendes SL. Ocelot (Leopardus pardalis) predation on primates in caratinga biological station, southeast Brazil. Am J Primatol. 2007; 69: 1–6.

16. Santos JL, Paschoal AMO, Massara RL, Chiarello AG. High consumption of primates by pumas and ocelots in a remnant of the brazilian atlantic forest. Braz J Biol. 2014; 74: 632–641. doi: 10.1590/bjb.2014.0094 PMID: 25296212

17. Bianchi RdC, Campos RC, Xavier-Filho NL, Olliers N, Gompper ME, Mourão G. Intraspecific, interspecific, and seasonal differences in the diet of three mid-sized carnivores in a large neotropical wetland. Acta Theriol. 2014; 59: 13–23. doi: 10.1007/s13364-013-0137-x

18. Chinchilla FA. La dieta del jaguar (Panthera onca), el puma (Felis concolor) y el manigordo (Felis pardalis) carnívoros: Felidae) en el Parque Nacional Corcovado, Costa Rica. Rev Biol Trop. 1997; 45: 1223–1229.

19. Emmons LH. Comparative feeding ecology of felids in a neotropical rainforest. Behav Ecol Sociobiol. 1987; 20: 271–283.

20. Oliveira TG, Tortato MA, Silveira L, Kasper CB, Mazim FD, Lucherini M, et al. Ocelot ecology and its effect on the small-felid guild in the lowland neotropics. In: MacDonald DW, Loveridge A, editors. Biology and conservation of wild felids. Oxford: Oxford University Press; 2010. pp. 563–584.

21. Oliveira-Santos LG, Graipel ME, Tortato MA, Zuczo CA, Cáceres NC, Goulart FVB. Abundance changes and activity flexibility of the oncilla, Leopardus tigrinus (carnivora: Felidae), appear to reflect avoidance of conflict. Zoologia 2012; 29: 115–120. doi: 10.1590/s1984-4670201200003

22. Ludlow ME, Sunquist ME. Ecology and behavior of ocelots in Venezuela. Natl Geogr Res. 1987; 3: 447–461.

23. Silva-Pereira JE, Moro-Rios RF, Bilski DR, Passos FC. Diets of three sympatric neotropical small cats: Food niche overlap and interspecies differences in prey consumption. Mamm Biol. 2011; 76: 308–312. doi: 10.1016/j.mambio.2010.09.001

24. Emmons LH. A field study of ocelots (Felis pardalis) in peru. Rev d'écologie. 1988; 43: 133–157.

25. Haines AM, Grassman LJ Jr., Tewes ME, Janečka JE. First ocelot (Leopardus pardalis) monitored with gps telemetry. Eur J Wildlife Res. 2006; 52: 216–218.

26. Machado ABM, Drummond GM, Paglia AP. Livro vermelho da fauna brasileira ameaçada de extinção. 1st ed. Brasília: Fundação Biodiversitas; 2008.

27. Chiarello AG. Effects of fragmentation of atlantic forest on mammal communities in south-eastern Brazil. Biol Conserv. 1999; 89: 71–82.
28. Di Bitetti MS, Angelo CDD, Blanco YED, Paviolo A. Niche partitioning and species coexistence in a neotropical felid assemblage. Acta Oecol. 2010; 36: 403–412.

29. Paschoal AMO, Massara RL, Santos JL, Chiarello AG. Is the domestic dog becoming an abundant species in the Atlantic Forest? A study case in southeastern Brazil. Mammalia. 2012; 76: 67–76.

30. Di Bitetti MS, Paviolo A, Angelo CDD, Blanco YED. Local and continental correlates of the abundance of a neotropical cat, the ocelot (Leopardus pardalis). J Trop Ecol. 2008; 24: 189–200.

31. Di Bitetti MS, Paviolo A, Angelo CD. Density, habitat use and activity patterns of ocelots (Leopardus pardalis) in the Atlantic forest of misiones, Argentina. J Zool. 2006; 270: 153–163.

32. Fusco-Costa R, Ingberman B, Couto HT, Nakano-Oliveira E, Monteiro-Filho EL. Population density of a coastal island population of the ocelot in Atlantic Forest, southeastern Brazil. Mamm Biol. 2010; 75: 358–362.

33. Goulart F, Graipel ME, Tortato MA, Ghizoni Jr I, Oliveira-Santos LG, Cáceres N. Ecology of the ocelot (Leopardus pardalis) in the Atlantic forest of southern Brazil. Tropical Biol Cons. 2009; 4: 137–143. doi: 10.4013/nbc.2009.43.03

34. Dillon A, Kelly MJ. Ocelot home range, overlap and density: Comparing radio telemetry with camera trapping. J Zool. 2008; 275: 391–398.

35. Schipper J. Camera-trap avoidance by kinkajous Potos flavus: Rethinking the “non-invasive” paradigm. Small Carniv Conserv. 2007; 1: 36–38.

36. Wegge P, Pokheral CP, Jnawali SR. Effects of trapping effort and trap shyness on estimates of tiger abundance from camera trap studies. Anim Conserv. 2004; 7: 251–256. doi: 10.1017/s1367943004001144

37. Goulart FVB, Cáceres NC, Graipel ME, Tortato MA, Ghizoni IR Jr., Gustavo L, et al. Habitat selection by large mammals in a southern Brazilian Atlantic forest. Mamm Biol. 2009; 74: 182–190.

38. Trolle M, Kéry M. Camera-trap study of ocelot and other secretive mammals in the northern Pantanal. Mammalia. 2005; 69: 405–412.

39. Hone JS, Haines AM, Tewes ME, Laack LL. Habitat partitioning by sympatric ocelots and bobcats: Implications for recovery of ocelots in southern Texas. Southwest Nat. 2009; 54: 119–126. doi: 10.1894/ps-49.1

40. Tökölyi J, Schmidt J, Barta Z. Climate and mammalian life histories. Biol J Linn Soc. 2014; 111: 719–736.

41. SOS Mata Atlântica. Relatório técnico do atlas dos remanescentes florestais da mata atlântica (período 2008–2010). 2011. Available: http://mapas.sosma.org.br/.

42. Miranda EE. Brasil em relevo. Embrapa monitoramento por satélite. 2005. Available: http://www.relevo.cnpm.embrapa.br.

43. IBGE. Mapas interativos do IBGE: Clima. Atualizado em 07/01/2012. 2012. Available: http://geoftp.ibge.gov.br/mapas_interativos.

44. IEF. Plano de manejo do Parque Estadual do Rio Doce. 2014. Available: http://www.ief.mg.gov.br/component/content/article/306.

45. Srbel-Araujo AC, Scoss LM, Hirsch A, Chiarello AG. Records of the giant-armadillo Priodontes maximus (Cingulata: Dasypodidae) in the Atlantic forest: Are Minas Gerais and Espirito Santo the last strongholds of the species? Zoologia. 2009; 26: 461–468.

46. SOS Mata Atlântica. Atlas dos remanescentes florestais da mata atlântica (período 2011–2012). 2014. Available: http://mapas.sosma.org.br/.

47. IBGE. Mapas temáticos: Municípios do Brasil. 2005. Available: http://downloads.ibge.gov.br/Esri/arcgisv92

48. Crawshaw PG, Quigley HB. Notes on ocelot movement and activity in the Pantanal region, Brazil. Biota tropica. 1989; 21: 377–379.

49. Foster RJ, Harmsen BJ. A critique of density estimation from camera-trap data. J Wildl Manage. 2012; 9999: 1–13. doi: 10.1002/jwmg.275

50. Harmsen BJ, Foster RJ, Doncaster CP. Heterogeneous capture rates in low density populations and consequences for capture-recapture analysis of camera-trap data. Popul Ecol. 2011; 53: 253–259. doi: 10.1007/s10144-010-0211-z

51. Huggins RM. On the statistical analysis of capture experiments. Biometrika. 1989; 76: 133–140.

52. Huggins RM. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics. 1991; 47: 725–732.
55. White GC, Burnham KP. Program mark: Survival estimation from populations of marked animals. Bird Study. 1999; 46: 120–139.

56. Erdas. Erdas imagine v. 8.4 field guide. 4th ed. Atlanta: Erdas; 1997.

57. Soisalo MK, Cavalcanti SMC. Estimating the density of a jaguar population in the brazilian pantanal using camera-traps and capture–recapture sampling in combination with gps radio-telemetry. Biol Conserv. 2006; 129: 487–496.

58. White GC. Population viability analysis: Data requirements and essential analysis. In: Fuller LBTK, editor. Research techniques in animal ecology: Controversies and consequences. New York: Columbia University Press; 2000. pp. 288–331.

59. Burnham KP, White GC. Evaluation of some random effects methodology applicable to bird ringing data. J Appl Statist. 2002; 29: 245–264. doi: 10.1080/02664760210165267

60. Gerber BD, Ivan JS, Burnham KP. Estimating the abundance of rare and elusive carnivores from photographic-sampling data when the population size is very small. Popul Ecol. 2014; 56: 463–470. doi: 10.1007/s10144-014-0431-8

61. Harverson PM, Tewes ME, Anderson GL, Laack LL. Habitat use by ocelots in south Texas: Implications for restoration. Wildl Soc Bull. 2004; 32: 948–954.

62. Maffei L, Noss AJ. How small is too small? Camera trap survey areas and density estimates for ocelots in the bolivian chaco. Biotropica. 2008; 40: 71–75.

63. Noss AJ, Gardner B, Maffei L, Cueliïar E, Montaño R, Romero-Muñoz A, et al. Comparison of density estimation methods for mammal populations with camera traps in the kaa-iya del gran chaco landscape. Anim Conserv. 2012; 15: 527–536. doi: 10.1111/j.1469-1795.2012.00545.x

64. Burnham KP, Anderson DR. Model selection and multimodel inference: A practical information-theoretical approach. 2nd ed. New York: Springer-Verlag; 2002.

65. Doherty PF, White GC, Burnham KP. Comparison of model building and selection strategies. J Ornithol. 2012; 152: S317–S323.

66. Otis DL, Burnham KP, White GC, Anderson DR. Statistical inference from capture data on closed animal populations. Wildlife Monogr. 1978; 62: 3–155.

67. White GC. Discussion comments on: The use of auxiliary variables in capture-recapture modelling. An overview. J Appl Statist. 2002; 29: 103–106.

68. Schwarz CJ, Amason AN. A general methodology for the analysis of capture-recapture experiments in open populations. Biometrics. 1996; 52: 860–873.

69. Ripple WJ, Beschta RL. Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. Biol Conserv. 2008; 141: 1249–1256. doi: 10.1016/j.bico.2008.02.028

70. Ripple WJ, Beschta RL. Hardwood tree decline following large carnivore loss on the great plains, USA. Front Ecol Environ. 2007; 5: 241–246.

71. Carbone C, Gittleman JL. A common rule for the scaling of carnivore density. Science. 2002; 295: 2273–2276. PMID: 11910114

72. Oliveira TGd. Ecología comparativa de la alimentación del jaguar y del puma en el neotrópico. In: Medellín RA, Echiquia C, Chetkiewicz C-LB Jr. PGC, Rabinowitz A, Redford KH, et al., editors. El jaguar en el nuevo milenio. Mexico: Wildlife Conservation Society; 2002. pp. 265–288.

73. Davis ML, Kelly MJ, Stauffer DF. Carnivore co-existence and habitat use in the mountain pine ridge forest reserve, Belize. Anim Conserv. 2011; 14: 56–65. doi: 10.1111/j.1469-1795.2010.00389.x

74. Negrões N, Sarmento P, Cruz J, Eira C, Revilla E, Fonseca C, et al. Use of camera-trapping to estimate puma density and influencing factors in central Brazil. J Wildl Manage. 2010; 74: 1196–1203. doi: 10.2193/2009-256

75. Foster VC, Sarmento P, Sollmann R, Tôrres N, Jácromo ATA, Negrões N, et al. Jaguar and puma activity patterns and predator-prey interactions in four brazilian biomes. Biotropica. 2013; 45: 373–379.

76. Sergio F, Caro T, Brown D, Clucas B, Hunter J, Ketchum J, et al. Top predators as conservation tools: Ecological rationale, assumptions, and efficacy. Annu Rev Ecol S. 2008; 39: 1–19.

77. Foster RJ, Harmen BJ, Valdes B, Pomilla C, Doncaster CP. Food habits of sympatric jaguars and pumas across a gradient of human disturbance. J Zool. 2010; 280: 309–318. doi: 10.1111/j.1469-7998.2009.00663.x

78. Young JK, Olson KA, Reading RP, Amgalanbaatar S, Berger J. Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. Bioscience. 2011; 61: 125–132.

79. Cassano CR, Barlow J, Pardini R. Forest loss or management intensification? Identifying causes of mammal decline in cacao agroforests. Biol Conserv. 2014; 169: 14–22. doi: 10.1016/j.biocon.2013.10.006
80. Vanak AT, Gompper ME. Dogs canis familiaris as carnivores: Their role and function in intraguild competition Mamm Rev. 2009; 39: 265–283.

81. Curi NH, Paschoal AM, Massara RL, Marcelino AP, Ribeiro AA, Passamani M, et al. Factors associated with the seroprevalence of leishmaniasis in dogs living around Atlantic forest fragments. PloS one. 2014; 9: e104003. doi:10.1371/journal.pone.0104003 PMID: 25089629.

82. Vanak AT, Gompper ME. Interference competition at the landscape level: The effect of free-ranging dogs on a native mesocarnivore. J Appl Ecol. 2010; 47: 1225–1232.

83. Srbek-Araujo A, Chiarello A. Domestic dogs in Atlantic forest preserves of south-eastern Brazil: A camera-trapping study on patterns of entrance and site occupancy rates. Braz J Biol. 2008; 68: 771–779. PMID: 19197494

84. Espartosa KD, Pinotti BT, Pardini R. Performance of camera trapping and track counts for surveying large mammals in rainforest remnants. Biodivers Conserv. 2011; 20: 2815–2829.

85. Dillon A, Kelly MJ. Ocelot Leopardus pardalis in Belize: The impact of trap spacing and distance moved on density estimates. Oryx. 2007; 41: 469–477.

86. Cenibra. RPPN Fazenda Macedônia. 2014. Available: http://www.cenibra.com.br/.

87. Hanski I, Simberloff D. The metapopulation approach. In: Hanski I, Gilpin M, editors. Metapopulation biology: Ecology, genetics and evolution. San Diego: Academic Press; 1997. pp. 5–26.

88. Maffei L, Noss AJ, Cuéllar E, Rumiz DI. Ocelot (Felis pardalis) population densities, activity, and ranging behaviour in the dry forests of eastern Bolivia: Data from camera trapping. J Trop Ecol. 2005; 21: 1–6.

89. Konecný MJ. Movement patterns and food habits of four sympatric carnivore species in Belize, central America. Adv Neotrop Mammal. 1989; 243–264.

90. Cullen LJ, Bodmer ER, Valladares-Padua C. Ecological consequences of hunting in Atlantic forest patches, Sao Paulo, Brazil. Oryx. 2001; 35: 137–144. doi:10.1046/j.1365-3008.2001.00163.x

91. Lyra-Jorge MC, Ciocheti G, Pivello VR. Carnivore mammals in a fragmented landscape in northeast of São Paulo state, Brazil. Biodivers Conserv. 2008; 17: 1573–1580.

92. Haines AM, Tewes ME, Laack LL, Horne JS, Young JH. A habitat-based population viability analysis for ocelots (Leopardus pardalis) in the United States. Biol Conserv. 2006; 132: 424–436.

93. Haines AM, Tewes ME, Laack LL, Grant WE, Young J. Evaluating recovery strategies for an ocelot (Leopardus pardalis) population in the United States. Biol Conserv. 2005; 126: 512–522.

94. Janecka JE, Tewes ME, Laack L, Caso A, Grassman LJ, Honeycutt RL. Loss of genetic diversity among ocelots in the United States during the 20th century linked to human-induced population reductions. PloS one. 2014; 9: e89384. doi:10.1371/journal.pone.0089384 PMID: 24586737; PubMed Central PMCID: PMC3935880.

95. Janecka JE, Tewes ME, Laack LL, Caso A, Grassman LJ Jr, Haines AM, et al. Reduced genetic diversity and isolation of remnant ocelot populations occupying a severely fragmented landscape in southern Texas. Anim Conserv. 2011; 14: 608–619. doi:10.1111/j.1469-1795.2011.00475.x

96. Janecka JE, Tewes ME, Laack LL, Grassman LJ, Haines AM, Honeycutt RL. Small effective population sizes of two remnant ocelot populations (Leopardus pardalis albescens) in the United States. Conserv Genet. 2007; 9: 869–878. doi:10.1007/s10592-007-9412-1

97. Araujo GR, Paula TAR, Deco-Souza T, Garay RM, Bergo LCF, Silva LC, et al. Criptorquidismo em jaguatirica de vida livre capturada no Parque Estadual do Rio Doce, Brasil. Arq Bras Med Vet Zootec. 2013; 65: 1–5.

98. Paolino RM. Importância das áreas de preservação permanente (APPs) ripárias para a mastofauna no nordeste do estado de São Paulo. M. Sc. Thesis, Universidade de São Paulo. 2015.