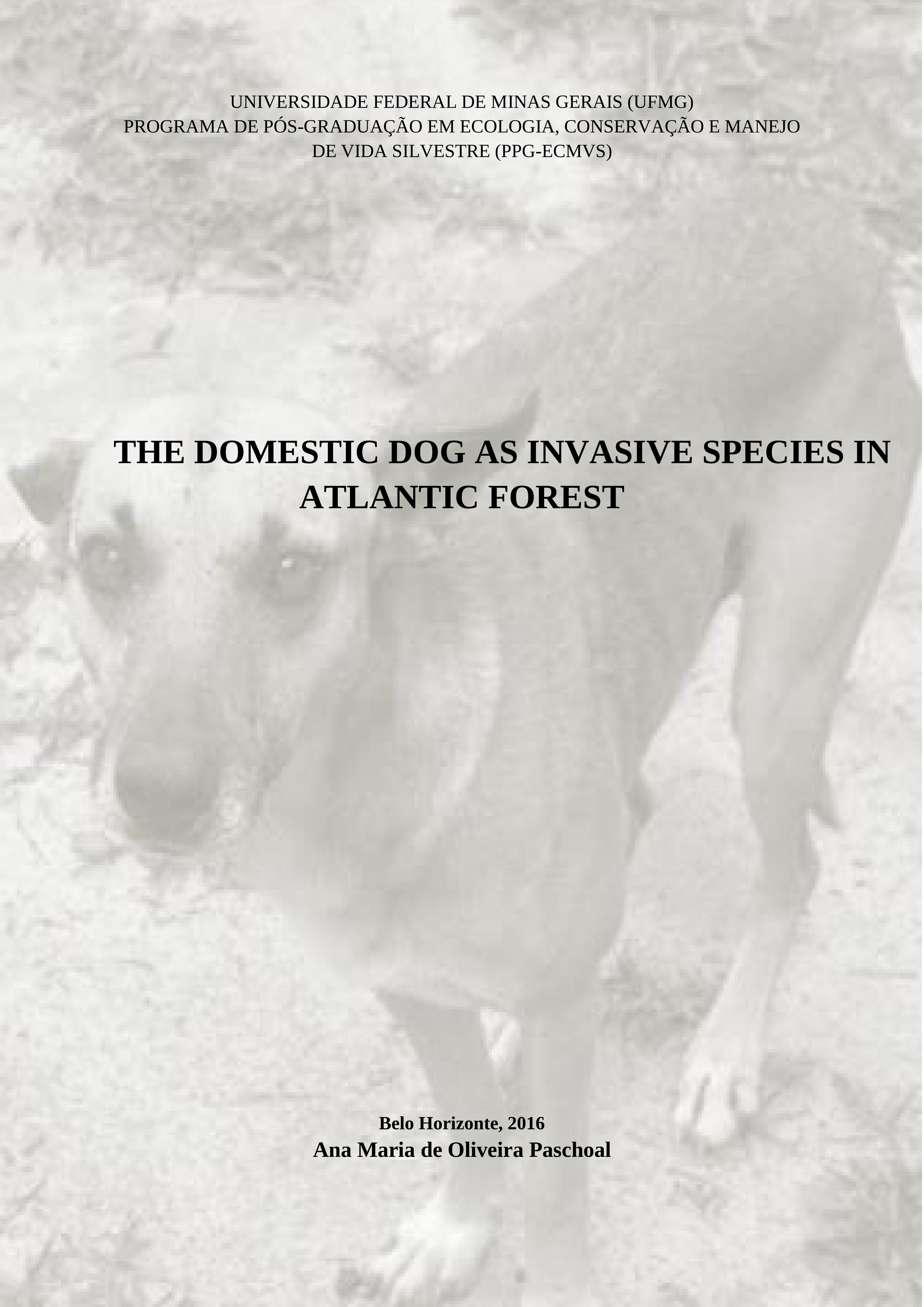

UNIVERSIDADE FEDERAL DE MINAS GERAIS (UFMG)
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DE VIDA SILVESTRE (PPG-ECMVS)

THE DOMESTIC DOG AS INVASIVE SPECIES IN ATLANTIC FOREST

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Ana Maria de Oliveira Paschoal

O cão doméstico como espécie invasora na Mata Atlântica

(Domestic dog as invasive species in Atlantic Forest)

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Co-orientadores: Dr. Adriano G. Chiarello (USP-Ribeirão Preto)
Dra. Larissa L. Bailey (CSU- Colorado State University)
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Contents

General Introduction

Domestic dog (*Canis familiaris,* Linneus 1798) was the first domesticated species by humans derived from Eurasian gray wolves (Shannon et al. 2015). Despite the origin and evolution of the domestic dog remains a controversial question, with basic aspects such as the place and date of origin, and the number of times dogs were domesticated, opens to dispute (Wang et al. 2016). There is no doubt that domestication occurred as a two-stage process where primitive dogs were first domesticated from their wild ancestors, the gray wolves, and in the second stage, the primitive forms were further selected to form dog breeds with specialized abilities and morphology (Lindblad-Toh *et al.* 2005; Wayne et al. 2007; Wang et al. 2014).

Since domestication (12 500 – 30 000 years; Vanak and Gompper 2010, Clutton-Brock 2012), dog has been subsidized and introduced (intentional or not) worldwide as a ubiquitous commensal of humans (Vanak and Gompper 2009; Vanak and Gompper 2010). Therefore, domestic dog population size and distributions mirror those of humans (Gompper 2004), consequently dog is one of the most common and widespread carnivoran on the planet (Vanak and Gompper 2010; Gompper 2014). The species is ubiquitous on all continents, except Antarctica, and in most human inhabited islands (Wandeler et al. 1993). With a global population size around 700 to 987 million (Hughes and Macdonald 2013, Gompper 2014), dogs outnumber all wild carnivoran populations in the world.

Due a combination of natural and strong artificial selection during multiple and independent processes of domestication, dog experienced morphological changes (e.g., body size and cranio-dental configuration (Clutton-Brock 2012) and was selected to has life history traits of *r*-selected species (Kitala et al. 2001; Gompper 2014), and a large niche breadth (Vázquez 2005). All these traits together allow dog to survive, reproduce and persist in a wide range of habitats (Ryall and Fahrig 2006; Ritchie et al. 2014) and make the dog one of the most successful invasive species (Miklósi 2007). However, the socio-ecology and diet of dog vary according with the way the species is managed, and its reliance degree on humans subsidizes (Vanak and Gompper 2009; Gompper 2014).

Vanak and Gompper (2009) suggested placing dog under one of six categories proposed: (1) dogs that are owned and restricted in movement to a proscribed area (owned dogs); (2) dogs that are not owned by humans, but are commensals, subsisting on human subsidies as their primary energetic source. They usually do not come into contact with native fauna, except in urban parks (urban free-ranging dog); (3) dogs that are owned or peripherally associated to human house, but are not restrained to a fixed area (rural free-ranging).Therefore, free-ranging dogs has a foraging behavior that can bring them into contact with native fauna more often than dog of other class; (4) Unconfined dogs that are associated to human houses in rural environments , but rarely leaves the immediate proximity of the village (village dogs); (5) Dogs that are wild and completely independent of human subsidies (feral dogs); (6) Dingoes and their hybrids in Asia and Australasia that are no longer considered domesticated.

Under conservation perspective, rural free-ranging dog (henceforth; dog) is a particular concern in exurban/rural landscape, because its allowed to range free through the landscape, thus is more likely to interact with native fauna, especially where human houses border natural habitats, as protected areas (Vanak and Gompper 2009; Gompper 2014). In addition, dog is a medium-sized generalist and opportunistic predator (Ryall and Fahrig 2006; Ritchie et al. 2014), that live primarily in human disturbed habitats (i.e., “matrix based”; Cantrell et al. 2001; Ryall and Fahrig 2006) where the species thrive and build up high local populations (Hughes and Macdonald 2013; Gompper 2014). Although, dog is considered an edge effect (Srbek-Araujo and Chiarello 2008; Lacerda et al. 2009; Vanak et al. 2014) it is not restricted to habitat edges. As a high mobile species, dog can easily cross edge boundaries events; Cantrell et al. 2001; Sepúlveda et al. 2015). Dog has been detected as far as 10 km from the edge (Vanak et al. 2014), and much further away in Australia (up to 30 km; Meek 1999). As consequence, its potential impact on native fauna is not necessarily restricted to the edge (Vanak et al. 2014). Moreover, dog impact within protected areas may be facilitated through complex pathways (e.g., habitat and community-mediated pathways) resulted from synergistic interactions between dog and other ecological disturbances (Didham et al. 2007; Doherty et al. 2015).

Abundance and ranging behavior of dog are recognized as important factors affecting its predator-prey and competitive interactions, which determines its cumulative impact on native fauna (Vanak and Gompper 2009; Gompper 2014). Dog has been reported to interact in multiple ways with native fauna trough predation, exploitative competition, interference competition, surplus killing, pathogen spillover and genetic introgression (Young et al. 2011; Hughes and Macdonald 2013; Ritchie et al. 2014). Dog may also alter native fauna behavior and activity patterns (Young et al. 2011, Hughes and Macdonald 2013). Dog suppression on native fauna has been reported worldwide (29 countries; Hughes and Macdonald 2013), although its impact is usually influenced by social-economic and political characteristics that varies among scales (e.g. national, regional, local; Jackman and Rowan 2007; Gompper 2014).

The dog impacts are usually exacerbated in regions possessing greater diversity (i.e., hotspots of biodiversity). These regions are mostly concentrated on undeveloped or developing countries and typically are under pressure of fast habitat loss and fragmentation, accelerated human population growth, and inefficient waste disposal management. Moreover, the absence of laws or enforcement that promotes responsible dog ownership in these countries increase their exposure and susceptibility to dog' invasion and its effects (Butler et al. 2004; Ritchie et al. 2014).

Among developing countries, Brazil stands out as one of the most diverse country in the world (Mittermeier et al. 2005). The dog was likely introduced from Andean societies to Brazil in ~ 1000 ybp, and posteriorly was widespread around late in the 16th century during European colonial empires (Crosby 1972; Dean 1995; Gompper 2014). Currently, the dog is a well-established species with a positive population growth in Brazil (PNS 2013). A crescent number of studies have been calling attention for the ordinary occurrence of dog within protected areas (Srbek-Araujo and Chiarello 2008; Lacerda et al. 2009; Espartosa 2009; Paschoal et al. 2012, 2016; Lessa et al. 2016), especially in Brazilian Atlantic Forest (Srbek-Araujo and Chiarello 2008; Paschoal et al. 2016; Lessa et al. 2016). This is an alarming evidence that protected areas, although considered and used as the cornerstone of biodiversity conservation (Chape et al. 2005; Loucks et al. 2008) and the primary strongholds of wilderness (Bruner et al. 2001), may be not effectively protected.

Despite the increasing number of studies targeting dogs (Paschoal et al. 2012; Frigeri et al.2014; Lessa et a. 2016) and its profound effect in natural ecosystems, there are still lacks of knowledge about dog ecology and surprisingly few studies targeting dog effects in Brazil (Gompper 2014; Lessa 2016; but see Paschoal et al. 2012; Massara et al 2015). Due to close and complex relationship between humans and dog, people often fail in recognize dog as integral part of carnivoran community, which partially explain the scarcity of studies (Gompper 2014; Lessa 2016; but see Paschoal et al. 2012; Massara et al 2015).

Particularly in Brazil we still need basic ecological information about dogs. How many dogs are effectively using protected areas? For how long dog use protected areas?

Which landscape structures may influence dog probability of use? The presence of dog affects the spatial and/or temporal distributions of potential native competitors and preys? If those dogs have an owner, who are they? What management factors contribute for dog invade protected areas? Can individual traits (e.g., age, height, nutritional condition) contribute for dog invasion? Based on the urgency of such information, the general aim of this study was assess and explore dogs' ecological roles and its effects on natural ecosystems within one of the most endanger Biome in the planet, the Atlantic Forest. Specifically:

(1) Investigate the *status quo* of dog population (Chapter 1 - Ecosphere);
(2) Explore dog-habitat relationship (Chapter 2 - Biological Invasions);
(3) Explore intraguild relationships;
(4) Explore predator-prey relationships;
(5) Explore and describe dog-owner relationship;
(6) Future scenario of dog distribution in Atlantic Forest: Are protected areas really protected?

Due to time constrain, my thesis is focused on the first two topics. This study is component of a larger project, titled: "Mesopredators in Atlantic Forest Protected Areas" which resulted in two more theses and one dissertation:

(1) "Abundance, habitat use and ecological interactions of the ocelot in Atlantic forest protected areas" - Dr. Rodrigo L. Massara (Universidade Federal de Minas Gerais, MG; Colorado State University, CO);
(2) "Domestic dog as invasive species in Atlantic Forest: sentinels of ecological health- Dr. Nelson A. Curi (Universidade Federal de Lavras, MG);

(3) "Ecology of domestic dog (*Canis familiaris*) in Atlantic Forest"- Msc. Julianna L. Santos (Pontifícia Universidade Católica de Minas Gerais, MG)

Collectively, we expect to help inform future management initiatives aimed at curbing the impacts of dog on native species in protected areas.

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Chapter 1 - Use of Atlantic Forest protected areas by free-ranging dogs: estimating abundance and persistence of use

Use of Atlantic Forest protected areas by free-ranging dogs: estimating abundance and persistence of use

Ana Maria O. Paschoal[1,2,3,†], Rodrigo L. Massara[1,2,3], Larissa L. Bailey[3], William L. Kendall[4], Paul F. Doherty, Jr.[3], André Hirsch[5], Adriano G. Chiarello[6], and Adriano P. Paglia[1]

[1] Universidade Federal de Minas Gerais, Departamento de Biologia Geral, Laboratório de Ecologia e Conservação, Avenida Antônio Carlos, no. 6627, Belo Horizonte, MG 31270901, Brazil.

[2] Instituto SerraDiCal de Pesquisa e Conservação, Rua José Hemetério de Andrade, no. 570, Belo Horizonte, MG 30493-180, Brazil.

[3] Colorado State University, Department of Fish, Wildlife, and Conservation Biology, 1474 Campus Delivery, 109 Wagar, Fort Collins, CO 80523, USA.

[4] U. S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, 1484 Campus Delivery, Fort Collins, CO 80523, USA.

[5] Universidade Federal de São João Del Rei, Programa Institucional de Bioengenharia, km 47 – Rodovia MG 424, Sete Lagoas, MG 35701-970, Brazil.

[6] Universidade de São Paulo, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Avenida Bandeirantes, no. 3900, Ribeirão Preto, SP 14040-901, Brazil.

[†] E-mail: anamuzenza@gmail.com

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Abstract

Worldwide, domestic dogs (*Canis familiaris*) are one of the most common carnivoran species in natural areas and their populations are still increasing. Dogs have been shown to impact native fauna populations negatively and their occurrence can alter the abundance, behavior, and activity patterns of native species. However, little is known about abundance and density of the free-ranging dogs that use protected areas. Here, we used camera trap data with an open-robust design mark-recapture model to estimate the number of dogs that used protected areas in Brazilian Atlantic Forest. We estimated the time period these dogs used the protected areas, and explored factors that influenced the probability of continued use (e.g., season, mammal richness, proportion of forest), while accounting for variation in detection probability. Dogs in the studied system were categorized as rural free-ranging and their abundance varied widely across protected areas (0–73 individuals). Dogs used protected areas near human houses for longer periods (e.g., >50% of sampling occasions) compared to more distant areas. We found no evidence that their probability of continued use varied with season or mammal richness. Dog detection probability decreased linearly among occasions, possibly due to the owners confining their dogs after becoming aware of our presence. Comparing our estimates to those for native carnivoran, we found that dogs were three to 85 times more abundant than ocelots (*Leopardus pardalis*), two to 25 times more abundant than puma (*Puma concolor*) and approximately five times more abundant than the crab-eating fox (*Cerdocyon thous*). Combining camera trapping data with modern mark-recapture methods provides important demographic information on free-ranging dogs that can guide management strategies to directly control dogs’ abundance and ranging behavior.

Key words*:* Brazil; camera traps; conservation; exotic species; invasive species; management; Neotropical Forest; reserves; robust design mark-recapture; subsidized predator.

Introduction

Invasive species are considered one of the greatest threats to biodiversity (Vitousek et al. 1997; McGeoch et al. 2010), and are one of the factors responsible for biotic homogenization (McKinney and Lockwood 1999). While researchers have debated whether invasive species are the cause or consequence of global change (Didham et al. 2005; MacDougall and Turkington 2005), there is no doubt that invasive species are causing considerable change to complex ecosystems, resulting in consequences that are difficult to predict (Simberloff 2001).

The domestic dog (*Canis familiaris,* Linnaeus 1758) is a generalist and opportunistic species (Ritchie et al. 2014) with large mobility (Meek 1999), high behavioral flexibility (Bentosela et al. 2008) and reproductive rates (Gompper 2014). It is the most successful invasive species (Miklósi 2007) and the most common carnivoran on the planet (Vanak and Gompper 2010; Gompper 2014). The species is ubiquitous on all continents, except Antarctica, and in most human inhabited islands (Wandeler et al. 1993). With a global population size around 700 to 987 million (Hughes and Macdonald 2013; Gompper 2014), dogs outnumber all wild carnivoran populations in the world.

The dogs' high population is a result of a complex association with humans; a relationship that has developed over 12,500–30,000 years (Vanak and Gompper 2010; Clutton-Brock 2012). Since dog domestication, humans have provided resources for the species (e.g., food, shelter), freeing it from density-dependent factors (e.g., resource availability and predator pressures; Gompper 2014). This relationship with humans has allowed dogs to become a subsidized predator, facilitating the maintenance of artificially high densities (Gompper 2014; Newsome et al. 2014), which increases their potential to influence biodiversity (Young et al. 2011; Hughes and Macdonald 2013; Gompper 2014).

The abundance and persistence of dogs in natural habitats results in interactions at multiple levels with native fauna (Vanak and Gompper 2009; Young et al. 2011). Dogs can affect native fauna through surplus killing (Ritchie et al. 2014), competition, predation, pathogen spillover and genetic introgression (Young et al. 2011; Hughes and Macdonald 2013). In addition, their occurrence can alter native fauna behavior and activity patterns (Young et al. 2011; Hughes and Macdonald 2013). Negative interactions between domestic dogs and native fauna populations can be dramatic in undeveloped or developing countries due to the absence of laws or enforcement that promote responsible dog ownership. The worst scenario is in rural areas where dogs that are owned or peripherally associated with human houses are rarely confined and roam freely through the landscape (i.e., rural free-ranging dogs; see Butler et al. 2004; Ritchie et al. 2014), often into natural areas (Butler et al. 2004; Paschoal et al. 2012).

Estimating abundance is a fundamental component of ecology and critical to the understanding and management of animal populations (Williams et al. 2002; O'Brien 2011). Often the impact of an invader is correlated with its population size as any biomass (or space, or energy) controlled by the invader constitutes resources no longer available to native competitors or prey (Parker et al.1999). However, most studies of dogs focus on understanding pathogen epidemiology or indirectly assess dog population through human questionnaires (see Gompper 2014). A recent review of free-ranging dogs and native fauna conservation found surprisingly few studies that attempted to estimate the demography and distribution of dogs beyond human houses in and around natural areas (Gompper 2014) and few studies have used an ecological approach to evaluate aspects of free-ranging dog demographics (but see Paschoal et al. 2012; Frigeri et al. 2014).

The impact of free-ranging dogs on native fauna in protected areas is associated with their population size and intensity of use within these areas. Here, we used data from camera traps with an open-robust design mark-recapture model (Kendall and Bjorkland 2001; Kendall 2004) to estimate the number of free-ranging dogs that use protected areas located within the Atlantic Forest Biome, a priority area for biodiversity conservation. In addition, we investigated factors that influenced their continued use (e.g., season, mammal richness, proportion of forest) and detection probability (e.g., protected area size, sex) within these protected areas. Collectively, this information will help inform future management initiatives aimed at curbing the impacts of free-ranging dogs on native species in protected areas.

Methods

Study areas

Brazil's Atlantic Forest is considered one of the most threatened hotspots of biodiversity on Earth (Mittermeier et al. 2005), but less than 17% of its original forest cover remains (Ribeiro et al. 2009). Forest remnants consist of small, isolated patches (most <50 ha) that are near populated areas and heavily influenced by edge effects (Ribeiro et al. 2009). We conducted our study across three state parks (Rio Doce - RD, Sete Salões - SS, Serra do Brigadeiro - SB) and three private protected areas (Feliciano Miguel Abdala - FMA, Mata do Sossego - MS and Fazenda Macedônia - FM; Table 1) all within the Atlantic Forest Biome in the State of Minas Gerais, southeastern Brazil (hereafter referred to as 'protected areas'; Fig. 1). Vegetation of all protected areas is classified as semi-deciduous seasonal forest (SOS Mata Atlântica 2014). The climate is humid tropical or semi-humid (IBGE 2012) and elevation of the protected areas vary between 230 m (FM) and 2075 m (SB; Miranda 2005).

Table 1. The total area, proportion of forest and relative abundance index for top predators (RAI) for six Atlantic Forest protected areas in southeastern Brazil. For each protected area, we report the mean distance to human house (MDH) and the effective sampling area (ESA) sampled with camera traps. We report estimates of the persistence of use ($\hat{R}$), the estimated number of occasions that a dog used the protected areas (and associated standard errors), and estimates of abundance and density of free-ranging dogs for dry and wet seasons, with the highest values in bold. No dogs were detected in Rio Doce (RD) during our 80-day sampling period.

Protected Area†	Total Area (ha)	Forest (%)	RAI (%)	MDH (m)	ESA (ha)	$\hat{R}$	Dogs Abundance (± 95% IC)		Dogs/km² (± 95% IC)	
							Dry	Wet	Dry	Wet
MS[1]	134	56.17	0	1,447	3,436	2.3(0.85)	10 (7–14)	16 (10–21)	0.30 (0.20– 0.41)	0.45 (0.29–0.61)
FM[2]	560	8.78	0.88	840	4,893	3.7(0.72)	22 (17–27)	20 (15–24)	0.45 (0.35–0.55)	0.41(0.32–0.50)
FMA[3]	**958**	**41.73**	**0.13**	**682**	**4,306**	**4.2 (0.81)**	**73 (57–88)**	**47 (37–57)**	**1.69 (0.85–2.05)**	**1.09 (0.85–1.33)**
SS[4]	12,520	58.45	0.25	570	4,950	4.5 (0.91)	6 (5–8)	19 (15–23)	0.13 (0.10–0.15)	0.38 (0.30–0.46)
SB[5]	14,985	55.28	1.00	714	5,445	4.1(0.78)	9 (7–10)	9 (7–10)	0.16 (0.12–0.19)	0.16 (0.12–0.19)
RD[6]	35,970	61.80	6.13	880	4,341	0	0	0	0	0

†[1] Mata do Sossego, [2] Fazenda Macedônia, [3] Feliciano Miguel Abdala, [4] Sete Salões, [5] Serra do Brigadeiro, [6] Rio Doce

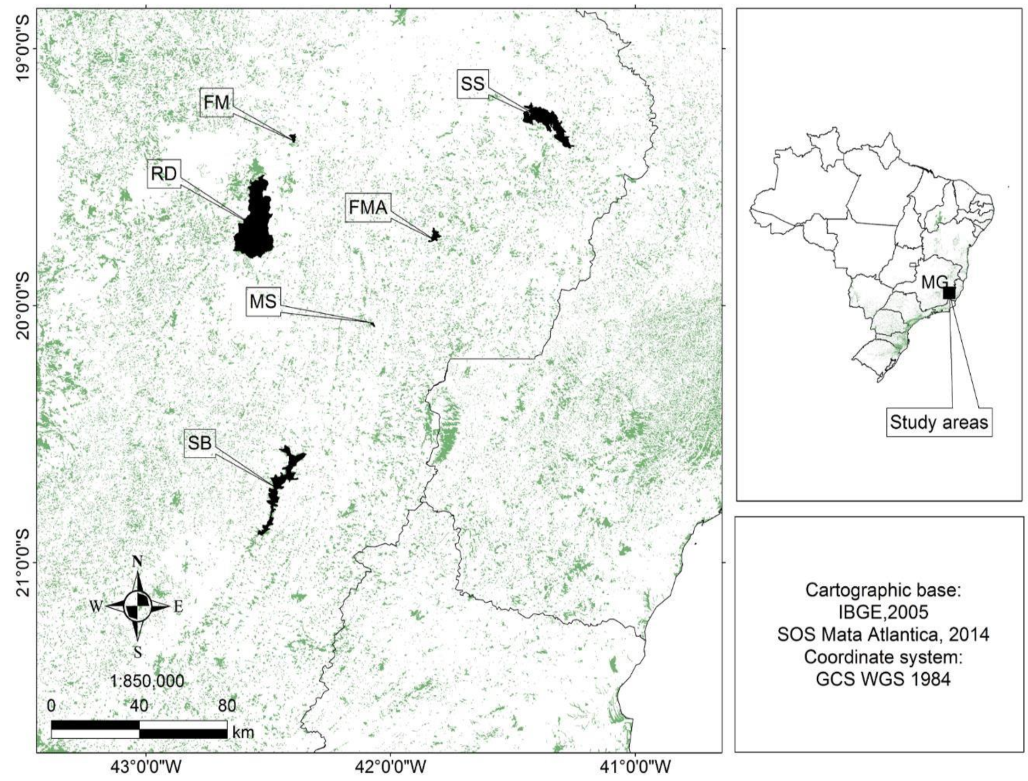

Fig. 1. Location of the six protected areas sampled for free-ranging domestic dogs in the Atlantic Forest, southeastern Brazil. FMA- Feliciano Miguel Abdala, MS- Mata do Sossego, FM- Fazenda Macedônia, SS- Sete Salões, SB- Serra do Brigadeiro, RD- Rio Doce. The insert shows the current distribution of the Atlantic Forest remnants in green (SOS Mata Atlântica 2014; Massara et al. 2015).

Sampling design and camera surveys

We used Tigrinus© camera traps (conventional model, passive infrared sensor; Tigrinus Research Equipment, Timbó, Brazil) to sample free-ranging dogs inside each of the protected areas. Twenty camera sites were established from a randomly selected starting location in each protected area using satellite images in ArcGIS 9.2 (ESRI 2008). The spacing of camera sites was designed to ensure approximately one site every 76 ha, a value similar to the average home range size of free-ranging dogs (~72 ha; Pal et al. 1998; Meek 1999; Dürr and Ward 2014), and other carnivores such as ocelots (*Leopardus* pardalis; Massara et al. 2015). Due to the small size of the private protected areas (e.g., Feliciano Miguel Abdala, Mata do Sossego and Fazenda Macedônia; Table 1), some camera sites were established on surrounding lands to standardize our sampling design (Appendix S1: Fig. S1). Cameras were placed at each randomly selected site unless there was a better position within 50–100 m that could improve detection (e.g., travel routes; Karanth and Nichols 1998; Sepúlveda et al. 2015). No bait or attractants were used that could produce heterogeneity in detection probability (Espartosa et al. 2011). Two cameras were placed at each site and operated 24 hours per day with a five-minute interval between photos.

Sampling occurred between 2008–2012; each protected area was sampled for 80 days in both the wet and dry seasons. Because we had a restricted number of cameras, we sampled five sites for 20 consecutive days, then replaced the film and batteries and moved the cameras to five different sites. This process was repeated until all 20 sites were sampled in each season (totaling 80 sampling days per season). We assume that this sampling strategy did not induce any heterogeneity among individuals.

Data analysis

Free-ranging dogs in our study exhibited a high degree of phenotypic diversity (Appendix S2: Fig. S2; Boyko and Boyko 2014). Photos of both left and right flanks were used to identify individuals. Detection records for each individual were summarized into a matrix of detection histories, reflecting whether each individual dog was detected (1) or not (0) on each sampling occasion (Otis et al. 1978). To promote independence among registers, only photos at one or more hour of interval was considered for analysis. We collapsed our 80 sampling days into 10-day occasions to increase detection probabilities and improve parameter estimates, as suggested by previous studies with carnivorans (Harmsen et al. 2011; Foster and Harmsen 2012).

In a preliminary analysis, we tested for demographic and geographic closure within seasons (wet or dry), using open-population mark-recapture models (Schwarz and Arnason 1996; Appendix S2).

Our results suggested that the closure assumption was not met; instead, individual dogs begin and cease to use the protected areas in a staggered manner within a season (Appendix S3: Table S3). Kendall et al. (1997) and Kendall (1999) described the potential biases produced by such non-random availability and advocate using an open-population robust design approach in these instances (Schwarz and Stobo 1997; Kendall 1999; Kendall and Bjorkland 2001).

Accordingly, we used a multi-state open-robust design model (hereafter MSORD; Kendall and Bjorkland 2001; Kendall 2004) in program MARK (White and Burnham 1999) to estimate population parameters for the dogs. This model relaxes the assumption of geographic closure, allowing individuals to enter and exit the area once during a season, but retains the demographic closure (no births and deaths) assumption over the 80 sampling days (Schwarz and Stobo 1997; Kendall 1999; Kendall and Bjorkland 2001).

Estimating abundance and persistence of use

The MSORD model provides an estimate of the population of dogs within a protected area (*N*, termed ‘superpopulation’) by modeling dynamic processes that occur at two different temporal scales. These scales are referred to as ‘between’ primary seasons or ‘within’ primary seasons. In our study, we consider only one primary season (the 80-day sampling period) and ignored the between seasons dynamics (survival and state transition probabilities), focusing only on those parameters that model dynamics within a season. These parameters include: $pent_j$ = represents the probability that a dog in the superpopulation (*N*) begins to use the protected area between occasions j and $j + 1$; φ_j = probability that a dog using the protected area at occasion j, continues to use the protected area during occasion $j + 1$; and p_j = probability that a dog in the protected area at occasion j is detected. Appropriate modelling of these parameters yields unbiased estimates of the derived parameters, the abundance (N; superpopulation) and 'residence time' (R) of dogs using each protected area (see Kendall 2006; http://www.phidot.org/software/mark/docs/book/pdf/chap15.pdf for details). Here, residence time is the estimated number of 10-day occasions that a free-ranging dog used a protected area and was interpreted as persistence of use.

Accordingly, we modelled factors that may influence the within-season parameters (*pent*, φ and p) and developed *a priori* hypotheses regarding potential variation in these parameters. First, we considered three possible model structures (hypotheses) for *pent*. We believed that once local dog-owners became aware of our study in a protected area, they would likely confine their dogs, keeping them out of the nearby protected area. This process could lead to a linear decline in the probability that a dog begins to use the protected area during a season. We also considered models where *pent* varied across occasions (time) in the absence of a specified pattern, and models where *pent* was relatively constant. We only considered these three temporal structures and assumed that the processes governing *pent* are similar across protected areas and seasons (wet or dry).

Next, we explored factors that may influence the probability that a dog continues to use the protected area between sampling occasions (φ). We expected that this could vary among protected areas and seasons. Specifically, we hypothesized that dogs will continue to use protected areas that: (1) are closer to humans' houses, since free-ranging dogs have a strong spatially relationship to humans and human houses are usually their home site (Woodroffe and Donnelly 2011; Silva-Rodríguez and Sieving 2012), (2) have a lower proportion of forest and/or higher richness of terrestrial mammal species (Silva-Rodríguez and Sieving 2012; Ritchie et al. 2014; Sepúlveda et al. 2015), (3) have a lower relative abundance of top predators, because these species can impose suppressive effects on dogs (Mazzolli 2009; Ritchie and Johnson 2009). To test these hypotheses regarding spatial variation in φ among protected areas, we mapped the land cover types by interpreting and classifying Landsat 5 images of each protected area, using the technique of supervised classification and a maximum similarity algorithm in program ERDAS Image 8.4 (ERDAS 1997).

We calculated the proportion of forest inside the effective sampling area in each protected area (see Table 1 and *Estimating density* section below). In addition, we used topographic maps at different resolutions (e.g., Ikonos, Google Earth and Landsat 5 Images) and previous known coordinates of human houses to calculate the mean distance between camera sites and the nearest human house (Table 1). We recorded all large and medium-sized terrestrial mammal species detected within each protected area and used the count of mammal richness (except top predator species) as a predictor variable for φ (also see Appendix S3: Table S2). Finally, we constructed a relative abundance index of top predators (*Puma concolor* and *Panthera onca*) for each protected area by calculating the encounter rate (number of photos per camera-day) and multiplying by 100 (Table 1).

In addition to the spatial hypotheses described above, we also tested for potential temporal variation in φ. We thought that dogs may continue to use protected areas more in the mild dry season, when heat stress is lower and dogs are more active (Oppenheimer and Oppenheimer 1975; Berman and Dunbar 1983). In addition, we: (1) allowed for 'transient' individuals, i.e., dogs that only used the protected area during one occasion, (2) modeled φ as a function of the number of occasions that an individual had spent in the protected area (time since-arrival) and (3) included the additive effects of both transient and time-since-arrival processes. For comparison, we also fit a constant model structure. These model structures represent reasonable scenarios for dogs in our study system because some individuals may only use the protected areas during one occasion (‘transients’), while other dogs may continue to use the protected areas for longer periods.

Finally, we suspected that detection probability (*p*) may vary among sex, protected areas, seasons, or sample occasions. We expected that detection probability may be higher for males than females since males are often more active, with larger home ranges (Sparkes et al. 2014; Pal 2015) which may increase their exposure to cameras and thus their detection probability. We also expected that detection probability may be higher in smaller protected areas (< 1,000 ha), because dogs have less space to move and consequently are more likely to be detected. Detection probability may be higher during the dry season because dogs are more active in mild temperatures (Oppenheimer and Oppenheimer 1975; Berman and Dunbar 1983).

In addition, our observation of owners’ tendency to restrain dogs after learning of our study during the pilot sampling, suggested that detection probability of dogs may decrease over occasions, yielding a negative linear trend in detection. We constructed models with these four detection structures and also considered a structure where detection probability was constant across protected areas, time, and individuals.

We tested for correlation among all covariates using a Pearson Correlation Matrix. None of the variables were highly correlated ($|r| \leq 0.50$ in all cases) so we developed a model set that included all possible combinations of the *pent*, φ, and *p* structures described above. We fit these models to our data, and used Akaike’s

Information Criterion adjusted for small sample size (AICc), the relative difference in AICc values among models (Δ AICc), and associated model weights (*w*) to assess strength of support for each candidate model (Burnham and Anderson 2002). The balanced model set allowed us to calculate the cumulative AICc weights for each predictor variable used to model our three parameters (Doherty et al. 2012). To account for model selection uncertainty, we report model-averaged estimates for modelled parameters (e.g., *pent*; Burnham and Anderson 2002).

There is no general goodness-of-fit test for the MSORD model and the median $\hat{c}$ procedure used to estimate overdispersion is not available for our data type in program MARK (Converse et al. 2009; Cooch and White 2015). Instead, we used the simpler Cormack-Jolly Seber model (CJS; Lebreton et al. 1992) that has well-known goodness-of-fit tests to assess model fit (e.g., independence among individuals). Using our most generalized MSORD model, we built a similar CJS model and used the median $\hat{c}$ procedure to estimate overdispersion. If there was no evidence of overdispersion using the simple CJS model, the more complex
MSORD model should fit even better.

Estimating density

We calculated the density of free-ranging dogs that used a protected area by dividing the derived estimate of abundance ($\hat{N}$) by the effective sampling area (ESA; Table 1). We calculated effective sampling area as the minimum convex polygon (MCP), using all camera traps sites, which covered on average 915.2 ha (range 433.8 to 1,334.5 ha), plus a buffer width defined by the mean maximum distance moved (MMDM; Soisalo and Cavalcanti 2006) by free-ranging dogs detected in all protected areas combined (1970 m). The effective sampling areas were calculated using ARCGIS 9.2 (ESRI 2008).

Results

Over our study resulted in a total of 1,249 records of 24 terrestrial mammal species. The domestic dog was the most detected species followed by tapeti (*Sylvilagus brasiliensis*) and ocelot (*L*. pardalis; Appendix S3: Table S2). Despite few differences in the number of terrestrial mammal species recorded among protected areas, the largest and more forested protected area (RD; Table 1) had a structurally more complex community, where large-bodied species such as tapirs (*Tapirus terrestris*), giant armadillos (*Priodontes maximus*), jaguars (*P. onca*) and red brocket deer were detected (*Mazama americana*; Appendix S3: Table S2). Overall, the relative abundance index (RAI) of top predators was low, but varied among protected areas (Table 1). In our study, *P. concolor* was the only large predator present in protected areas where dogs were detected (Appendix S3: Table S2).

Our CJS analysis revealed no overdispersion ($\hat{c}$ = 1.02; $S\hat{E}$ = 0.03), so we used AICc values and associated metrics from the MSORD analysis for biological inference. The top two models accounted for approximately 99% of the AICc weight (w_+ = 0.99) and Δ AICc values suggested that both models are plausible, given our study system (Table 2). We found uncertainty between *pent* model structures (Table 2); however, model-averaged estimates of *pent*, indicate that the probability that a dog begins to use the protected area between occasions *j* and *j* + 1 were relatively uniform (Fig. 2A).

Consistent with our *a priori* hypothesis, we found strong support for a negative relationship between the probability that a dog continues to use a protected area (φ) and distance to human houses (w_+ = 0.99; Table 2, Fig. 2B). There was little or no support that any other factor influenced φ. As expected, detection probability (*p*) decreased linearly across occasions, possibly due to owners becoming aware of our study and confining their dogs (Table 2, Fig. 2C).

Estimates of free-ranging dog abundance and densities varied among protected areas (Table 1), with the highest values found at FMA, where estimated abundance was 73 dogs (95% CI = 57–88) and estimated density was 1.69 dogs/km^2 (95% CI = 0.85–2.05). In contrast, no dogs were detected in the sampled area at Rio Doce (RD) during our study. Our data also indicated a weak effect of seasonality on abundance and, consequently, density of free-ranging dogs (Table 1). Dogs persisted for longer periods in protected areas near human houses (> 50% of the eight occasions) compared to protected areas more distant from human dwellings (< 30% of occasions; Table 1).

Table 2. Models selection results for factors expected to influence: *pent*, the probability that a dog from the superpopulation (N) begins to use the protected area between occasions j and j +1; φ, the probability that a dog in the protected area at occasion j, continues to use the protected area during occasion $j + 1$; and p, probability that a dog in the protected area during occasion j is detected. Models with little support ($w < 0.05$) are not shown. The AICc values and their respective weights (w) are shown for models with the following effects: time trend (T) for p and mean distance between camera locations and the nearest human house (MDH) for φ. Parameter estimates (β) and standard errors (in parenthesis) are shown for mean distance to human house (φ) and time trend (p).

Model	K	AICc	Δ AICc	*w*	Deviance	Parameter estimates (β)	
						MDH	Trend
{*pent*(.), φ(MDH),*p*(T)}	5	684.84	0	0.74	692.58	-0.001 (0.96E-003)	-0.21 (0.06)
{*pent*(T),φ(MDH),*p*(T)}	6	687.01	2.17	0.25	690.94	-0.001 (0.96E-003)	-0.29 (0.09)

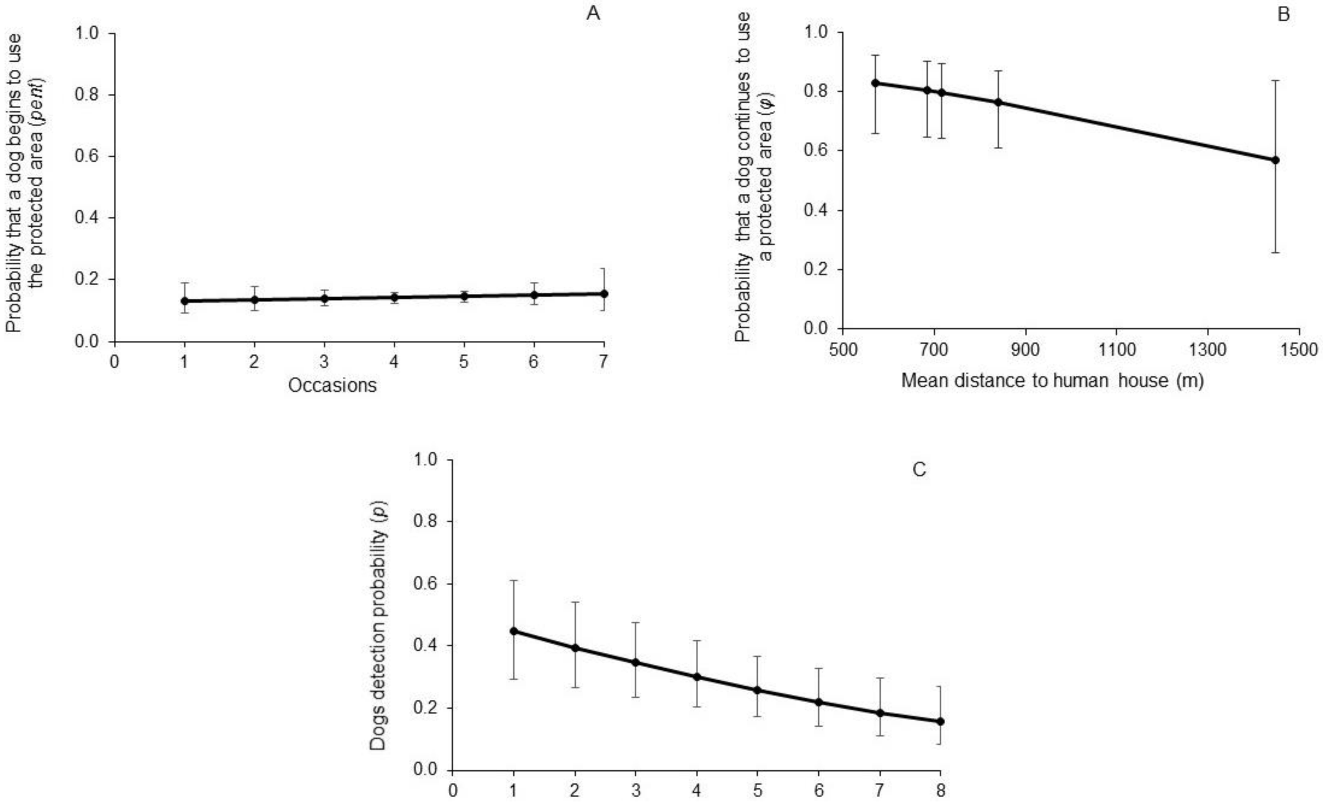

Fig. 2. Model-averaged estimates of the probability that a dog in the superpopulation (N) begins to use the protected area between occasions j and $j + 1$ (*pent*; **A**). Estimates of the probability of a free-ranging dog continues to use a protected area (φ) as a function of mean distance to human houses (m; **B**) and probability of detecting a dog (p) within a protected area during a given occasion (10-day period; **C**). Estimates of φ and p are from the best model that included the specified covariate.

Discussion

Abundance and ranging behavior of domestic dogs are recognized as important factors determining their cumulative impact on wild communities (Vanak and Gompper 2009; Gompper 2014). Our results show that free-ranging dogs are much more common than native carnivorans in sampled protected areas. Specifically, dog densities were approximately three to 85 times higher than ocelot densities (*L. pardalis*) in the same protected areas (Massara et al. 2015) and approximately five to 25 times higher than crab-eating fox (*Cerdocyon thous*, 0.35 fox/km^2; Beiseigel et al. 2013) and puma (*P. concolor*, 0.007 puma/km^2; Kelly et al. 2008) densities observed in other Atlantic Forest areas. In our study, *P. concolor* was the only large predator present in protected areas where dogs were detected and *C. thous* is the only native Canidae we detected (Appendix S3: Table S2). Comparing our results with estimates from a companion study conducted at the same time, we found that *L. pardalis* was rare in our protected areas where free-ranging dogs were abundant and vice versa (Massara et al. 2015), indicating an inverse pattern in abundance (i.e., abundance-asymmetry hypothesis; Vázquez et al. 2007).

While our estimates of free-ranging dog densities are much higher than those reported for wild carnivorans within protected areas (Massara et al. 2015; Kelly et al. 2008; Beiseigel et al. 2013), higher densities of free-ranging dogs have been reported in rural systems (Kitala et al. 2001; Acosta-Jamett et al. 2010). Density differences are likely a function of different sampling methods (Gompper 2014) as previous studies used household questionnaire to determine human: dog ratios and then extrapolated dog abundance from human population censuses (Kitala et al. 2001; Acosta-Jamett et al. 2010). Resulting estimates represent the number of dogs in rural areas, but not the abundance or density of free-ranging dogs that actually used protected areas. Several studies suggest that just a portion of free-ranging dogs' population foray into protected areas (Woodroffe and Donnelly 2011; Ruiz-Izaguirre et al. 2014; Sepúlveda et al. 2015), suggesting that the population of free-ranging dogs outside the protected areas may be much higher than the densities we report here. Dog densities can vary widely across regions and are influenced by human densities and their demand for dogs (Vanak and Gompper 2009; Gompper 2014). The cultural, economic and social factors controlling the rates of acquisition and disposal of dogs (and thus, ownership) are still not well understood and necessitate further investigation (Morters et al. 2014). Future studies should aim to linking these societal characteristic to the density of dogs within protected areas and/or the probability that a dog uses protected areas.

The rationale for a numerical dominance of free-ranging dogs within protected areas are directly (e.g., intentional) and indirectly (e.g., unintentional) related to human activities (Sakai et al. 2001; Hulme et al. 2008). Dogs can be directly introduced into protected areas by accompanying humans (e.g., for hunting, logging or company); however, in our system, free- ranging dogs were usually detected without human presence, indicating an indirect introduction. Rural free-ranging dogs are released and kept unrestrained in the landscape for different reasons (e.g., protection against human intruders, native “pests” and predators; Paschoal *personal observation*). Under these circumstances, free-ranging dogs interact synergistically with other ecological disturbances, resulting in a variety of complex pathways for dog invasion into protected areas (Didham et al. 2007; Hulme et al. 2008; Doherty et al. 2015).

We found that the abundance and density of dogs was highest in small, private protected areas (Table 1). The expansion and intensification of land-use activities establish a trend toward ever-increasing proximity between human modified habitats and Atlantic Forest protected areas (Wittemeyer et al. 2008; Mcdonald et al. 2009).

Among ecological disturbances, alteration on natural habitat structure and composition (i.e., habitat-mediated pathway) and those that arise due to composition of the ecological community (i.e., community-mediated pathway) have been recognized as particularly likely to lead to an increase in dog abundance and distribution which may cause a numerical impact on native fauna (Didham et al. 2007; Doherty et al. 2015). Land-use around protected areas and habitat edges are important habitat mediated pathways. Land-use activities (e.g., land clearing, farmland production or expanding urban centers) increase human modified habitats which benefits dogs, likely increasing their total population size and thus the number of individuals that are likely to use adjacent protected areas (Lockwood et al. 2005; Didham et al. 2007).

In addition, anthropogenic habitat modification result in community-mediated pathways, where changes in the community structure of native fauna favor dog numerical dominance within protected areas (Didham et al. 2007; Doherty et al. 2015). In this case, the underling mechanism is declines in top predators (Doherty et al. 2015; Wallach et al. 2015). Top predators regulate trophic structures of ecosystems by limiting herbivores through predation and suppressing mesopredators, both native and introduced, via intraguild interaction (e.g., Ritchie and Johnson 2009; Ripple et al. 2014).

Top predator status in Atlantic Forest protected areas is critically low, with unprecedented rates of local extinctions (Canale et al. 2012). While we found no effect of relative abundance of top predators on dog population parameters, puma (*P. concolor*) was rare among protected areas and jaguar (*P. onca*) were only present at the biggest protected areas (RD) were we did not detected dogs (Appendix S3: Table S2). Our inability to show a relationship between top predators and dog population parameters may simply reflect that top predators were rare or absent at all protected areas where dogs existed, and dogs were rare or absent in the sampled area in RD, the only protected area with an intact top predator community.

We found that dogs used protected areas for longer periods (i.e., higher probabilities of continued use) if the area was closer to human houses. For protected areas where the average distance to nearest house was < 750 m, we estimated that dogs in the superpopulation used protected areas approximately half of the time (R >4 occasions; eight total occasions). This is not surprising, given the life-history traits and foraging behavior of free-ranging dogs. Dogs have a high degree of behavioral flexibility (Bentosela et al. 2008) and a large dietary and habitat breadth (Gehring and Swihart 2003; Ritchie et al. 2014).

Typically, free-ranging dog center their activity around their home site (Meek 1999; Woodroffe and Donnelly 2011; Dürr and Ward 2014). Due to their home site fidelity they are thought to behave like central place foragers (Ruiz-Izaguirre et al. 2014). According to the optimal foraging theory, travel time is an important constrain for central place foragers, influencing the time that dogs should spent in a habitat if energy is to be maximized (Pyke et al. 1977). Dogs home ranges will likely overlap protected areas in close proximity to a dog’s home site, allowing them to exploit the high-quality and abundant resources found in these areas for longer time periods while minimizing energy expended (Pyke et al. 1977). In rural areas, even the most predictable resources (e.g., human food subsidies) present some fluctuation (Oro et al. 2013); therefore, it may be advantageous for dogs to capitalize on different food resources available in protected areas, especially if those areas are within close proximity. We found no support for transients within protected areas, which further suggests that free-ranging dogs probably came from adjacent habitats.

We found no evidence that other variables (e.g., season, mammal richness) influences the probability that a dog continues to use a protected area, when compared to the strong relationship with human houses. Short travel routes to protected areas in close proximity may have mitigated overheating (Spotte 2012) that was expected to occur in the wet season, resulting in little effect on dogs' activity and persistence of use. Likewise, no consistent pattern in the abundance and density of dogs using the protected areas were observed among seasons. There were few differences in the number of terrestrial mammal species recorded among protected areas (Appendix S3: Table S2), so this variable was not useful in describing the difference in dog population parameters in our system.

In addition to proximity to human houses, we found that owner attitudes may effect protected area use by dogs and thus dog-native fauna interactions (Miller et al. 2014; Ritchie et al. 2014). Once local dog-owners became aware of our study, they confined their dogs, limiting their frequency of use of the nearby protected area. This behavior likely led to a negative trend in detection probabilities, and suggests that our results may underestimate the true persistence of use, abundance and density of dogs in protected areas.

While free-ranging dog abundance, density and persistence of use varied among protected areas, we use the two extreme scenarios to highlight the variety of scenarios that exist for Atlantic Forest remnants. The worst scenario occurred at one of the smaller protected areas, Feliciano Miguel Abdala (FMA), which protects one of the most threatened primate species in the world, the northern muriqui (*Brachyteles hypoxanthus*). Here, free-ranging dog densities were four to 10 times higher than any other protected area, and dogs exhibited the second highest persistence of use (Table 1). Feliciano Miguel Abdala (FMA) is representative of other small private protected areas, with agriculture areas (e.g., coffee, livestock and sugar cane crops) surrounding the natural area. It was legally protected in 1983 (Nery and Tabacow 2012), and despite efforts to conserve biodiversity, it still contains and is surrounded by anthropogenic features which are strongly associated with dogs (Pita et al. 2009; Sepúlveda et al. 2015). In contrast, Rio Doce State Park (RD) is the largest and best preserved protected area in our study and, represents the best scenario for native fauna.

Our inability to detect free-ranging dogs during the sample period suggests that few or no dogs exist in the sampled area (Table 1). Several factors may have contributed to such low densities; first, Rio Doce was the only protected area where top predators, known to kill dogs, were common (Appendix S3: Table S2). Second, a large *Eucalyptus* plantation surrounds the sampled area in Rio Doce (Barros et al. 2006), a type of land cover that may act as a buffer limiting dog access and occurrence (Srbek-Araujo and Chiarello 2008; Torres and Prado 2010).

In summary, our study reinforces the existence of a gradient in dog encounter risk, where native fauna is exposed to more free-ranging dogs in higher densities in small private protected areas (Table 1). Given that people live within the boundaries of 70% of protected areas in the tropics (Terborgh and Peres 2002), few areas are free of the influence of dogs (but see Rio Doce State Park; Ribeiro et al. 2009; Sampaio and Schmidt 2013; Lessa et al. 2016).

Since human populations continue to expand, especially at the edge of protected areas (Wittemyer et al. 2008; Laurance 2015), additional opportunities for invasion by dogs are being created (Hansen and DeFries 2007; Macdonald et al. 2009). Protected areas are one of the cornerstones for conserving the world's remaining biodiversity (DeFries et al. 2005). Our results suggest that many protected areas may be not functioning as originally envisioned (Hansen and DeFries 2007), especially small ones, which appeared to be more vulnerable to invasion by dogs (this study, Hansen and DeFries 2007; Srbek-Araujo and Chiarello 2008).

Free-ranging dogs usually originate from adjacent habitats outside the boundaries of protected areas but are often linked to negative effects on ecological function and biodiversity within protected areas (Lovejoy 2006; Hansen and DeFries 2007). We demonstrate how a commonly used native fauna sampling method (camera traps) can be used to estimate the number of free-ranging dogs using protected areas, even when individual dogs do not remain in the sampling area for the duration of study (i.e., when the closure assumption is not met). Given the numerous camera trapping studies that exist or are ongoing in the Atlantic Forest region, and other areas worldwide, our technique could be used to evaluate potential negative effects and density differences between free-ranging dogs and native species in various types of habitats.

Free-ranging dogs are clearly abundant in protected areas near human houses. Any efficient conservation paradigm must incorporate human-modified landscapes in assessments of biodiversity, and buffer zones, and restoration of degraded lands. We advocate a cross-boundary management approaches that look beyond individual habitat types to the linkages and dynamics across habitat types and landscapes (DeFries et al. 2007). Given that exotic species are legally prohibited in Brazilian protected areas (Federal Law No. 9,985, Sistema Nacional de Unidades de Conservação - SNUC 2000), we believe that dog-owners restrained their dogs out of fear of punishment by the government, and/or to avoid exposing their dogs to danger (e.g., culling; Paschoal *personal observation*). This response of dog owners to our presence suggests that the human dimension is an important component of the dog problem in protected areas.

Due to the complex bond between humans and dogs, it is necessary to manage people and their dogs as a cooperative social unit, using multiple and complementary strategies (e.g., educational programs, neutering campaigns, application and enforcement of laws and buffer zones; Bekoff and Meaney 1997; Miller et al. 2014). Understanding the complexity of the relationship between dogs and local people is essential before implementing any action aimed at reducing dog populations in protected areas and the associated dog-native fauna conflicts (Reece 2005).

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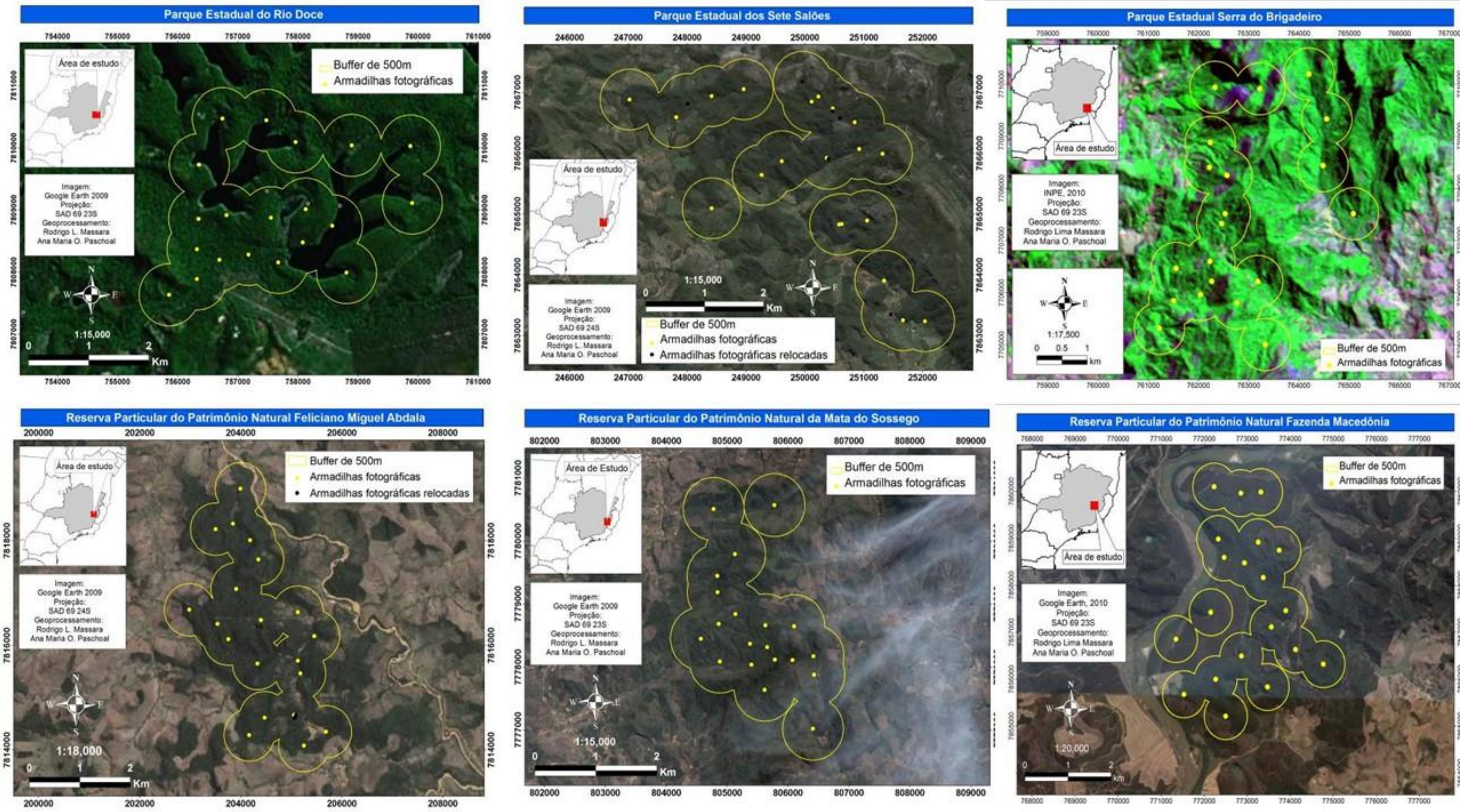
Appendices

Appendix S1



Appendix S1: Fig. S1. Camera trap sites and their respective buffer (500 m) for the six protected areas sampled for free-ranging domestic dogs in the Atlantic Forest, southeastern

Brazil. FMA- Feliciano Miguel Abdala, MS- Mata do Sossego, FM- Fazenda Macedônia, SS- Sete Salões, SB- Serra do Brigadeiro, RD- Rio Doce.

Appendix S1

Fig. S1. Examples of photos of free-ranging dogs using protected areas in Brazilian Atlantic Forest. Individuals were identified uniquely based on high phenotypic diversity found in the species.

Appendix S2

We tested for demographic and geographic closure within a season (wet or dry season), using open-population mark-recapture models (Schwarz and Arnason 1996) in program MARK using the POPAN formulation (White and Burnham 1999). In POPAN formulation φ, represents the probability that a dog in the protected area survives and remains in the area between occasions j and j+1. This parameter is not identical to parameter (φ) in the MSORD models (see text). We fit two models (*sensu* Stanley and Burnham 1999), one where φ and *pent,* the probability that a dog from the superpopulation (N) begins to use the protected area between occasions j and j + 1, were fixed to one and zero, respectively (representing a closed population), and another where these probabilities were estimated, representing an open population. We compared the relative weight of evidence for each model using Akaike's weights adjusted for small sample size (*w*) and the relative AICc difference among models (Δ AICc) to evaluate which model was better supported by our data (Burnham and Anderson 2002). The open-population model was better supported (*w* = 1.00; Table S1 below), and resulting parameter estimates suggested that individual dogs begin and cease to use the protected areas in a staggered manner throughout the season.

Table S1. Model selection results using the POPAN formulation in program MARK. The first model represents an open population, where φ and *pent* probabilities were estimated. The second model represents a closed population where we assumed all dog survive and remain in the study area ($\varphi = 1$) and no new dogs enter (*pent* = 0) the population during our sampling.

Model	K	AICc	Δ AICc	*w*	Deviance
φ (.),*p*(.),*pent*(.),N(.)	4	328.04	0	1.00	692.58
φ (1),*p*(.),*pent*(0),N(.)	2	343.08	15.03	0.00	690.94

Appendix S3

Table S2. The table below contains the number of records and corresponding percentage of mid-sized terrestrial mammal species detected by camera traps in the six Atlantic Forest protected areas in southeastern Brazil. All large and medium-sized terrestrial mammal species detected within each protected area (i.e., except top predator species) were recorded and the count of mammal richness was used as predictor variable for estimating the probability of continued use (φ). The detection success was estimated as the total number of detections multiplying by 100 and divided by the sampling effort. No dogs were detected in RD during the sampling period.

Species	**FMA**		**MS**		**FM**		**SS**		**SB**		**RD**		**TOTAL**	
	N‡	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
DIDELPHIMORPHIA														
Didelphis aurita	8	2.05	3	1.70	2	0.77	3	2.83	3	3.26	_	_	19	1.52
CINGULATA														
Cabassous tatouay	2	0.51	7	3.98	_	_	_	_	_	_	_	_	9	0.72
Dasypus novemcinctus	38	9.74	1	0.57	9	3.47	5	4.72	5	5.43	10	4.42	68	5.44
Euphractus sexcinctus	2	0.51	_	_	1	0.40	_	_	_	_	_	_	3	0.24
Priodontes maximus	_	_	_	_	_	_	_	_	_	_	4	1.77	4	0.32
PILOSA														
Tamandua tetradactyla	3	0.77	3	1.70	5	1.93	1	0.94	_	_	_	_	12	0.96
CARNIVORA														
Canis familiaris †	169	43.33	17	9.66	21	8.10	30	28.30	12	13.04	_	_	249	19.94
Cerdocyon thous	14	3.60	3	1.70	19	7.34	_	_	1	1.09	_	_	37	2.96
Leopardus guttulus	1	0.26	5	2.84	1	0.39	_	_	6	6.52	_	_	13	1.04
Leopardus pardalis	3	0.77	15	8.52	43	16.60	9	8.49	16	17.40	36	15.93	122	9.77
Puma concolor	1	0.26	_	_	7	2.70	2	1.89	8	8.70	39	17.26	57	4.56
Puma yagouaroundi	10	2.56	5	2.84	8	3.09	2	1.89	2	2.17	3	1.33	30	2.40
Panthera onca	_	_	_	_	_	_	_	_	_	_	8	3.54	8	0.64
Nasua nasua	4	1.03	24	13.64	21	8.10	29	27.36	9	9.78	_	_	87	6.97
Procyon cancrivorus	26	6.67	20	11.36	13	5.02	3	2.83	1	1.09	_	_	63	5.04
Eira barbara	4	1.03	35	19.90	9	4.47	11	10.38	9	9.78	8	3.54	76	6.08
ARTIODACTYLA														
Mazama americana	_	_	_	_	_	_	_	_	_	_	3	1.33	3	0.24
Mazama gouazoubira	_	_	1	0.57	33	12.74	_	_	_	_	_	_	34	2.72
Pecari tajacu	_	_	_	_	_	_	_	_	14	15.22	12	5.31	26	2.08
PERISSODACTYLA														
Tapirus terrestris	_	_	_	_	_	_	_	_	_	_	47	20.80	47	3.76
RODENTIA														
Cuniculus paca	16	4.10	37	21.02	1	0.39	6	5.66	5	5.43	8	3.54	73	5.84
Dasyprocta leporina	24	6.15	_	_	_	_	4	3.77	_	_	32	14.16	60	4.80
Hydrochoerus hydrochaeris	_	_	_	_	4	1.54	_	_	_	_	1	0.44	5	0.40
LAGOMORPHA														
Sylvilagus brasiliensis	65	16.67	_	_	62	23.94	1	0.94	1	1.09	15	6.64	144	11.53
Total records	390	31.22	176	14.09	259	20.74	106	8.49	92	7.37	226	18.09	1249	100
Detection success (%)	_	48.75	_	22.00	_	32.38	_	13.25	_	11.50	_	28.25	_	26.02
Total native species	16	66.67	13	54.17	16	66.67	12	50.00	13	54.17	14	58.33	24	100

† Invasive species

‡ N= number of records (considering minimum interval of one hour between photographs)

Chapter 2 - Landscape structure shape habitat use by free-ranging dog in protected areas of Brazilian Atlantic Forest

Landscape structure shape habitat use by free-ranging dog in protected areas of Brazilian Atlantic Forest

Ana Maria O. Paschoal[a,b*], Rodrigo L. Massara[a,b], Larissa L. Bailey [c], Paul F. Doherty, Jr.[c], Paloma M. Santos[a], Adriano P. Paglia[a], André Hirsch[d], Adriano G. Chiarello[e]

[a] Universidade Federal de Minas Gerais, Programa de Pós-graduação em Ecologia, Conservação e Manejo de Vida Silvestre, Avenida Antônio Carlos, no. 6627, Belo Horizonte, MG 31270-901, Brazil.

[b] Instituto SerraDiCal de Pesquisa e Conservação, Rua José Hemetério de Andrade, no. 570, Belo Horizonte, MG 30493-180, Brazil.

[c] Colorado State University, Department of Fish, Wildlife, and Conservation Biology, 1474 Campus Delivery, 109 Wagar, Fort Collins, CO 80523, USA.

[d] Universidade Federal de São João Del Rei, Programa Institucional de Bioengenharia, km 47 – Rodovia MG 424, Sete Lagoas, MG 35701-970, Brazil.

[e] Universidade de São Paulo, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Avenida Bandeirantes, no. 3900, Ribeirão Preto, SP 14040-901, Brazil.

*Corresponding author: Universidade Federal de Minas Gerais, Programa de Pós-graduação em Ecologia, Conservação e Manejo de Vida Silvestre, Avenida Antônio Carlos, no.6627, Belo Horizonte, MG 31270-901, Brazil. Tel.: *55 31 34092569. E-mail addresses: anamuzenza@gmail.com

Abstract

Domestic dog is the most successful invasive predator species, thus reduce its ecological impacts on native fauna is a central conservation goal globally. The threat of free-ranging dog is often intensified in disturbed habitat. They can negatively interact with native fauna at multiple levels posing issues for biodiversity conservation in tropical forests, especially in Atlantic Forest. To optimize future control programs, it is necessary to understand how dog is distributed across a highly heterogeneous landscape and which factors influence its habitat use. We combined a camera trapping data and occupancy models to characterize habitat use of dogs. Dogs did not use sample sites randomly; instead our results indicated a selective pattern of habitat use, where dog was more likely to use sites strongly influenced by human activities. Sites with higher rural housing expansion (≥ 4.00 houses/km^2; Fig. 2a) or higher proportion of croplands and pasture ($\geq 72\%$) were more likely to be used by dog ($\hat{\Psi} \geq 0.90$) than sites with no houses ($\hat{\Psi} = 0.23 \pm 0.10$) or agricultural activities ($\hat{\Psi} = 0.34 \pm 0.08$). There was little evidence that any other covariate tested influenced dog probability of use (Ψ, $w+ < 0.20$; e.g., top predators, mammal richness, distance to edge). In addition, we found moderated evidence for effects of camera location ($w+ = 0.51$), rural housing density ($w+ = 0.46$) and protected area size ($w+ = 0.40$) on dog detection probability (Table 3). Dog was more detected at sites located on unpaved roads ($\hat{p} = 0.33 \pm 0.05$) than off-road sites ($\hat{p} = 0.18 \pm 0.04$). As expected, sites within small protected areas and with higher house density, thus more disturbed sites, had higher detection probabilities. All other covariates had little support ($w+ <$ 0.25; e.g., top predators, mammal richness, distance to edge), and thus did not strongly influenced the detection probability of dog at used sites. Our findings suggest that the probability of a site be used by a dog is a function of the human activity type and its intensity. This work brings into focus the importance to account for landscape scale to achieve an effective management plan on control and reduction of dog distribution within protected areas.

Keywords: invasive species; *Canis familiaris*; Brazil; occupancy models; biological invasions

Introduction

Invasive species is considered one of the greatest threat to global biodiversity, and mammalian predators have contributed disproportionately to the decline and extinction of native species in a variety of ecosystems (Vitousek et al. 1997; Wilcove et al. 1998). In particular, domestic dog (*Canis lupus*, Linnaeus 1758) stand out among invasive mammalian predators, inducing drastic changes in communities and ecosystems around the world (Ritchie et al. 2014; Vanak et al. 2014), interacting at multiple levels with native fauna (Vanak and Gompper 2009). These interactions often result in negative impacts, such as predation, competition, surplus killing, pathogen spillover and genetic introgression (Vanak and Gompper 2009; Young et al. 2011; Gompper et al. 2014) contributing to the decline of biodiversity (Doherty et al. 2015).

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

Dog is a particular concern in exurban/rural areas, where they are commonly owned and associated with particular human housing, but they are allowed to range free through the landscape (i.e., *free-ranging*; see Vanak and Gompper 2009; Gompper 2014) increasing the probability of contact with native fauna (Vanak and Gompper 2009; Gompper 2014). In this scenario, the influence of free-ranging dog (i.e., hereafter dog) on native fauna has been reported to be higher at the boundary of native and disturbed habitats, thus dog is considered a type of edge effect (Srbek-Araujo and Chiarello 2008; Lacerda et al. 2009; Vanak et al. 2014). However, dog effect is not restricted to habitat edge (Vanak et al. 2014).

As a high mobile species, dog can easily cross edge boundaries and invade adjacent habitats, including protected areas (Cantrell et al. 2001; Sepúlveda et al. 2015) been detected as far as 10-30 km from the edge (Vanak et al. 2014, Meek 1999). Furthermore, dog impacts in natural habitats, mainly within protected areas may be enhanced through complex pathways (e.g., habitat and community-mediated pathways) resulted from synergistic interactions between dog and other ecological disturbances, especially at the habitat edges (Didham et al. 2007; Doherty et al. 2015).

Dog has been described as a common species within protected areas (Vanak et al., 2014; Paschoal et al. 2012, 2016). Although protected areas are generally considered the cornerstone of biodiversity conservation and the primary strongholds of wilderness (Bruner et al. 2001), they are ecologically linked to the surrounding habitats and vulnerable to many anthropogenic disturbances emanating from outside their borders (Lovejoy 2006; Laurance et al. 2012). Indeed, if dogs are common within protected areas, these areas are no longer functionally protected (Hansen and DeFries 2007; Cantrell et al. 2001). Although few ecosystems are free of the influence and disturbance of dogs (Silva-Rodríguez and Sieving 2012; Hughes and Macdonald 2013), some are more invasible than others (Pyšek and Richardson 2010).

Tropical forests are the richest ecosystems on Earth and unique in their provision of key ecosystem services (DeFries et al. 2005; Laurance 2015). Ongoing landscape modification and habitat degradation caused by socioeconomic demands (Wright 2005; Newbold et al. 2014; Laurance 2015) make tropical forests one of the most fragile and susceptible ecosystems to dog invasion (Pyšek and 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 (Ribeiro et al. 2009; Canale et al. 2012).

Atlantic Forest has experienced a long history of intense landscape modification for commodity exports, which has been accelerated through the last century via coffee and sugarcane monocultures (Gibbs et al. 2010; Tabarelli et al. 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 and DeFries 2007; Macdonald et al. 2009).

In this scenario, the dog has become a major issue and represent one of the greatest challenges for biodiversity conservation in Atlantic Forest (Lessa et al. 2016; Paschoal et al. 2012, 2016), giving urgency to reducing its ecological impacts. The species distribution and habitat use defines 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 et al. 2005; With 2002; González-Bernal et al. 2016).

In the last decades, dog become a major research theme in conservation biology (Hughes and Macdonald 2013), yielding some information related to its space use and distribution (Silva-Rodríguez and Sieving 2012; Sepúlveda et al. 2015). 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, that accounts for imperfect detection probability (MacKenzie et al. 2002, 2006), to achieve a better understanding of dog-habitat relationship in Atlantic Forest. Our main goals were to explore landscape structures and other environmental factors that may influence dog occupancy (i.e., hereafter probability of use) in a highly heterogeneous tropical forest. Additionally, we tested for variables that may account for variation in dog detection probabilities (MacKenzie et al. 2006).

Materials and methods

Study Areas

Our study was conducted in six protected areas considered priority areas for Atlantic Forest biological conservation (Drummond et al. 2005). We sampled three state parks (Rio Doce - RD, Sete Salões - SS, Serra do Brigadeiro - SB) and three private protected areas (Feliciano Miguel Abdala - FMA, Mata do Sossego - MS and Fazenda Macedônia - FM) in the State of Minas Gerais, southeastern Brazil (Table 1, Fig. 1). Vegetation of all protected areas are classified as semi-deciduous seasonal forest (SOS Mata Atlântica 2014). The climate is humid tropical or semi-humid (IBGE 2012) and elevation varies between 230 m (FM) and 2075 m (SB; Miranda 2005).

The protected areas are predominately native forest remnants, surrounded mostly by disturbed habitats including pasture, croplands and eucalyptus plantations (Massara et al. 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 to the native forest (Table 1). Rural houses are found in both the protected areas and surrounding habitats. Dog density in the study system was previously estimated via camera traps, and varied among protected areas with the highest densities found at FMA (1.69 dogs/km^2; 95% CI = 0.85–2.05; Paschoal et al. 2016).

Sampling design and field methods

Twenty camera sites were established from a randomly selected starting location in each protected area using satellite images in ArcGIS 9.2 (ESRI 2008), yielding a total of 120 camera sites among the six protected areas. We used Tigrinus$^©$ camera traps (conventional model, passive infrared sensor; Tigrinus Research Equipment, Brazil) to detect dogs within protected areas. At the small private protected areas (<1,000 ha, FMA, MS, FM) some camera sites were established on surrounding lands to maintain our standardized sampling design. When cameras could not be placed in their original locations due to logistic constraints (e.g., no site access), we relocated them within 50–100 m and recorded the actual camera location using a GPS unit.

Cameras were installed in pairs at each site to improve detection probabilities (Harmsen et al. 2011; Foster and Harmsen 2012) and were set to operate for 24 hours with an interval of five minutes between photos. No bait or attractants were used that could produce heterogeneity in detection probability (Espartosa et al. 2011). Protected areas were 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 five random sites for 20 consecutive days, then replaced the photographic film and batteries before moving them to another five random sites in the protected area. We repeated this process until all 20 camera sites were sampled, totaling 80 days per season.

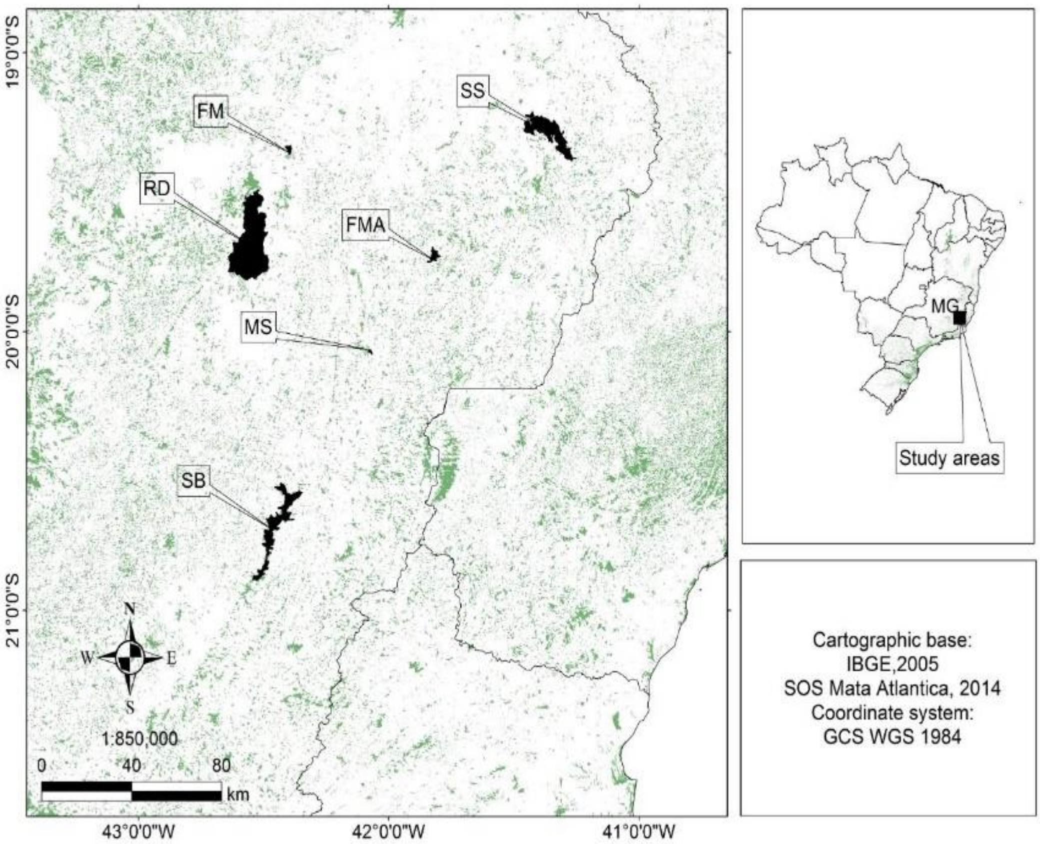


Fig. 1. Location of the six protected areas sampled for free-ranging domestic dog in the Atlantic Forest, southeastern Brazil. FMA- Feliciano Miguel Abdala, MS- Mata do Sossego, FM- Fazenda Macedônia, SS- Sete Salões, SB- Serra do Brigadeiro, RD-

Rio Doce. The insert shows the current distribution of the Atlantic Forest remnants in green (SOS Mata Atlântica 2014; Massara et al. 2015).

Modelling probability of use (Ψ) and detection probability (p) as a function of predictor covariates

We attempted to limit the number of covariates to those 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 natural history of the dog. We assessed correlations among covariates using Pearson's correlation coefficient to develop the candidate model set. Covariates with correlation coefficients greater than $|r| = 0.7$ were considered collinear (Whittington et al. 2005) and one of the covariates was eliminated from further analyses (see results section). Using the retained covariates, we modelled factors that could influence dogs' probability of use *(Ψ)* and detection probability *(p)*.

Dogs probability of use (Ψ)

We modelled factors that may influence dogs' probability of use and developed nine *a priori* hypotheses regarding factors that may influence this parameter. To explore the influence of landscape composition on probability that dogs use a site, we classified the land cover within each protected area by interpreting Landsat5-TM satellite image using the supervised classification technique and a maximum similarity algorithm in program ERDAS Image 8.4 (ERDAS 1997). Using a 500 m radius buffer around each camera site, we quantified the proportion of unpaved road, agricultural lands and eucalyptus (Table 1). We chose a 500 m radius buffer because we believe that this buffer size is sufficient to account for the relative contribution of landscape composition on dog distribution. We did not test scales with larger radii to avoid confounding spatial auto-correlation as larger radii increased the overlapping between sampling sites (Fortin and Dale 2009).

We considered agriculture lands as areas of cultivated soil, crop production or with domestic livestock, primarily cattle. We expected a positive relationship between probability that dogs use a site and the proportion of unpaved roads and agricultural lands. Dogs, like other carnivores, move preferentially along roads and trails, even if these features represent a small proportion of habitat in the study area. Therefore, unpaved roads could be an important determinant of dog distribution (Moreira-Arce et al. 2015; Sepúlveda et al. 2015).

Moreover, the dog is a generalist and opportunistic predator, and thus can benefit from the abundance of food and other available resources (e.g., shelter) in agricultural lands (Pita et al. 2009; Torres and Prado 2010; Soto and Palomares 2015). Conversely, we expected lower probability that dogs use a site in close canopy areas, such as eucalyptus areas (Pita et al. 2009; Torres and Prado 2010).

To investigate the influence of landscape configuration on probability that dogs use a site we measured each protected area size and categorized them into two groups (i.e., small; <1,000 ha and large; >10,000 ha). We expected probability that dogs use a site may be higher at sites located within smaller protected areas, because small patches of natural habitats tend to be more vulnerable to edge effects, thus more susceptible to cross-edge incursions by dogs.

Table 1 Covariates used to model the variation in probability of use (Ψ) and detection probability (p) of free-ranging dogs in six priority areas for Brazilian Atlantic Forest. 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 8 total) 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).

	FMA[1]	MS[2]	FM[3]	SS[4]	SB[5]	RD[6]
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 (0.56–6.53)	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 (160.53–1,273)	846.10 (96.89–1,574)	1,007 (227.52–2,000)	747.71(53.26–1,632)	898.79 (212–2,000)	880.77 (240–1,542.60)
Ψ conditional of top predators*	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 (0.20–1.00)
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

[1] Feliciano Miguel Abdala, [2]Mata do Sossego, [3]Fazenda Macedônia,[4] Sete Salões, [5] Serra do Brigadeiro, [6] Rio Doce.

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

Furthermore, dogs often reach high densities and consequently high propagule pressure where human population is high (Odell and Knight 2001; Ordeñana et al. 2010). Thus, dogs should show higher levels of probability that dogs use a site with higher housing intensity. We also estimated the linear distance between each camera site and the nearest house or forested edge. We expected probability that dogs use a site to be positively influenced by the proximity to human houses and forested edge, because dogs are owned and usually live at human houses (Odell and Knight 2001; Sepúlveda et al. 2015).

In addition to human activities, we explored environmental factors that may influence probability that dogs use a site. We expected that probability that dogs use a site could vary according to the number of terrestrial mammal species and the conditional occupancy of top predators. The number of terrestrial mammal species detected at each site, except top predators (jaguars - *Panthera onca* and pumas *Puma concolor*), was used as site covariate.

We also estimated conditional occupancy probability ($\Psi_{conditional}$) of top predators for each camera site using the 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 dog (Butler et al. 2014). Specifically, we expected a positive relationship between terrestrial mammal richness and probability that dogs use a site because high mammal richness may indicate habitats with more potential resources that could supplement dog's diet (Hughes and Macdonald 2013, Ritchie et al. 2014). Additionally, we expected dogs to avoid sites where top predators occur because they can impose suppressive effects on dogs, via consumptive (direct predation; Mazzolli

2009; Foster et al. 2010) and non-consumptive (fear-mediated) effects (Estes et al. 2011; Ritchie and Johnson 2009).

Dogs detection probability (p)

We developed eight *a priori* hypotheses regarding factors that may influence dog detection probability (*p)* at used sites. We model potential variation in detection probability as a function of many of the same covariates used for the probability that dogs use a site (Table 1). Specifically, we expected that sites within smaller protected areas, close to human housing (distance or density) and edge or with higher terrestrial mammal richness, may have higher detection probability than sites within larger protected areas, distant to houses, with lower rural housing intensity, or lower terrestrial mammal richness. 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.

Among all protected areas, we expect 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 to more remote sites (Odell and Knight 2001; Ordeñana et al. 2010). Moreover, these sites would be used by more individuals due to increased influx of dogs. Consequently, these sites would have higher dog detection probability compared to sites within large protected areas (Odell and Knight 2001; Ordeñana et al. 2010).

Three additional covariates were only used 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 worked for longer periods may have higher detection probability. Dogs preferentially move via roads and trails, which may increase their detection probability (Silva-Rodríguez and Sieving 2012; Sepúlveda et al. 2015; Moreira-Arce et al. 2015). Finally, we constructed a covariate for each site and occasion indicating whether top predators were detected (1) or not (0; Table 1). We expected a negative relationship between detection probability and top predator detection since 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. 2006), where detection records (i.e., photographs) of dog were summarized into a matrix of detection histories, reflecting if a dog was detected (1) or not (0) during each occasion of our 120 study sites. We defined an occasion as a 5-day period, so each site had four occasions per season. This model has several assumptions that should be met to avoid biased estimates and incorrect inferences about probability that dogs use a site and detection probability (see MacKenzie et al. 2006).

One of the critical assumptions is that probability that dogs use a site at each site does not change over the study period (i.e., sampled sites are closed to changes in probability that species use a site; MacKenzie et al. 2006). We assessed the potential violation of this model assumption exploring possible changes in the occupancy state between dry and wet seasons, using a dynamic occupancy model (MacKenzie et al. 2003). We fitted four models, where colonization and extinction parameters were either estimated (non-zero) or fixed to 0 (i.e., occupancy state is static between seasons) and we allowed p to vary or not between seasons.

We used Akaike's Information Criterion adjusted for small sample size (AICc) and the relative AICc difference among models (Δ AICc) to evaluate which model was better supported by our data (Burnham and Anderson 2002). The static occupancy model was better supported (Δ AICc for the dynamic model = 2.85), and *p* was constant between seasons (Δ AICc 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 Δ AICc, none of interactive models were supported by our data, so we built a set of models consisting of all possible additive covariate combinations (Doherty et al. 2012) for probability that dogs use a site and detection probability and fit these in Program MARK (White and Burnham 1999). This approach resulted in a balanced model set essential to interpret the cumulative AICc weights ($w+$) for each covariate (Burnham and Anderson 2002).

We assessed goodness of fit (GOF) for our most parameterized model structure (composed of all covariates for probability that dogs use a site and detection probability) via Pearson's GOF test and evaluated overdispersion (i.e., lack of independence among camera sites) using the $\hat{c}$ value, incorporated in Program PRESENCE (Mackenzie and Bailey 2004).

Results

We found strong correlation between proportion of forest cover and proportion of agricultural lands (e.g., r = -0.70). Since dog occurrence is often inversely correlated with vegetation (McKinney 2002, 2006; Ryall and Fahrig 2006) and closely related to human activities (Pita et al., 2009; Soto and Palomares 2015), we retained the proportion of agricultural lands and removed proportion of forest cover from further analyses. Our goodness-of-fit test revealed no evidence of lack of fit and little overdispersion in the data (χ^2 = 350.73; *p*-value = 0.09; $\hat{c}$ =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 of other model in our candidate set (Table 2). Consistent with a *priori* hypothesis, 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).

Table 2 Model selection results for the top 10 models expected to influence: *Ψ*, the probability that a dog use a site during the sampling period and *p*, 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:* proportion of agricultural lands (AG), proportion of eucalyptus (EU), rural housing density (house/km²; RD) and *p;* camera site location (On or off unpaved road; CL), rural housing density (RD), protected area size (RS), distance to edge (DE), distance to house (DH). The plus signal (+) means an additive effect between two or more tested covariates.

Model	AICc	Δ AICc	*w*	K	Deviance
{*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

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 priorities areas for Brazilian Atlantic Forest. Estimates of covariate effects (*β* parameters) are given for the most parsimonious model that included the covariate.

Covariate	Cumulative AICc Weights (%)	*β* parameters		
		Estimate	Lower 95%CL	Upper 95%CL
Free-ranging dog use (*Ψ*)				
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) **	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
Free-ranging dog detection (*p*)				
Camera site location*	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)**	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

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

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

Sites with high rural housing density (≥ 4.00 houses/km^2; Fig. 2a) or higher proportion of croplands and pasture (≥ 72%) were more likely to be used by dog (*Ψ* ≥ 0.90) compared to sites with no houses (*Ψ* = 0.23 ± 0.10; Fig. 2a) or agricultural activities (*Ψ* = 0.34 ± 0.08; Fig. 2b). There was little evidence that any other covariate influenced dogs' probability of use (*Ψ, w+* < 0.20; Table 3).

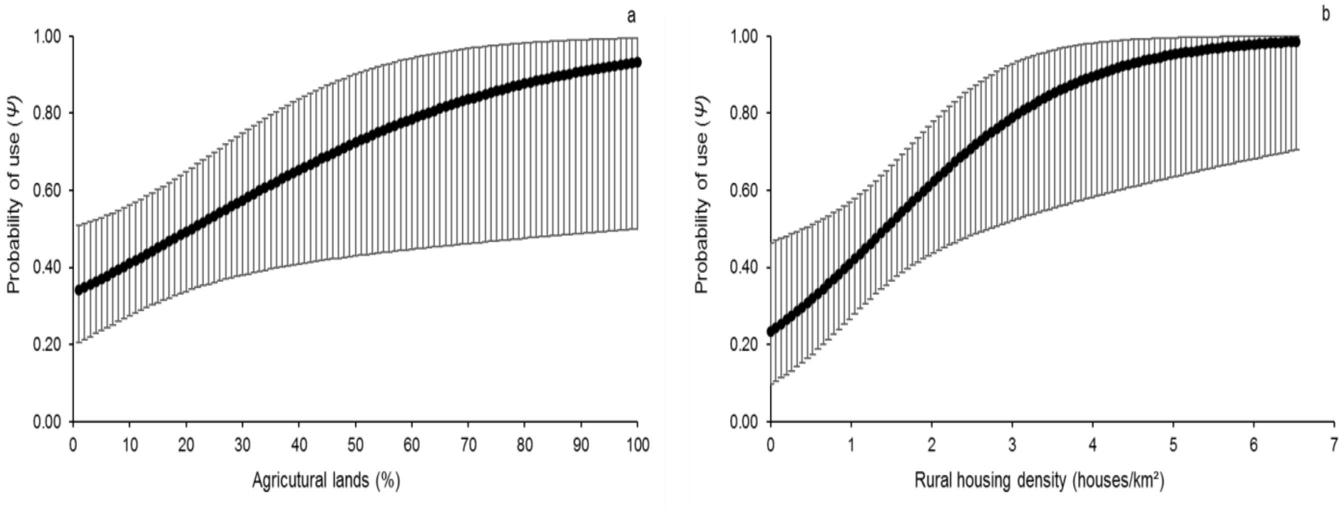


Fig. 2. Probability of free-ranging dog use as a function of site-specific proportion of agricultural lands (a) and rural housing density (b) in Brazilian Atlantic Forest. Estimates are from the most parsimonious model that included those covariates, proportion of agricultural lands and rural housing density.

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

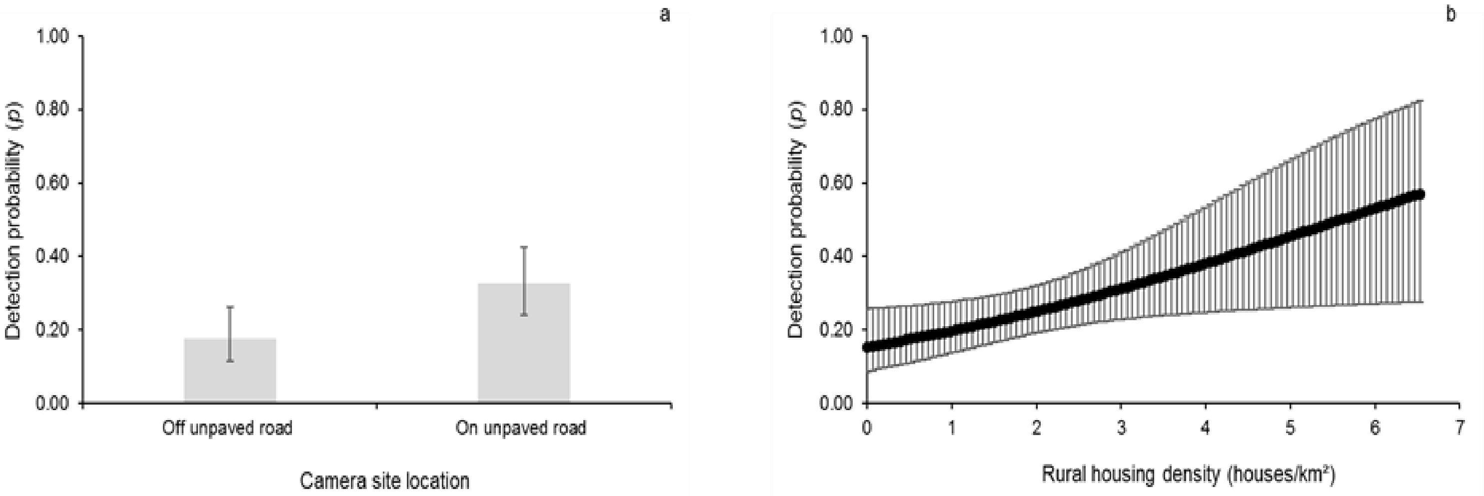


Fig. 3. Detection probability of free-ranging dog as a function of site-specific camera site location; on or off unpaved road (a) and rural housing density (b) in Brazilian Atlantic Forest. Estimates are from the most parsimonious model that included those covariates, camera site location, and rural housing density.

Discussion

Despite having been described previously as habitat generalist with wide habitat breadth (Shea and Chesson 2002), dogs did not use sites randomly. Instead, our result suggested a spatial heterogeneity in dogs' use between camera sites and between protected areas. A heterogeneity among sites may indicate a selective pattern of habitat use. Typically, many of the most troublesome invasive species have relatively broad patterns of habitat use, but often with clear preferences for certain kinds of habitat (Fuller et al. 2011). Habitat selection is a decision-making process where the non-random use of the space by a species is resulted from individuals' choices that differ not only in terms of habitat quality, but also in terms of the energetics costs and benefits of habitat use (Fretwell and Lucas 1970, Kennedy and Gray 1994).

Dogs are thought to behave like central place foragers (Ruiz-Izaguirre et al. 2014). According to the optimal foraging theory, time and distance are an important constrain for central place foragers, influencing the time that dogs should spent in a habitat if energy is to be maximized (Pyke et al. 1977), thus resulting in spatial heterogeneity. In addition, cultural, political and socio-economic traits of local human population have been related to influence habitat selection by dogs. Individual heterogeneity may also occur and have been reported by previous study (Meek et al. 1999; Sepúlveda et al. 2015).

Among predictor variables human activities showed to be important, in shaping dogs' habitat use, where dog was more likely to use sites strongly influenced by human activities. In this context, human housing and agricultural lands are closely associated with two factors that are thought to lead to thriving dog populations and thus, may increase dogs' probability to use: (1) increased food supply that results in augmented propagule pressure and (2) providing favorable habitat for dogs, through modifications in the landscape (Hansen et al. 2005; McKinney 2002, 2006; Vanak and Gompper 2009). The dog is highly adapted to anthropogenic habitats, where it usually lives (Vanak and Gompper 2010; Silva-Rodríguez and Sieving 2012). Consequently, they are spatially related to human activities, such as rural housing and agricultural lands (Vanak and Gompper 2010; Silva-Rodríguez and Sieving 2012; Paschoal et al. 2016).

The strong association found between dog and human activities is consistent with previous studies conducted in different systems worldwide, indicating a consistent pattern (Espartosa 2009; Vanak and Gompper 2010). According to our results, dog's probability of use is a function not only of activity type (e.g. agriculture), but also its magnitude (intensity) in the landscape (e.g., housing density), even in low-density rural areas (≤ 7 houses/km^2; Hansen et al. 2005). Sites composed by ≥ 50% of agriculture and with density of houses ≥ 4 houses/km^2 were respectively ~ 2 to 4 times more likely to be used by a dog when compared to sites with no agriculture or no rural housing.

Rural housing and agriculture are *per se* land-use activities responsible for profound and long-lasting modification of the landscape; thus they are important habitat-mediated pathways. These activities tend to intensify with local human population density and human demand for food resources, increasing the degree of human disturbance even in protected areas. In addition to increased dog abundance (i.e., propagule pressure), land-use intensification leads to a landscape mosaic with increased habitat edges that juxtaposes disturbed and natural habitats facilitating dog occurrence within protected areas through cross-edge incursions (Cantrell et al. 2001; Sepúlveda et al. 2015), where dog 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).

The Atlantic Forest is facing a critical scenario. Protected areas are under continued anthropogenic pressures due to the relentless human population growth resulting in increased proximity to human-disturbed habitats. Furthermore, natural areas provide ecosystem services (e.g., water, soil quality, temperature) that beneficiates human activities, inducing a clustering of these activities at the borders of or encroaching on, protected areas (Hansen et al. 2005; Wittemeyer et al. 2008) increasing the probability of cross-edge incursions events. In contrast to previous studies (Lacerda et al. 2009; Vanak and Gompper 2010; Sepúlveda et al. 2015), dog probability of use showed no relationship to distance to houses or edge proximity.

Although nearly all camera sites (85%) were located in native habitat within protected areas, all sites were within 2.5 km of edge or rural houses which may explain the lack of any distance effects on dogs' probability of use. This is not surprising, since ~ 80% of forest fragments in Atlantic Forest consist of small patches where almost half of them is less than 100 m from a forested border, thus heavily influenced by edge effects (Ribeiro et al. 2009). Despite the lack of relationship between dog probability of use and distance to houses, Paschoal et al. (2016) found that if a dog used a protected area, its probability of continued use was related to the average distance to houses in the protected area.

In addition to habitat-mediated pathways, habitat modification caused by an intense land-use can result in community-mediated pathways, where changes in the community structure of native fauna favor dog numerical dominance (Didham et al. 2007) and consequently its probability of use at a site (Doherty et al. 2015; Kowalski et al. 2015). In this case, the underling mechanism is declines in top predators in fragmented landscapes that would result in the ecological release of dog (Doherty et al. 2015).

Top predators are intolerant to anthropogenic landscapes even in low-density rural areas (Hansen et al. 2005). Their status in Atlantic Forest is critically low, even in protected areas, with unprecedented rates of local extinctions (Canale et al. 2012). This alarmingly status of top predators can also explain our inability to show a direct relationship between top predators and dog probability of use. We found no evidence that other variables (e.g., eucalyptus, mammal richness, roads) influences the probability that a dog use a site within protected area, when compared to the strong relationship with rural housing density and proportion of agricultural lands.

Our results showed that used sites located on unpaved roads were ~ 2 times more likely to detect dog than used sites off roads, 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 corridor and hunting grounds for carnivorans in general (Karanth 1995; Soisalo and Cavalcanti 2006).

Dog seems to preferentially move through habitats/areas via roads (paved or not) and trails (Srbek-Araujo and Chiarello 2008; Silva-Rodríguez and Sieving 2012; Sepúlveda et al. 2015). Therefore, our results are consistent with similar patterns observed in other systems that reported roads and trails as an important conduit improving the access to protected areas and facilitating dog movement within these habitats, directly influencing their impact on native fauna (i.e., expanded edge effect; Červinka et al. 2013; Vanak et al. 2014).

Dog detection probability was ~ 3 times more detectable at sites with ≥ 4 houses/km^2 than sites with no houses, given that these sites are used. This pattern can be related by two factors. First, dog density is directly linked to human density (Odell and Knight 2001; Ordeñana et al. 2010) and an increased in local dog abundance raises the species detection probability in a predictable way (Royle et al. 2005). Overall, small protected areas presented higher house density (Table 1) and higher abundance/density of dogs (10–47 dogs; 0.30–1.69 dogs/km^2; Paschoal et al. 2016). Second, dog usually center their activity around their home site (i.e., rural housing; Meek 1999; Dürr and Ward 2014), where they spend most of their time (Ruiz-Izaguirre et al. 2014; Sepúlveda et al. 2015). This spatial aggregated activity pattern, likely lead to a higher frequency of use at sites with higher number of houses resulting in a higher detection probability of dogs.

Our study provides important information about dog distribution in a highly heterogeneous landscape, providing insights into how human activities indirectly promote the invasion and spread of the species within natural areas, in particular, protected areas. Our study also suggests that the degree of human modification in and around protected areas is a crucial factor to understand and predict dog distribution and likely their impact on native fauna. This finding is a valuable and concerning information considering that people live within the boundaries of 70% of protected areas in the tropics (Bruner et al. 2001), and that human populations in biodiversity hotspots, like Atlantic Forest, are continually expanding especially at the edges of protected areas (Wittemyer et al. 2008; Laurance 2015), and so dog population (Gompper 2014). Moreover, the human population growth creates greater demand for food leading to conversion of lands to agricultural use (Foley et al. 2005; Grau et al. 2008), mostly via high-intensity crop production (Foley et al. 2005). This dynamic increases the susceptibility of a natural habitats, especially protected areas, to new and subsequent dog invasions.

The dog is already considered one of the most common species within protected areas in different biomes, including Atlantic Forest (Srbek-Araujo and Chiarello 2008; Lacerda et al. 2009; Paschoal et al. 2016; Lessa et al. 2016) and their occurrence, and thus their impact, will likely be enhanced due to increasing anthropogenic pressure in the coming decades (Hansen and DeFries 2007), which could reduce their conservation effectiveness (Bruner et al. 2001; DeFries et al. 2005; Hansen and DeFries 2007).

Our findings also suggest that local residents have important roles in controlling the impact of dog on native fauna (Ritchie et al. 2014) and are an essential component for long term dog management (Schwartzman et al. 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 and DeFries 2007). Previous studies suggest that the reduction of dog abundance and ranging behavior are crucial management strategies for dogs (i.e., species-centered approach; Silva-Rodríguez and Sieving 2012; Paschoal et al. 2016).

We advocate the importance to incorporate landscape structure perspective on management strategies given dog impact is largely driven by landscape configuration and composition. Moreover, since dog can interact with diverse ecological disturbances, other valuable approach is considering a pathway-centered approaches (i.e., habitat-mediated pathway and community mediated pathway; Doherty et al. 2015). Since the dog is locally established and widespread in Atlantic Forest, prioritization should focus on feasible complementary strategies considering different approaches for its eradication or containment (McGeoch et al. 2016).

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Final Considerations

Our findings suggest that dog is an important component of carnivoran guild in sensitive areas for conservation within Atlantic Forest. Although some studies suggested that dog incursion in protected areas is a sporadic event, make by few individuals of the local population (Ruiz-Izaguirre et al., 2014; Sepúlveda et al. 2015). Our findings suggest that dog reached high numbers, within protected areas boundaries, overcoming population of native carnivoran like crab-eating fox, ocelot and puma. However, this estimate may be negative biased due to owners' tendency to restrained dogs after learning of our study.

Dogs also seems to came from near distance, likely from human houses within or around protected areas. Unlike native carnivoran, free-ranging dogs in our system is a subsidized predator and do not depend exclusively on natural resources (e.g., food; Vanak and Gompper 2009; Gompper 2014). Therefore, as previously reported in other rural ecosystems (Pita et al. 2009; Odell and Knight 2001; Woodroffe and Donnelly 2011), the dog is highly associated to human activities like human houses and agricultural lands. The increase on intensity of these activities is followed by an increase on dog population and the amount of suitable habitat for the species; consequently, increasing the probability of dog to use a site.

In addition, the continued use of an area/site by a dog is higher with the proximity to human houses where they usually live (Silva-Rodríguez and Sieving 2012); and its frequency of use is higher at unpaved roads, what likely increase the probability of interactions between dog and native fauna, mainly intraguild-interactions, since native carnivoran is widely reported using roads and trails to move (Srbek-Araujo and Chiarello 2008; Goulard et al. 2009).

This strong association with human activities make dog distribution highly predictable in Atlantic Forest. Despite few areas are free of the influence of dog (Sampaio and Schmidt 2013; Lessa et al. 2016). Our study reinforces the existence of a gradient in dog encounter risk, where native fauna is exposed to higher dog effect in small protected areas, which present a suit of conditions, like increased house density, increased proximity with disturbed habitats, and increased dog population (propagule pressure), that favor dog occurrence, persistence and abundance. Given that most Atlantic Forest remnants consist of small, isolated patches that are near populated areas and heavily influenced by edge effects (Ribeiro et al. 2009); dog is likely ubiquitous and overabundant in almost protected areas in this Biome.

Our findings also suggest that dog occurrence and presence should be considered as a priority on management of protected areas in Atlantic Forest. Since dog usually originate from adjacent habitats outside the boundaries of protected areas, the human dimension is an important component of the dog problem in Atlantic Forest protected areas. Therefore, we advocate a cross-boundary management approaches that look beyond protected areas boundaries to the linkages and dynamics across habitat types and landscapes (DeFries et al. 2007). According to our data local people are aware of dog issues when those uses protected areas. However, owners keep dogs unrestrained due to services these animals provide to them, including protection, companionship, and pest control (Paschoal personal obs.). The lack of enforcement of existing law (Federal Law No. 9,985, Sistema Nacional de Unidades de Conservação - SNUC 2000), and specific laws targeting dogs may encourage local people to keep dog ranging free through the landscape.

Moreover, due the complex bond between humans and dogs, it is necessary to manage people and their dogs as a cooperative social unit, using multiple and complementary strategies. These strategies should be applied at species and landscape levels. However, the fact that most dogs are owned restricts or at least complicates management options. For example, lethal control (e.g. culling) is generally not feasible in our protected areas, or in protected areas around the world where dog owners live nearby

(Lacerda et al. 2009; Silva-Rodríguez and Sieving 2012; Vanak and Gompper 2010). In addition, culling programs might increase birth rates via compensatory recruitment, increase immigration rates (Barlow 1996; Lloyd-Smith et al. 2005), or result in local conflicts (Ibama and Funatura 1998; Paschoal personal obs.).

Neutering programs is a population control option that is more plausible since dog owners near the protected areas were very receptive to the idea (Paschoal personal obs.). However, this option requires a long-term investment, low immigration rates and a high proportion of neutered dogs (Amaku et al. 2009), but continuous neutering and education programs can achieve these necessities (Silva-Rodríguez and Sieving 2012). Furthermore, neutering programs can also reduce the duration of protected area use by males (R), since gonadectomized dogs tend to roam or escape less often and spend more time at home (Maarschalkerweerd et al. 1997; Spain et al. 2004). Although, Silva-Rodríguez and Sieving (2012) suggested that neutering just females could be more efficient and less expensive, it may be better to neuter both sexes since free-ranging dog populations are highly male biased (Reece 2005; Gompper 2014; Curi et al. 2014). Doing so would reduce both dog abundance and ranging behavior.

Other important point is controlling dog movement through kennels around backyard or farm animal enclosures (e.g. henhouses) would allow dogs to effectively perform their primary guarding duty, while also minimizing roaming and hunting behaviors, but socio-cultural barriers to implementing this management could be difficult to overcome. In addition, as previous studies, our data suggested that specific traits of landscape (e.g., house density, agricultural lands) can function as conduit for dog invasions. Therefore, another strategy for controlling dog–native fauna interactions could be selective use of habitat or other movement barriers. Management action plans could reduce dog access into protected areas by reducing the proximity of human houses and protected areas applying buffer zones, and restoration of degraded habitat and native community (Bekoff and Meaney 1997; Miller et al. 2014; Sepúlveda et al. 2015). Such landscape manipulation, of course, could lead to conflict with local communities and therefore a participatory community-based approach should be used.

Understanding the complexity of the relationship between local people-dogs-native fauna is essential before implementing any action aimed at reducing dog occurrence and its populations within protected areas (Reece 2005). Therefore, we should overcome the lack of knowledge about dog ecology as invasive species. For this reason, we claim for more studies targeting dog within protected areas in Atlantic Forest and other ecosystems in Brazil exploring other variables that may influence dog occurrence and abundance within protected areas. For this reason, besides the present information, our study is already exploring potential spatial and temporal interactions among dog and native fauna (e.g., predation, intraguild interactions); exploring how individual traits of dogs (e.g., health condition, age, sex), as well as, owner management to their dog could influence dog probability of use and abundance in sensitive areas for conservation. We also expect to develop a map of potential distribution of dog in Atlantic Forest. Finally, we expected to contribute for a better understanding of dog in natural ecosystems and provide important information for future managements.

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