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Authors: Paschoal, Ana M. O., Massara, Rodrigo L., Bailey, Larissa L., Doherty, Paul F., Santos, Paloma M., et al.

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Ana M. O. Paschoal^{1,2}, Rodrigo L. Massara^{1,2} , Larissa L. Bailey³, Paul F. Doherty Jr.³, Paloma M. Santos¹, Adriano P. Paglia¹, André Hirsch⁴ , and Adriano G. Chiarello⁵

Abstract

Domestic dog is the most successful invasive mammalian predator species, and reducing its ecological impacts on wildlife is a central conservation goal globally. Free-ranging dogs can negatively interact with wildlife at multiple levels, posing issues for biodiversity conservation in tropical forests, especially in fragmented Atlantic Forest. To optimize future control programs, it is necessary to identify the main factors influencing their habitat use, particularly in natural reserves. We combined camera trapping data and occupancy models to characterize habitat use of dogs in six Atlantic Forest protected areas (134–36,000 ha). Our results show that dogs were more likely to use sites ($\hat{\psi} \geq 0.90$) having higher housing density (≥ 4.00 houses/km²) or higher proportion of croplands and pasture ($\geq 75\%$) relative to sites with no houses ($\hat{\psi} = 0.23 \pm 0.10$) or lower proportion of croplands and pasture ($\hat{\psi} = 0.34 \pm 0.08$). In addition, dogs had higher detection probability at camera locations on unpaved roads ($\hat{p} = 0.33 \pm 0.05$) relative to off-road sites ($\hat{p} = 0.18 \pm 0.04$), and in small protected areas with high housing density, that is, more disturbed sites, dogs had higher detection probabilities. Our findings indicate that the probability of dogs using a site within protected area is mainly driven by type and intensity of human activity in the surroundings. Given the urgent need to control free-ranging dogs within protected areas, we strongly recommend that managers target sites/areas within and near protected areas that have a rural housing density ≥ 4.00 houses/km² or higher proportion of croplands and pasture ($\geq 75\%$).

Keywords

domestic species, *Canis familiaris*, Brazil, occupancy models, biological invasions

Introduction

Invasive species are considered one of the greatest threats to global biodiversity, and mammalian predators have contributed disproportionately to the decline and extinction of native species in a variety of ecosystems (Vitousek, D'Antonio, Loope, Rejmanek, & Westbrooks, 1997). The domestic dog (*Canis familiaris*, Linnaeus 1758) stands out among invasive mammalian predators, inducing drastic changes in communities and ecosystems around the world (Ritchie, Dickman, Letnic, & Vanak, 2014; Vanak, Dickman, Silva-Rodríguez, Butler, & Ritchie, 2014). They interact with native fauna at multiple levels (Vanak & Gompper, 2009), often resulting in negative impacts, such as predation, competition, surplus killing, pathogen spillover, and genetic introgression (Vanak & Gompper, 2009; Young, Olson, Reading,

¹Laboratório de Ecologia e Conservação, Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil

²Instituto SerraDiCal de Pesquisa e Conservação, Belo Horizonte, Brazil

³Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, USA

⁴Programa Institucional de Bioengenharia, Universidade Federal de São João Del Rei, Sete Lagoas, Brazil

⁵Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Brazil

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Corresponding Author:

Ana M. O. Paschoal, Programa de Pós-graduação em Ecologia, Conservação e Manejo de Vida Silvestre, Universidade Federal de Minas Gerais, Avenida Antônio Carlos, No. 6627, Belo Horizonte, MG 31270-901, Brazil.
Email: anamuzenza@gmail.com



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Amgalanbaatar, & Berger, 2011), contributing to the decline of biodiversity (Doherty, Dickman, Nimmo, & Ritchie, 2015; Doherty et al., 2017).

The dog derived from Eurasian gray wolves (*Canis lupus*; Shannon et al., 2015), and since domestication, it has been subsidized and introduced worldwide as a ubiquitous commensal of humans (Vanak & Gompper, 2009, 2010). Nowadays, it is the most common and widespread carnivoran on the planet (Vanak & Gompper, 2010). Under a combination of natural and strong artificial selection during multiple and independent processes of domestication, the dog now has life history traits of *r*-selected species (Kitala et al., 2001). They also have high behavioral flexibility (Wright, Eberhard, Hobson, Avery, & Russello, 2010) and large niche breadth (Vázquez, 2005). Together these traits allow dogs to survive, reproduce, and persist in a wide range of habitats (Ritchie et al., 2014; Ryall & Fahrig, 2006), making them one of the most successful invasive species (Miklósi, 2007).

The dog is a concern in exurban/rural areas, where they are commonly owned and associated with human housing, but they are allowed to range freely through the landscape, increasing the probability of contact with native fauna (i.e., *free-ranging*; see Vanak & Gompper, 2009). The influence of free-ranging dogs (i.e., hereafter dogs) on native fauna is usually higher at the boundary of native and disturbed habitats; thus, the dog is considered a type of edge effect (Lacerda, Tomas, & Marinho-Filho, 2009; Srbek-Araujo & Chiarello, 2008; Vanak et al., 2014), although this effect is not restricted to habitat edges (Vanak et al., 2014). As a highly mobile species, the dog can easily cross edge boundaries and invade adjacent habitats, including protected areas (Cantrell, Cosner, & Fagan, 2001; Sepúlveda, Pelican, Cross, Eguren, & Singer, 2015) and thus be detected 10 to 30 km from the edge (Meek, 1999; Vanak et al., 2014). Furthermore, the dog's impact within protected areas may be enhanced through complex pathways (e.g., habitat- and community-mediated pathways) resulting from synergistic interactions between dogs and other ecological disturbances, especially at the habitat edges (Didham, Tylianakis, Gemmill, Rand, & Ewers, 2007; Doherty et al., 2015).

Although protected areas are generally considered the cornerstone of biodiversity conservation and the primary strongholds of wilderness (Bruner, Gullison, Rice, & de Fonseca, 2001), they are ecologically linked to the surrounding habitats and vulnerable to many anthropogenic disturbances emanating from outside their borders (Laurance et al., 2012; Lovejoy, 2006). Indeed, if dogs are common within protected areas, these areas are no longer functionally protected (Cantrell et al., 2001; Hansen & DeFries, 2007). Although few ecosystems are free of the influence and disturbance of dogs (Hughes & Macdonald, 2013; Silva-Rodríguez & Sieving, 2012), some are more prone to invasion than others (Pyšek &

Richardson, 2010). Among tropical forests, one of the worst scenarios may be found at Brazilian Atlantic Forest, which is one of the most threatened and fragmented ecosystems (Canale, Peres, Guidorizzi, Gatto, & Kierulff, 2012; Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009).

Atlantic Forest has experienced a long history of intense landscape modification for commodity exports, which has been accelerated through the past century via coffee and sugarcane monocultures (Gibbs et al., 2010; Tabarelli, Aguiar, Ribeiro, Metzger, & Peres, 2010). Currently, ~120 million people (70% of the Brazilian population) live in regions previously dominated by Atlantic Forest, resulting in unprecedented levels of habitat loss and other human disturbances (Tabarelli et al., 2010) creating opportunities for dog invasion in the remaining protected areas (Hansen & DeFries, 2007; Macdonald et al., 2009). The dog has become a major issue and represents one of the greatest challenges for biodiversity conservation in Atlantic Forest (Lessa, Guimarães, Bergallo, Cunha, & Vieira, 2016; Paschoal, Massara, Santos, & Chiarello, 2012; Paschoal et al., 2016), giving urgency to reducing its ecological impacts. The species distribution and habitat use define the types and degree of interactions that may occur between dog and native fauna (Vanak et al., 2014), thus understanding dog-habitat relationships is crucial for future action plans aimed at mitigating the dog's impact on native fauna (Simberloff, Parker, & Windle, 2005).

In the past decade, dogs have become a major research theme in conservation biology (Hughes & Macdonald, 2013), yielding some information related to its space use and distribution (Sepúlveda et al., 2015; Silva-Rodríguez & Sieving, 2012). However, there is still limited knowledge about its habitat use and factors that determine its distribution within protected areas, especially in Brazil. Here, we used a combination of camera trapping data and occupancy models, which accounts for imperfect detection probability (MacKenzie et al., 2002, 2006), to achieve a better understanding of dog-habitat relationships in Atlantic Forest. Our main goals were to explore environmental factors that may influence dog occupancy (i.e., hereafter probability of use) in a highly heterogeneous tropical forest. In addition, we explored for variables that may account for variation in dog detection probabilities (MacKenzie et al., 2006).

Methods

Study Areas

We conducted our study across three state parks (Rio Doce, Sete Salões, and Serra do Brigadeiro) and three private protected areas (Feliciano Miguel Abdala, Mata do Sossego, and Fazenda Macedônia), all within the

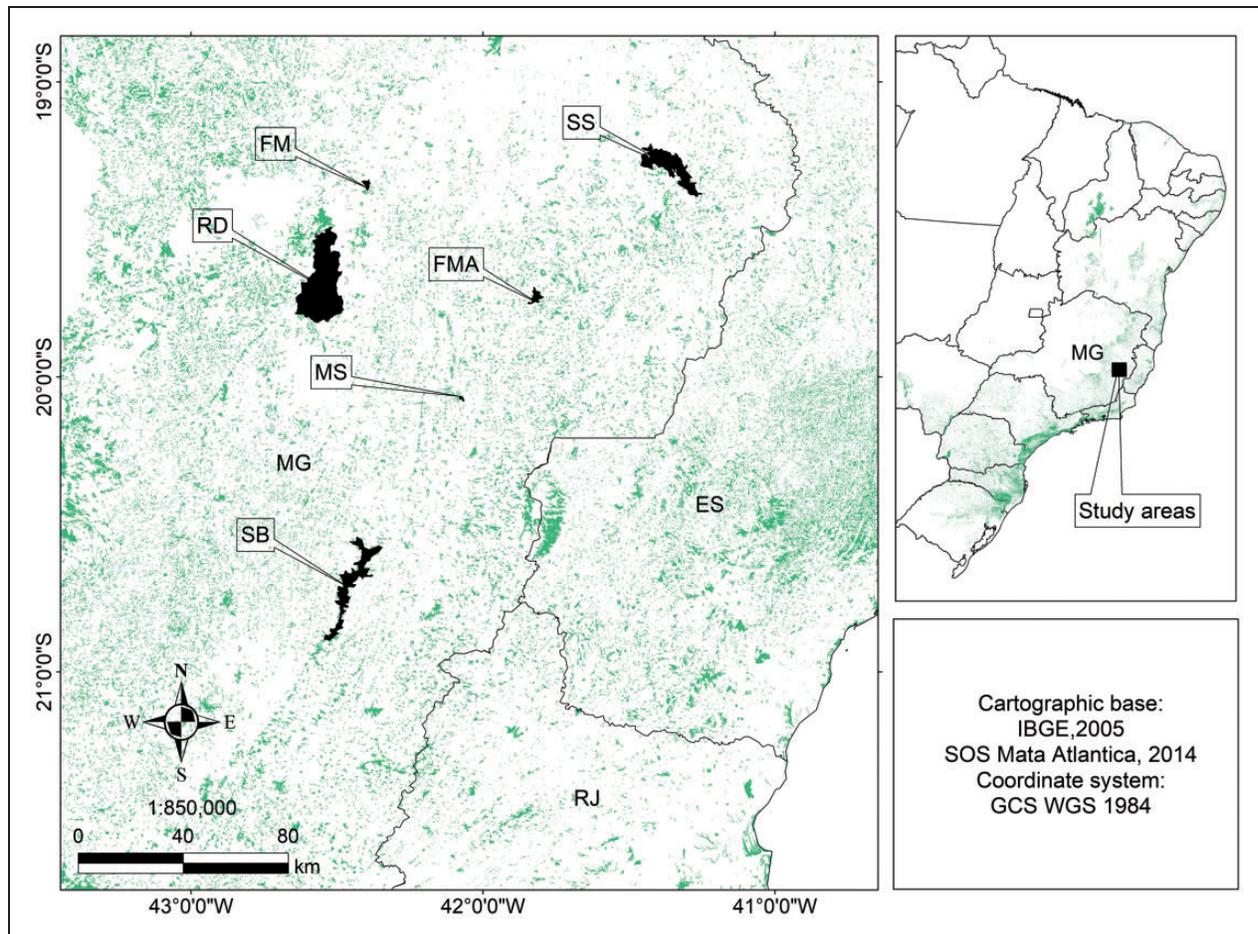


Figure 1. Location of the six protected areas sampled for free-ranging domestic dog in the Atlantic Forest, southeastern Brazil. The inset shows the current distribution of the Atlantic Forest remnants in green. FMA = Feliciano Miguel Abdala; MS = Mata do Sossego; FM = Fazenda Macedônia; SS = Sete Salões; SB = Serra do Brigadeiro; RD = Rio Doce. Adapted from Massara et al. (2015).

Atlantic Forest Biome in the state of Minas Gerais, southeastern Brazil (hereafter referred to as *protected areas*; Figure 1). These areas are predominately native forest remnants, surrounded mostly by disturbed habitats including pasture, croplands, and eucalyptus plantations (Massara, Paschoal, Doherty, Hirsch, & Chiarello, 2015). Abandoned pasture, small subsistence crops, some eucalyptus stands, and a network of trails and roads also occur within our protected areas, but in relatively small proportions compared with the native forest. Rural houses are found in both the protected areas and surrounding habitats (Figure 2).

Sampling Design and Field Methods

We sampled 120 camera sites (i.e., our sampling units), consisting of 20 camera sites randomly selected within each of the 6 protected areas. The minimum and mean distance between cameras was 200.55 m and 571.98 m, respectively. At each site, we placed two cameras (Tigrinus© conventional model, passive infrared sensor;

Tigrinus Research Equipment, Brazil), except when we encountered logistical constraints (e.g., no site access). In these cases, cameras were relocated 50 to 100 m from the original location, and we recorded the actual camera site using a GPS unit. At two small private protected areas (i.e., Mata do Sossego and Fazenda Macedônia), some camera sites were established on surrounding lands to maintain our sampling design. Cameras were operated for 24 hours with an interval of 5 minutes between photographs. No bait or attractants were used that could produce heterogeneity in detection probability (Espartosa, Pinotti, & Pardini, 2011). Sampling occurred between 2008 and 2012. Each protected area was sampled for 80 days in both dry (April–September) and wet (October–March) seasons. Because we had a restricted number of cameras ($n=10$), we rotated them among our random sites within each protected area. We sampled 5 sites for 20 consecutive days and then replaced the photographic film and batteries before moving them to another 5 sites in the protected area. We repeated this process until all 20 camera sites were sampled, totaling 80 days per season.



Figure 2. Protected areas sampled for free-ranging domestic dog in the Atlantic Forest, southeastern Brazil (photo by Ana M. O. Paschoal/Rodrigo L. Massara).

Modeling Probability of Use (Ψ) and Detection Probability (p) as a Function of Predictor Covariates

We chose covariates that were biologically important or those that reflected potential management actions in the protected areas or the surrounding habitat. We developed preliminary list of potential covariates using past studies and the dog's natural history. We assessed correlations among covariates using Pearson's correlation coefficient to develop the candidate model set. Covariates with correlation coefficients ($|r|$) greater than .7 were considered collinear (Whittington, St Clair, & Mercer, 2005), and one of the covariates was eliminated from further analyses (see Results section). Using the retained covariates, we modeled factors that could influence dogs' probability of use (Ψ) and detection probability (p).

Dogs' Probability of Use (Ψ)

We expected that dogs' probability of use (Ψ) could vary with (a) landscape composition (the proportion of

unpaved road, agricultural lands, eucalyptus, and size of protected areas); (b) proximity and intensity of human activities (rural housing density, distance to edge, and distance to house); and (c) other coexisting species (top predators and native mammal species). Specifically, we developed nine a priori hypotheses regarding factors that may influence dogs' use of a site within protected areas (see the following).

To investigate the influence of protected area size on probability that dogs use a site, we measured the size of each protected area and categorized them into two groups (i.e., small, <1,000 ha and large, >10,000 ha). We expected that dogs' use may be higher at sites located within smaller protected areas because those small patches of natural habitats tend to be more vulnerable to edge effects, thus more susceptible to cross-edge incursions by dogs. We also measured the linear distance between each camera site and the nearest house or forest edge. Dogs often reach high densities—and consequently high propagule pressure—where human population is high and in close proximity (Ordeñana et al., 2010). Thus, dogs should show higher levels of use at

sites with higher housing density or near forested edge (Sepúlveda et al., 2015).

In addition to human activities, dog use might be influenced by other species. Specifically, we expected that the probability of dog use could vary according to the number of terrestrial mammal species and the occurrence of top predators. We expected a positive relationship between terrestrial mammal richness and probability of dog use because high mammal richness may indicate habitats with more potential resources that could supplement dog's diet (Hughes & Macdonald, 2013; Ritchie et al., 2014). We calculated the number of terrestrial mammal species detected at each site and used this measure as a site covariate in our analysis. We also estimated the conditional occupancy probability ($\Psi_{conditional}$) of top predators (jaguars—*Panthera onca* and pumas—*Puma concolor*) for each camera site using a single-season occupancy model (Table 1; MacKenzie et al., 2002) incorporated into Program PRESENCE (Hines, 2006). Due to limited detections, we could not estimate different occupancy probabilities for each species; however, we believed that both top predators represent the same ecological

relationship with dogs (Butler et al., 2014). Specifically, we expected dogs to avoid sites where top predators occur because they can impose suppressive effects on dogs, via consumptive (direct predation; Foster, Harmsen, Valdes, Pomilla, & Doncaster, 2010; Mazzolli, 2009) and nonconsumptive (fear-mediated) effects (Estes et al., 2011; Ritchie & Johnson, 2009).

Dog Detection Probability (p)

We developed eight a priori hypotheses regarding factors that may influence dog detection probability (p) at used sites. We model variation in detection probability as a function of many of the same covariates used for the probability of dogs' use (Table 1). Among all protected areas, we expected that sites located closer to edge or human habitats would be used by more dogs and consequently would have higher dog detection probability (or p) compared with more remote sites (Ordeñana et al., 2010).

Specifically, we expected that sites within smaller protected areas, close to human housing (distance or density)

Table 1. Covariates Used to Model the Variation in Probability of Use (Ψ) and Detection Probability (p) of Free-Ranging Dogs in Six Protected Areas for Brazilian Atlantic Forest.

	FMA	MS	FM	SS	SB	RD
Proportion of agricultural lands (%)	13.00 (0–50.50)	2.46 (0–15.40)	35.00 (0–84.80)	14.48 (0–62.12)	8.70 (0–44.00)	0.08 (0–1.67)
Proportion of eucalyptus (%)	0 (0–0)	0 (0–0)	27.60 (0–98.57)	0 (0–0)	0 (0–0)	5.81 (0–31.85)
Proportion of unpaved road (%)	0.18 (0–3.85)	0 (0–0)	0 (0–0)	0 (0–0)	0.78 (0–5.34)	0 (0–0)
Rural housing density (houses/km ²)	2.06 (0–3.66)	2.11 (0.5–6.53)	1.04 (0–3.34)	0.94 (0.16–3.66)	1.05 (0–2.31)	0.06 (0–1.19)
Distance to edge (m)	249.45 (10–569)	571.70 (0–969)	84.94 (0–499)	286.26 (0–692)	245.31 (20–697)	909.60 (67–2,360)
Distance to house (m)	595.88 (161–1,273)	846.10 (96.89–1,574)	1,007 (227.52–2,000)	747.71 (53–1,632)	898.79 (212–2,000)	880.77 (240–1,542)
Ψ conditional of top predators ^a	0.10 (0.05–1.00)	0 (0–0)	0.50 (0.33–1.00)	0.10 (0.02–1.00)	0.41 (0.09–1.00)	0.64 0. (0.20–1.00)
Detection of top predators	0.01 (0–0.13)	0 (0–0)	0.04 (0–0.25)	0.01 (0–0.13)	0.05 (0–0.25)	0.19 (0–0.75)
Number of native mammal species	3.54 (1–7)	3.9 (1–9)	5.15 (1–9)	1.96 (0–5)	2.7 (0–7)	5 (2–10)
Days of camera operation	32 (2–40)	40 (40–40)	40 (40–40)	30 (9–40)	39 (20–40)	40 (40–40)
Cameras located on unpaved road	13	0	11	1	0	7
Protected area size (ha)	958	134	560	12,520	14,985	35,970

Note. FMA = Feliciano Miguel Abdala; MS = Mata do Sossego; FM = Fazenda Macedônia; SS = Sete Salões; SB = Serra do Brigadeiro; RD = Rio Doce. Mean and range (minimum–maximum) values are given for each protected area. The values for *Detection of top predators* are the proportion of occasions (out of eight total occasions) with top predator detections, averaged across sites. *Camera located on unpaved road* indicates the number of camera sites that were installed on unpaved roads in each protected area (out of 20 total sites).

^a Ψ conditional is the probability that a site is used by top predators, given its detection history in each protected area.

or edge, and with higher terrestrial mammal richness, may have higher detection probability than used sites within larger protected areas, further from houses or with lower rural housing density. While we might expect small, private protected areas to suffer more from edge effects, the covariates related to rural housing density and distance to edge and nearest house were not highly correlated.

Three additional covariates were used only to model potential variation in detection probability among sites. First, we recorded the camera site as either on (1) or off (0) unpaved roads and the number of days that cameras were operable. We expect that sites located on unpaved roads or sites where cameras operated for longer periods may have higher detection probability. Dogs preferentially move via roads and trails, which may increase their detection probability (Moreira-Arce, Vergara, & Boutin, 2015; Sepúlveda et al., 2015; Silva-Rodríguez & Sieving, 2012). Finally, we constructed a covariate for each site indicating whether top predators were detected (1) or not (0; Table 1) during each occasion. We expected a negative relationship between detection probability and top predator detection because dog may temporally avoid a site during occasions when top predators were detected (Lewis et al., 2015).

Model Fitting and Data Analysis

We used single-species single-season occupancy models to estimate probability that dogs use a site and detection probability (MacKenzie et al., 2002, 2006). Dog detection records (i.e., photographs) were summarized into a matrix of detection histories, reflecting if a dog was detected (1) or not (0) during each occasion at our 120 study sites. We defined an occasion as a 5-day period, so each site had 4 occasions per season.

A critical assumption of this model is that dogs' use at each site is static and does not change during the study period (i.e., a site is either used or not during the study period; MacKenzie et al., 2006). We assessed the potential violation of this model assumption by exploring possible changes in the occupancy state between dry and wet seasons, using a dynamic occupancy model (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). We fitted four models, where colonization and extinction parameters were either estimated (nonzero) or fixed to 0 (i.e., occupancy state is static between seasons), and we allowed p to vary or not between seasons. Models were fit using Program MARK (White & Burnham, 1999), and we used the relative difference in Akaike's Information Criterion adjusted for small sample size (AICc) among models (ΔAICc) to evaluate which model was better supported by our data (Burnham & Anderson, 2002). The static occupancy model, suggesting that dog use did not

change between seasons, was better supported (ΔAICc for the dynamic model = 2.85), and p was constant between seasons (ΔAICc for detection varying between seasons = 4.72). Therefore, we used the single-season occupancy approach with eight occasions (both seasons) and did not test for seasonality effect in detection probability in our subsequent analysis.

Initially, we considered models with an interaction between distance to housing and housing density for probability that dogs use a site; however, based on the ΔAICc , none of interactive models were supported by our data. Consequently, we developed a set of models consisting of all possible additive covariate combinations (Doherty, White, & Burnham, 2012) for our two parameters: Ψ , the probability that dogs use a site, and p , detection probability. This approach resulted in a balanced model set essential to interpret the cumulative AICc weights (w_+) for each covariate (Burnham & Anderson, 2002).

We assessed goodness of fit (GOF) and evaluated overdispersion (i.e., lack of independence among camera sites) using our most parameterized model and the Pearson's GOF test incorporated in Program PRESENCE (MacKenzie & Bailey, 2004).

Results

We found strong negative correlation between proportion of forest cover and proportion of agricultural lands (e.g., $r = -.70$). Because dog occurrence is often inversely correlated with vegetation (McKinney, 2006; Ryall & Fahrig, 2006) and closely related to human activities (Pita, Mira, Moreira, Morgado, & Beja, 2009; Soto & Palomares, 2015), we retained the proportion of agricultural lands and removed proportion of forest cover in our analyses. Our GOF test revealed no evidence of lack of fit and little overdispersion in the data ($\chi^2 = 350.73$; p value = .09; $\hat{c} = 1.20$), so we used AICc values and associated metrics for biological inference.

Our analyses showed uncertainty among Ψ and p model structures, but our most parsimonious model ($w_+ = 0.13$), was ~ 3 times more likely than any other model in our candidate set (Table 2). Consistent with a priori hypotheses, the probability of dog use showed a strong positive relationship with rural housing density ($w_+ = 0.82$) and proportion of agricultural lands ($w_+ = 0.65$; Table 3).

Sites with high rural housing density (≥ 4.00 houses/km²; Figure 3(a)) or higher proportion of croplands and pasture ($\geq 75\%$; Figure 3(b)) were likely to be used by dogs ($\hat{\Psi} \geq 0.90$) compared with sites with no houses ($\hat{\Psi} = 0.23 \pm 0.10$; Figure 3(a)) or agricultural activities ($\hat{\Psi} = 0.34 \pm 0.08$; Figure 3(b)). There was little evidence that any other covariate influenced dogs' probability of use ($w_+ < 0.20$; Table 3; Figure 4).

Table 2. Model Selection Results for the Top 10 Models in the Candidate Set.

Model	AICc	Δ AICc	w	K	-2Log(L)
{ Ψ (AG + RD), p (CL + RD)}	569.68	0.00	0.13	6	556.98
{ Ψ (AG + RD), p (CL + DH)}	571.83	2.16	0.04	6	559.14
{ Ψ (AG + RD), p (RS + RD)}	572.55	2.88	0.03	6	559.86
{ Ψ (AG + RD + EU), p (CL)}	572.80	3.13	0.03	6	560.11
{ Ψ (AG + RD + EU), p (RS)}	572.82	3.15	0.03	6	560.13
{ Ψ (AG + RD), p (CL + RS)}	573.25	3.58	0.02	6	560.56
{ Ψ (RD), p (CL + RD + DH)}	573.49	3.82	0.02	6	560.80
{ Ψ (AG + RD), p (RS + DE)}	573.51	3.83	0.02	6	560.81
{ Ψ (AG + RD), p (CL)}	573.64	3.96	0.02	5	563.14
{ Ψ (AG + RD), p (RS + DH)}	573.68	4.01	0.02	6	560.99

Note. AICc = Akaike's Information Criterion adjusted for small sample size.

Ψ denotes the probability that a dog used a site during the sampling period, and p is probability of detecting a dog during occasion j , given the site was used. AICc and Δ AICc values and their respective weights (w) are shown for models with the following effects for Ψ or p : proportion of agricultural lands (AG), proportion of eucalyptus (EU), rural housing density (house/km²; RD), camera site location (on or off unpaved road; CL), protected area size (RS), distance to edge (DE), and distance to house (DH). The plus signal (+) means an additive effect between two or more covariates. K denotes the number of parameters in each model.

Table 3. Cumulative AICc Weights ($w+$) for Covariates Used to Model the Variation in Probabilities of Use (Ψ) and Detection (p) of Free-Ranging Dog in Six Protected Areas of Brazilian Atlantic Forest.

Covariate	Cumulative AICc weights (%)	β parameters		
		Estimate	Lower 95% CL	Upper 95% CL
<i>Free-ranging dog use (Ψ)</i>				
Rural housing density (house/km ²)	0.82	0.84	0.26	1.41
Proportion of agricultural lands (%)	0.65	0.04	0.01	0.07
Protected area size (ha) ^a	0.17	0.72	-0.29	1.73
Proportion of eucalyptus (%)	0.17	-0.02	-0.05	0.01
Distance to edge (m)	0.07	-0.1×10^2	-0.3×10^2	0.3×10^3
Distance to house (m)	0.04	-0.8×10^4	-0.9×10^3	0.8×10^3
Ψ conditional of top predators	0.04	-0.21	-1.54	1.12
Proportion of unpaved roads (%)	0.04	-0.09	-0.74	0.55
Number of terrestrial mammal species	0.04	-0.04	-0.29	0.21
<i>Free-ranging dog detection (p)</i>				
Camera site location ^b	0.57	0.81	0.28	1.34
Rural housing density (house/km ²)	0.46	0.30	0.07	0.54
Protected area size (ha) ^a	0.33	0.83	0.16	1.51
Distance to house (m)	0.22	-0.6×10^3	-0.1×10^2	-0.6×10^4
Distance to edge (m)	0.09	-0.7×10^3	-0.2×10^2	0.2×10^3
Days of camera operation	0.06	-0.02	-0.05	0.01
Detection of top predators	0.06	-1.03	-3.08	1.01
Number of terrestrial mammal species	0.06	0.04	-0.09	0.17

Note. AICc = Akaike's Information Criterion adjusted for small sample size. Estimates of covariate effects (β parameters) are given for the most parsimonious model that included the covariate.

^a β parameter value based on protected areas considered small (<1,000 ha).

^b β parameter value based on camera sites that were installed on unpaved road.

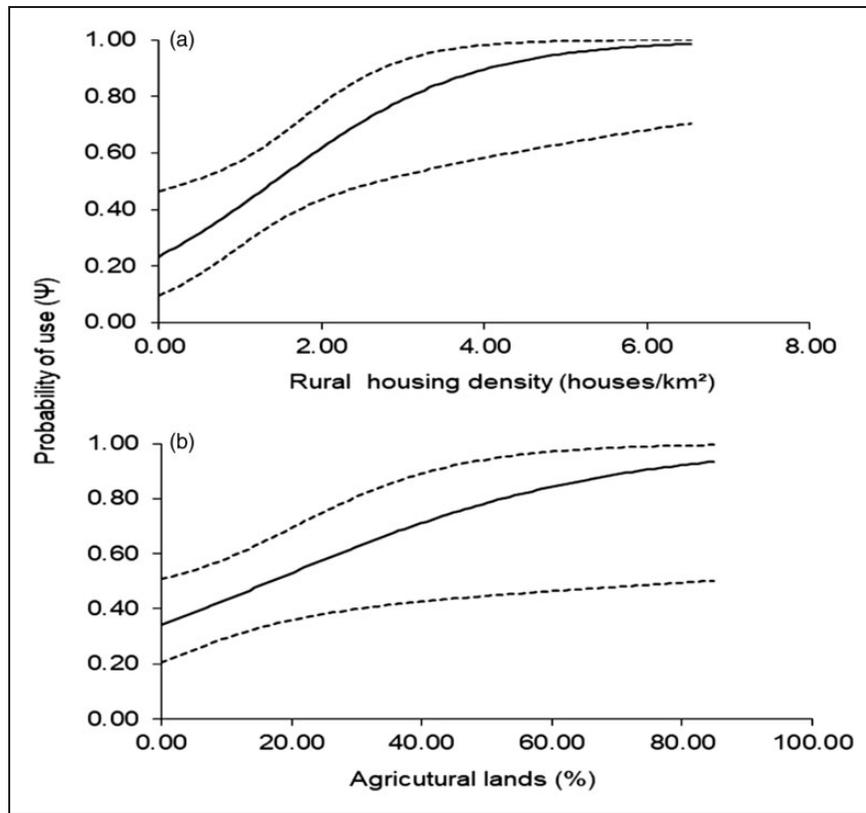


Figure 3. Probability of free-ranging dog use as a function of site-specific proportion of rural housing density (a) and agricultural lands (b) in Brazilian Atlantic Forest. Estimates are from the most parsimonious model that included the covariates, $\psi(\text{AG} + \text{HD})$ and $p(\text{CL} + \text{HD})$.

In addition, we found moderate evidence for effects of camera location ($w+ = 0.57$) and rural housing density ($w+ = 0.46$) on dog detection probability (Table 3). Dogs had higher detection probability at used sites located on unpaved roads ($\hat{p} = 0.33 \pm 0.05$) than off-road sites ($\hat{p} = 0.18 \pm 0.04$; Figure 5). As expected, sites with higher house density had higher detection probabilities (Figure 5). All other covariates had little support ($w+ < 0.35$) and thus did not strongly influence the detection probability of dogs at used sites (Table 3).

Discussion

Accordingly, our predictor variables associated with human activities were the most important in shaping dogs' habitat use within protected areas. Dogs are highly adapted to anthropogenic habitats (Silva-Rodríguez & Sieving, 2012; Vanak & Gompper, 2010), and consequently, their spatial distribution is strongly influenced by human activities, such as rural housing and agricultural lands (Paschoal et al., 2016; Silva-Rodríguez & Sieving, 2012; Vanak & Gompper, 2010). These activities reflect two factors that are thought to lead to thriving dog populations, namely, increased food supply resulting in augmented propagule pressure

and favorable habitat for dogs derived from modifications in the landscape (Hansen et al., 2005; McKinney, 2006; Vanak & Gompper, 2009).

Further, the dogs' probability of use is a function not only of activity type (e.g., agriculture) but also of its magnitude (intensity) in the landscape (e.g., housing density), even in low-density rural areas (≤ 7 houses/km²; Hansen et al., 2005). Our sites composed by $\geq 50\%$ agriculture and with ≥ 4 houses/km² were respectively ~ 2 to 4 times more likely to be used by a dog when compared with sites with no agriculture or rural housing. In addition to increased dog abundance, land-use intensification leads to a landscape mosaic with increased habitat edges that juxtapose disturbed and natural habitats. This facilitates dog occurrence within protected areas through cross-edge incursions (Cantrell et al., 2001; Sepúlveda et al., 2015), where dogs may cross habitat edges and move from a human modified habitat to an adjacent protected area, exacerbating potential impacts on native fauna (Cantrell et al., 2001). This cross-edge incursion events might be further increased at the borders of protected areas (Hansen et al., 2005; Wittemyer, Elsen, Bean, Burton, & Brashares, 2008) because protected areas provide ecosystem services such as water and soil quality, lower



Figure 4. Some detected free-ranging domestic dog in the Atlantic Forest, southeastern Brazil.

temperature, among others, that beneficiates human activities.

We found no evidence that other variables (e.g., eucalyptus, mammal richness, roads) influence the probability that a dog uses a site within protected area. Our inability to show a direct relationship between top predators and dogs' probability of use may be explained by the alarmingly low population status of these top predators. Due to fragmentation, habitat loss, overexploitation, and persecution, top predators' populations are declining worldwide (Hansen et al., 2005; Ritchie & Johnson, 2009), even in areas with low human densities, due to their intolerance to anthropogenic landscapes (Hansen et al., 2005; Ritchie & Johnson, 2009). Population of these two large cats in Atlantic Forest are critically low, even in protected areas, leading to unprecedented rates of local extinctions (Canale et al., 2012; Hansen et al., 2005). This current scenario may enhance the impact of dogs on native fauna (Doherty et al., 2015) because the collapse of top predators can result in outbreaks of mesopredators (mesopredator release), leading to detrimental impacts on the underlying prey community (Crooks & Soulé, 1999; Estes et al., 2011).

Our detection results also show a preponderant influence of anthropogenic features, particularly roads and house density. Used camera sites located on unpaved roads were ~ 2 times more likely to detect dogs than off-road cameras, even though a small proportion of our camera sites (25%) were placed on unpaved roads. Bare ground and linear features associated with disturbed habitats (e.g., unpaved roads, trails) can act as movement corridors and hunting grounds for carnivorans (Soisalo & Cavalcanti, 2006). Elsewhere, dogs also seem to preferentially move through habitats/areas via roads (paved or not) and trails (Sepúlveda et al., 2015; Silva-Rodríguez & Sieving, 2012; Srbek-Araujo & Chiarello, 2008). Therefore, our results are consistent with similar patterns observed in other studies where roads and trails facilitate dog movement within protected areas (Vanak et al., 2014). In addition, dog detection probability was ~ 3 times higher at sites with housing density ≥ 4 houses/km² than at sites with no houses. This pattern could be related to two factors: First, dog density is directly linked to human density (Ordeñana et al., 2010), and an increase in local dog abundance raises the species detection probability in a predictable way (Royle, Nichols, & Kéry, 2005).

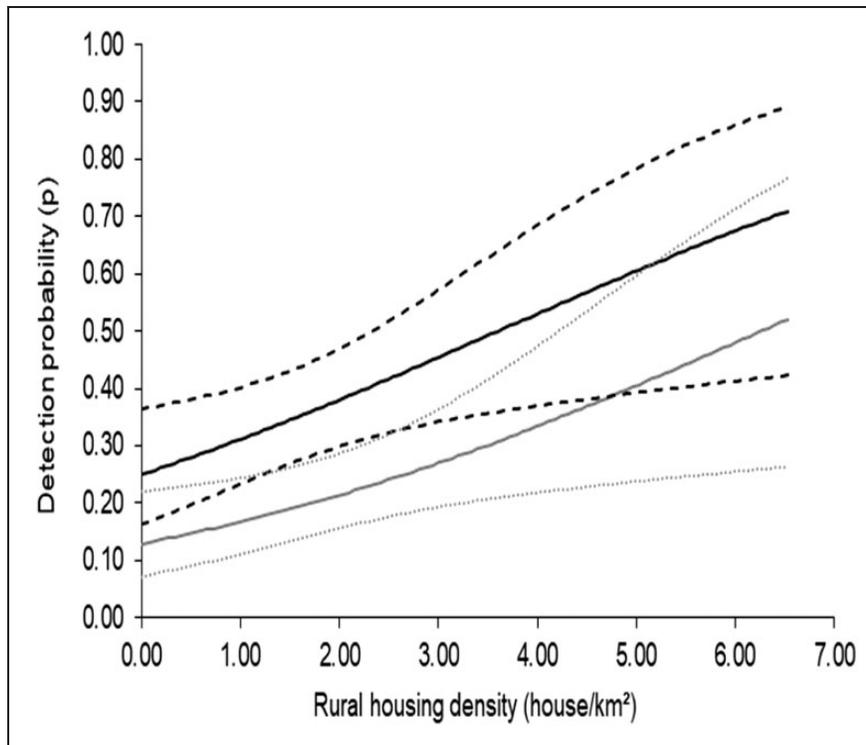


Figure 5. Detection probability of free-ranging dog as a function of rural housing density in Brazilian Atlantic Forest using the most parsimonious model that included this covariate, $\psi(\text{AG} + \text{HD})$ and $p(\text{CL} + \text{HD})$. Estimates are based on either camera sites installed on (black line) or off (gray line) unpaved roads. Dashed lines represent the 95% confidence intervals.

Typically, small protected areas have higher housing density (Table 1) and higher abundance/density of dogs (Paschoal et al., 2016). Second, dog usually center their activity around their homesite (i.e., rural housing; Dürr & Ward, 2014; Meek, 1999), where they spend most of their time (Ruiz-Izaguirre et al., 2014; Sepúlveda et al., 2015). This spatially aggregated activity pattern likely leads to a higher frequency of use and thus a higher detection probability.

Our study also sheds light on links or insights between dog and wildlife distribution in these areas. In other words, it is known that free-ranging dog occurrence negatively affects the distribution of native species, such as maned wolf (*Chrysocyon brachyurus*) and giant anteater (*Myrmecophaga tridactyla*) in the Brazilian Cerrado (Lacerda et al., 2009) and margay (*Leopardus wiedii*), oncilla (*Leopardus tigrinus*), naked-tailed armadillo (*Cabassous* sp.), and golden-headed lion tamarin (*Leontopithecus chrysomelas*) in the Brazilian Atlantic Forest (Cassano, Barlow, & Pardini, 2014).

Specifically for our studied protected areas, a companion study conducted at the same time and with the same sampling design, found that dog densities were approximately 3 to 85 times higher than ocelot (*Leopardus pardalis*) densities (Massara et al., 2015; Paschoal et al., 2016), and ocelots were rare where free-ranging dogs were abundant and vice versa (Massara et al., 2015;

Paschoal et al., 2016), indicating an inverse pattern in abundance (i.e., abundance-asymmetry hypothesis; Vázquez et al., 2007).

In addition, ocelot occupancy at sites with a high number of dogs was almost 4 times lower than at sites with no dogs (Massara et al., 2018a), and the species tended to be even more nocturnal at sites where the landscape was intensively altered by human activities (i.e., rural housing and agriculture; Massara et al., 2018b). Therefore, ocelots may restrict their activity in these areas or use them only at night hours, when encounters with humans or with free-ranging dogs associated with human residences are diminished.

However, it is unlikely that these changes in ocelot behavior per se might be enough to guarantee long-term persistence of the species, especially in the current scenario of the Atlantic Forest biome, and, therefore, the outlook for ocelots in these forest remnants may be extremely pessimistic if management actions are not implemented. For example, the degree of human modification within and surrounding protected areas is a crucial factor to understand and anticipate dog occurrence and its impact, therefore, can promote support for effective management strategies aiming native fauna conservation.

This finding is a valuable and concerning information, given that people live within the boundaries of 70% of

protected areas in the tropics (Bruner et al., 2001) and that human populations continue to grow near the edges of biodiversity hotspots, like Atlantic Forest protected areas (Laurance, 2015; Wittemyer et al., 2008). Human population growth creates greater demand for food, leading to conversion of natural lands to agricultural use (Foley et al., 2005; Grau, Gasparri, & Aide, 2008), mostly via high-intensity crop production (Foley et al., 2005). This dynamic increases the susceptibility of natural habitats, especially protected areas, to subsequent dog invasions. Our findings reinforce that domestic dog is one of the most species within protected areas in different biomes, including Atlantic Forest (Lacerda et al., 2009; Lessa et al., 2016; Paschoal et al., 2016; Srbeek-Araujo & Chiarello, 2008).

The Atlantic Forest is heavily influenced by edge effects because about 80% of its fragments consist of small patches, and nearly half of the remaining area is less than 100 m from the nearest edge (Ribeiro et al., 2009). Thus, dog occurrence and their corresponding impact will likely be enhanced, not only because of this exposure to edge but also due to increasing anthropogenic pressure in the coming decades (Hansen & DeFries, 2007), reducing the conservation effectiveness of protected areas (DeFries, Hansen, Newton, Hansen, & Townshend, 2005; Hansen & DeFries, 2007).

Implications for Conservation

Due to the current scenario of the Atlantic Forest protected areas, our findings highlight the importance of buffer zones for deterring and minimizing the use of protected areas by free-ranging dogs. However, protocols associated with the implementation of buffer zones, suggested by the Brazilian system of protected areas (Federal Law# 9985; July 18, 2000; Federal Resolution# 428; December 17, 2010), are not effective for protecting species from this external threat (Massara et al., 2018a).

Furthermore, dogs in our study areas were not feral, suggesting that human residents play an important role in curbing the impact of dogs on native fauna (Ritchie et al., 2014) and are an essential component for long-term dog management (Schwartzman, Moreira, & Nepstad, 2000). The future ability of protected areas to maintain current biodiversity requires the understanding that protected areas are components of larger ecosystems and are often ecologically linked to their surrounding habitats (Hansen & DeFries, 2007).

Given the urgent need to control free-ranging dogs within natural areas, we strongly recommend that managers prioritize zones, within a buffer of ~10 km surrounding protected areas, that have ≥ 4.00 houses/km² or a higher proportion of croplands and pasture ($\geq 75\%$). In these zones, managers should work with local residents aiming at free-ranging dog eradication or

containment (McGeoch et al., 2016), applying multiple and complementary strategies (e.g., educational programs, neutering campaigns, application and enforcement of laws; Miller, Ritchie, & Weston, 2014).

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ORCID iD

Rodrigo L. Massara  <http://orcid.org/0000-0003-1221-2185>
 André Hirsch  <http://orcid.org/0000-0001-9237-201X>

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