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

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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 wildlife 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.

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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 high 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 700–987 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 yr (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 result in interactions at multiple levels with native fauna (Vanak and Gompper 2009, Young et al. 2011). Dogs can affect wildlife 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 wildlife behavior and activity patterns (Young et al. 2011, Hughes and Macdonald 2013). Negative interactions between domestic dogs and wildlife populations can be dramatic in undeveloped or developing countries due to the absence of laws or enforcement that promotes 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 wildlife 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 wildlife 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; and 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 semideciduous seasonal forest (SOS Mata Atlântica 2014). The climate is humid tropical or semihumid (IBGE 2012), and elevation of the protected areas varies between 230 m (FM) and 2075 m (SB; Miranda 2005).

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., FMA, MS, and FM; Table 1), some camera sites were established on surrounding lands to standardize our sampling design. Cameras were placed at each randomly selected site unless there was a better position within 50–100 m that could improve carnivoran 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 h per day with a 5-min interval between photographs.

Sampling occurred between 2008 and 2012; each protected area was sampled for 80 d in both the wet and dry seasons. Because we had a restricted number of cameras, we sampled five sites for 20 consecutive days and 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.

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.

Protected area†	Total area (ha)	Forest (%)	RAI (%)	MDH (m)	ESA (ha)	$\hat{R}$	Dogs abundance (± 95% CI)		Dogs/km^2 (± 95% CI)	
							Dry	Wet	Dry	Wet
MS[1]	134	56.17	0	1447	3436	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	4893	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**	**4306**	**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	4950	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	5445	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	4341	0	0	0	0	0

Notes: 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 ($\widehat{R}$), 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-d sampling period.

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

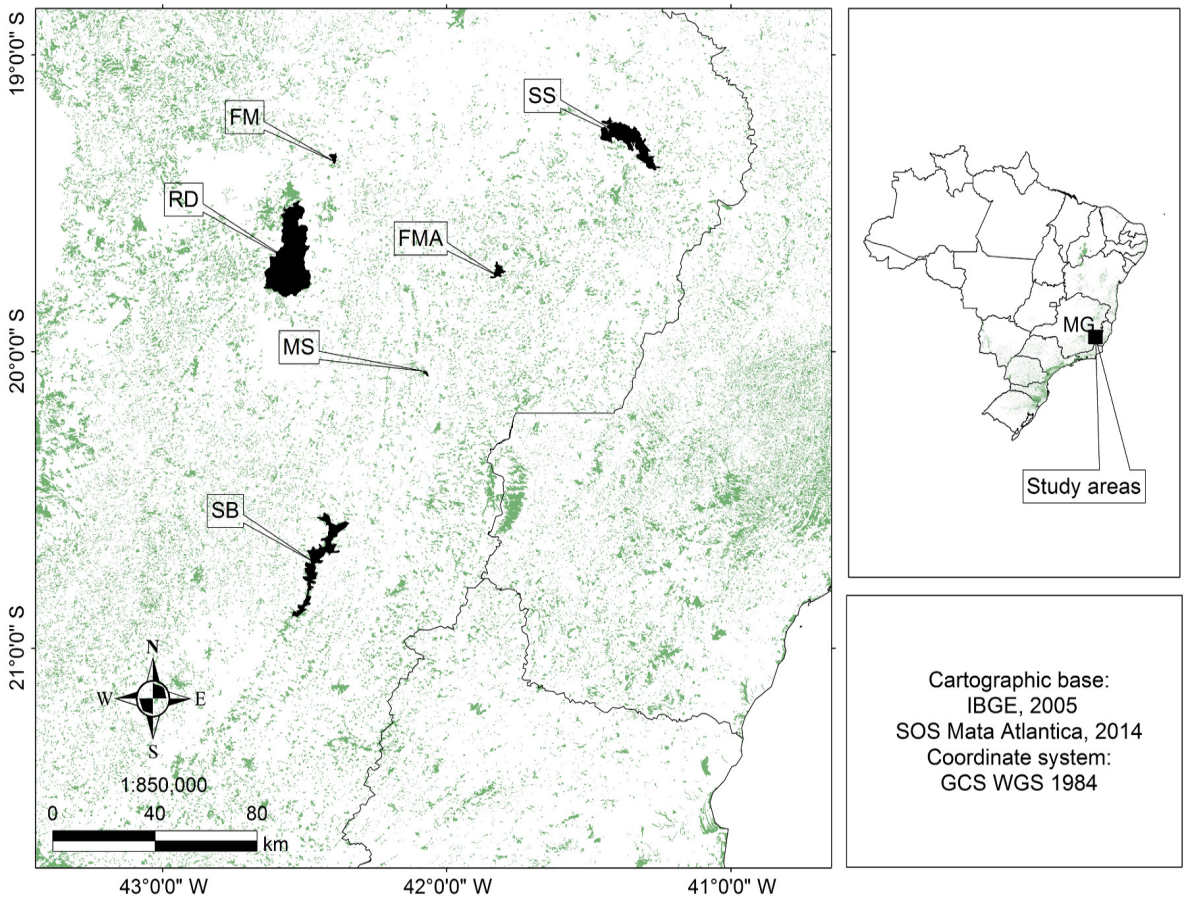

Fig. 1. Location of the six protected areas sampled for free-ranging domestic dogs in the Atlantic Forest, southeastern Brazil. FMA—Feliciano Miguel Abdala; MS—Mata do Sossego; FM—Fazenda Macedônia; SS—Sete Salões; SB—Serra do Brigadeiro; RD—Rio Doce. The inset shows the current distribution of the Atlantic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

Data analysis

Free-ranging dogs in our study exhibited a high degree of phenotypic diversity (Appendix S1: Fig. S1; Boyko and Boyko 2014). Photographs 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 photographs at one or more hour of interval was considered for analysis. We collapsed our 80 sampling days into 10-d 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 S2: Table S1). Kendall et al. (1997) and Kendall (1999) described the potential biases produced by such nonrandom 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 multistate open-robust design model (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-d 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 the following: $pent_j$ = 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 modeling 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-d occasions that a free-ranging dog used a protected area and was interpreted as persistence of use.

Accordingly, we modeled 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, as 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); and (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 (ESA) 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 (RAI) of top predators (*Puma concolor* and *Panthera onca*) for each

protected area by calculating the encounter rate (number of photographs 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, that is, 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 as 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 (<1000 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 corrected for small sample size (AIC_c), the relative difference in AIC_c values among models (ΔAIC_c), 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 AIC_c 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 modeled 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 ESA (Table 1). We calculated ESA as the minimum convex polygon, using all camera traps sites, which covered on average 915.2 ha (range 433.8–1334.5 ha), plus a buffer width defined by the mean maximum distance moved (Soisalo and Cavalcanti 2006) by free-ranging dogs detected in all protected areas combined (1970 m). The ESAs were calculated using ArcGIS 9.2 (ESRI 2008).

Results

Overall, our study resulted in a total of 1249 records of 24 terrestrial mammal species. The domestic dog was the most detected species

Table 2. Model 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*, the probability that a dog in the protected area during occasion *j* is detected.

Model	K	AIC_c	ΔAIC_c	*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)

Notes: Models with little support ($w < 0.05$) are not shown. The AIC_c values and their respective weights (*w*) are shown for models with the following effects: time trend (T) for *p* and mean distance between camera sites 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*).

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 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 AIC_c values and associated metrics from the MSORD analysis for biological inference. The top two models accounted for approximately 99% of the AIC_c weight (w_+ = 0.99) and ΔAIC_c 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 was 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 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).

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; Beisiegel 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

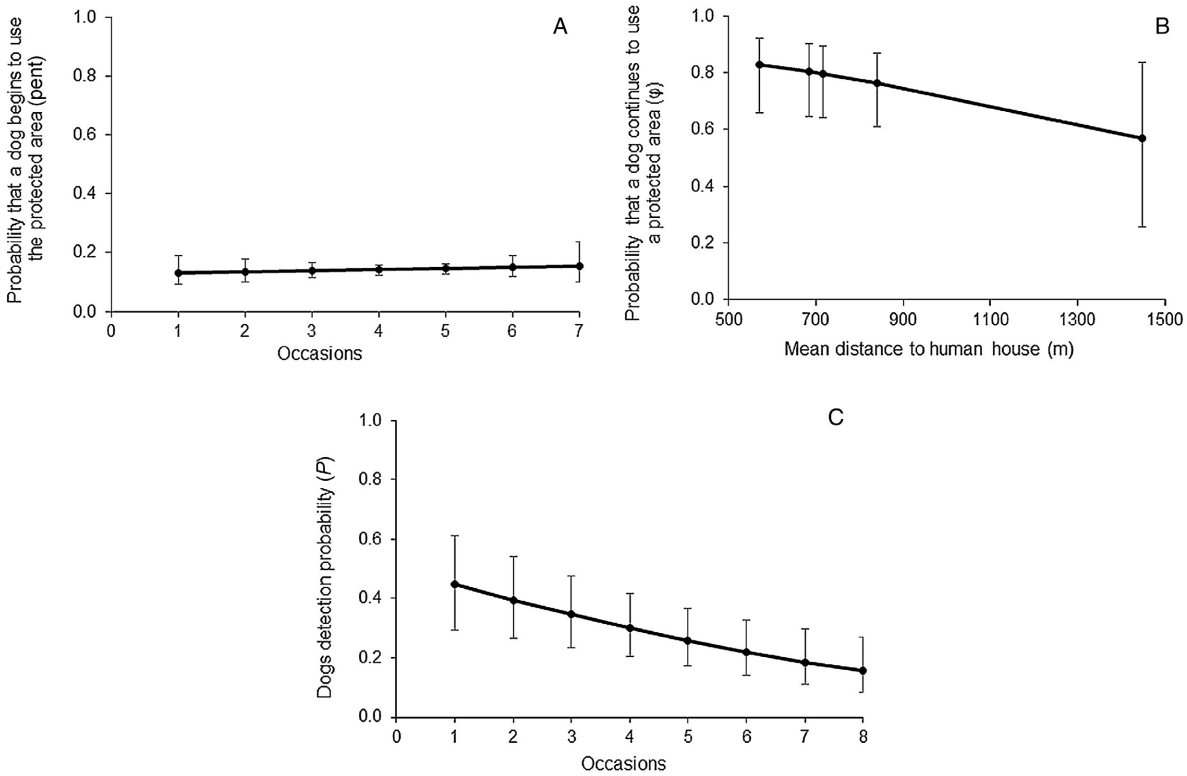

Fig. 2. Model-averaged estimates of the probability that a dog in the superpopulation (*N*) begins to use the protected area between occasions *j* and *j* + 1 (*pent*; A). Estimates of the probability that a free-ranging dog continues to use a protected area (φ) as a function of mean distance to human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

(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 (Kelly et al. 2008, Beisiegel et al. 2013, Massara et al. 2015), 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 is 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; A. M. O. 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 (Wittemyer 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 uses 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 results 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) where we did not detect 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 dogs 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) influenced 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 was 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 affect protected area use by dogs and thus dog–wildlife 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, 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 ten 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 sugarcane 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 wildlife. 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, RD 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 RD (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). As 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, Mcdonald 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 wildlife 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, buffer zones, and restoration of degraded lands. We advocate 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. 9985, 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; A. M. O. 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–wildlife conflicts (Reece 2005).

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Literature Cited

Acosta-Jamett, G., S. Cleaveland, and A. A. Cunningham. 2010. Demography of domestic dogs in rural and urban areas of the Coquimbo region of Chile and implications for disease transmission. Preventive Veterinary Medicine 94:272–281.

Barros, C. F. A., M. B. G. Souza, and F. A. R. Barbosa. 2006. Seasonal mechanisms driving phytoplankton size structure in a tropical deep lake (Dom Helvécio Lake, South-East Brazil). Acta Limnologica Brasiliensia 18:55–66.

Beisiegel, B. M., F. G. Lemos, F. C. Azevedo, D. Queirolo, and R. S. P. Jorge. 2013. Avaliação do risco de extinção do Cachorro-do-mato *Cerdocyon thous* (Linnaeus, 1766) no Brasil. Biodiversidade Brasileira 3:138–145.

Bekoff, M., and C. A. Meaney. 1997. Interactions among dogs, people, and the environment in Boulder, Colorado: a case study. Anthrozoos 10:23–31.

Bentosela, M., G. Barrera, A. Jakovcevic, A. M. Elgier, and A. E. Mustaca. 2008. Effect of reinforcement, reinforcer omission and extinction on a communicative response in domestic dogs (*Canis familiaris*). Behavioural Processes 783:464–469.

Berman, M., and I. Dunbar. 1983. The social behaviour of free-ranging suburban dogs. Applied Animal Ethology 10:5–17.

Boyko, R. H., and A. R. Boyko. 2014. Dog conservation and the population genetic structure of dogs. Pages

185–207 *in* M. E. Gompper, editor. Free-ranging dogs and wildlife conservation. Oxford University Press, Oxford, UK.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer Verlag, New York, New York, USA.

Butler, J. R. A., J. T. du Toit, and J. Bingham. 2004. Free-ranging domestic dogs (*Canis familiaris*) as predators and prey in rural Zimbabwe: threats of competition and disease to large wild carnivores. Biological Conservation 115:369–378.

Canale, G. R., C. A. Peres, C. E. Guidorizzi, C. A. F. Gatto, and M. C. M. Kierulff. 2012. Pervasive defaunation of forest remnants in a tropical biodiversity hotspot. PLoS One 7:e41671.

Clutton-Brock, J. 2012. Animals as domesticates: a world view through history. Michigan State University Press, East Lansing, Michigan, USA.

Converse, S. J., W. L. Kendall, P. F. Doherty, and P. G. Ryan. 2009. Multistate models for estimation of survival and reproduction in the Grey-Headed Albatross (*Thalassarche chrysostoma*). Auk 126:77–88.

Cooch, E., and G. White. 2015. Program MARK: a gentle introduction. Fourteenth edition. Colorado State University, Fort Collins, Colorado, USA. http://www.phidot.org/software/mark/docs/book

DeFries, R., A. Hansen, A. C. Newton, and M. Hansen. 2005. Increasing isolation of protected areas in tropical forests over the past twenty years. Ecological Applications 15:19–26.

DeFries, R., A. Hansen, B. L. Turner, R. Reid, and J. Liu. 2007. Land use change around protected areas: management to balance human needs and ecological function. Ecological Applications 17:1031–1038.

Didham, R. K., J. M. Tylianakis, N. J. Gemmell, T. A. Rand, and R. M. Ewers. 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends in Ecology and Evolution 22:489–496.

Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmell. 2005. Are invasive species the drivers of ecological change? Trends in Ecology and Evolution 20:470–474.

Doherty, T. S., C. R. Dickman, D. G. Nimmo, and E. G. Ritchie. 2015. Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. Biological Conservation 190:60–68.

Doherty, P. F., G. C. White, and K. P. Burnham. 2012. Comparison of model building and selection strategies. Journal of Ornithology 152:317–323.

Dürr, S., and M. P. Ward. 2014. Roaming behaviour and home range estimation of domestic dogs in Aboriginal and Torres Strait Islander communities in northern Australia using four different methods. Preventive Veterinary Medicine 117:340–357.

ERDAS [Earth Resources Data Analysis System]. 1997. ERDAS imagine version 8.4 field guide. Fourth edition. ERDAS, Atlanta, Georgia, USA.

Espartosa, K. D., B. T. Pinotti, and R. Pardini. 2011. Performance of camera trapping and track counts for surveying large mammals in rainforest remnants. Biodiversity and Conservation 20: 2815–2829.

ESRI [Environmental Systems Research Institute]. 2008. ArcViewGISv.9.2. Environmental Systems Research Institute, Redlands, California, USA.

Foster, R. J., and B. J. Harmsen. 2012. A critique of density estimation from camera-trap data. Journal of Wildlife Management 76:224–236.

Frigeri, E., C. R. Cassano, and R. Pardini. 2014. Domestic dog invasion in an agroforestry mosaic in southern Bahia, Brazil. Tropical Conservation Science 7:508–528.

Gehring, T. M., and R. K. Swihart. 2003. Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. Biological Conservation 109:283–295.

Gompper, M. E. 2014. The dog-human-wildlife interface: assessing the scope of the problem. Pages 9–45 *in* M. E. Gompper, editor. Free-ranging dogs and wildlife conservation. Oxford University Press, Oxford, UK.

Hansen, A. J., and R. DeFries. 2007. Ecological mechanisms linking protected areas to surrounding lands. Ecological Applications 17:974–988.

Harmsen, B., R. Foster, and C. Doncaster. 2011. Heterogeneous capture rates in low density populations and consequences for capture-recapture analysis of camera-trap data. Population Ecology 53:253–259.

Hughes, J., and D. W. Macdonald. 2013. A review of the interactions between free-roaming domestic dogs and wildlife. Biological Conservation 157:341–351.

Hulme, P. E., et al. 2008. Grasping at the routes of biological invasions: a framework for integrating pathways into policy. Journal of Applied Ecology 45:403–414.

IBGE [Instituto Brasileiro de Geografia e Estatística]. 2012. Mapas interativos do IBGE: Clima. http://mapas.ibge.gov.br/interativos

Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852–2862.

Kelly, M. J., A. J. Noss, M. S. Di Bitetti, L. Maffei, R. L. Arispe, A. Paviolo, C. D. De Angelo, and Y. E. Di Blanco. 2008. Estimating puma densities from camera trapping across three study sites: Bolivia,

Argentina, and Belize. Journal of Mammalogy 89:408–418.

Kendall, W. L. 1999. Robustness of closed capture-recapture violations of closure assumption. Ecology 80:2517–2525.

Kendall, W. L. 2004. Coping with unobservable and mis-classified states in capture-recapture studies. Animal Biodiversity and Conservation 27: 97–107.

Kendall, W. L. 2006. The robust design. Pages 15.2–15.50 *in* E. G. Cooch and G. C. White, editors. Program MARK: a gentle introduction. Colorado State University, Fort Collins, Colorado, USA. http://www.phidot.org/software/mark/docs/book/pdf/chap15.pdf

Kendall, W. L., and R. Bjorkland. 2001. Using open robust design models to estimate temporary emigration from capture-recapture data. Biometrics 57:1113–1122.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration and breeding proportions using capture-recapture data with Pollock's robust design. Ecology 78:563–578.

Kitala, P., J. McDermott, M. Kyule, J. Gathuma, B. Perry, and A. Wandeler. 2001. Dog ecology and demography information to support the planning of rabies control in Machakos District, Kenya. Acta Tropica 78:217–230.

Laurance, W. F. 2015. Emerging threats to tropical forests. Annals of the Missouri Botanical Garden 100:159–169.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals. A unified approach with case studies. Ecological Monographs 62:67–118.

Lessa, I., T. C. S. Guimarães, H. G. Bergallo, A. Cunha, and E. Vieira. 2016. Domestic dogs in protected areas: A threat to Brazilian mammals? Natureza & Conservação. *In press*. http://dx.doi.org/10.1016/j.ncon.2016.05.00

Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20:223–228.

Lovejoy, T. E. 2006. Protected areas: a prism for a changing world. Trends in Ecology and Evolution 21:329–333.

MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42–55.

Massara, R. L., A. M. O. Paschoal, P. F. Doherty, A. Hirsch, and A. G. Chiarello. 2015. Ocelot population status in protected Brazilian Atlantic forest. PLoS One 11:e0141333.

Mazzolli, M. 2009. Mountain lion *Puma concolor* attacks on a maned wolf *Chrysocyon brachyurus* and a domestic dog in a forestry system. Mastozoologia Neotropical 16:465–470.

Mcdonald, R. I., R. T. Forman, P. Kareiva, R. Neugarten, D. Salzer, and J. Fisher. 2009. Urban effects, distance, and protected areas in an urbanizing world. Landscape and Urban Planning 93:63–75.

McGeoch, M. A., S. H. M. Butchart, D. Spear, E. Marais, E. J. Kleynhans, A. Symes, J. Chanson, and M. Hoffmann. 2010. Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. Diversity and Distributions 16:95–108.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14:450–453.

Meek, P. D. 1999. The movement, roaming behavior and home range of free-roaming domestic dogs, *Canis lupus familiaris*, in coastal New South Wales. Wildlife Research 26:847–855.

Miklósi, A. 2007. Dog behaviour, evolution, and cognition. Oxford University Press, Oxford, London, UK.

Miller, K. K., E. G. Ritchie, and M. A. Weston. 2014. The human dimensions of dog-wildlife interactions. Pages 286–301 *in* M. E. Gompper, editor. Free-ranging dogs and wildlife conservation. Oxford University Press, Oxford, UK.

Miranda, E. E. 2005. Brasil em Relevo. Embrapa Monitoramento por satélite. http://www.relevobr.cnpm.embrapa.br

Mittermeier, R. A., P. G. Gil, M. Hoffman, J. Pilgrim, T. Brooks, C. G. Mittermeier, J. Lamoreux, G. A. B. Fonseca, P. A. Seligmann, and H. Ford. 2005. Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions. CEMEX, Mexico City, Mexico.

Morters, M. K., T. J. McKinley, O. Restif, A. J. Conlan, S. Cleaveland, K. Hampson, H. R. Whay, I. M. Damriyasa, and J. L. Wood. 2014. The demography of free-roaming dog populations and applications to disease and population control. Journal of Applied Ecology 51:1096–1106.

Nery, M. S., and F. P. Tabacow. 2012. Plano de Manejo: RPPN Feliciano Miguel Abdala. Caratinga, Preserve Muriqui, Fundação SOS Mata Atlântica, Conservação Internacional do Brasil, Fundação Biodiversitas, Caratinga, Minas Gerais, Brazil.

Newsome, T. M., G. A. Ballard, P. J. Fleming, R. van de Ven, G. L. Story, and C. R. Dickman. 2014. Human-resource subsidies alter the dietary preferences of a mammalian top predator. Oecologia 175:139–150.

O'Brien, T. G. 2011. Abundance, density and relative abundance: a conceptual framework. Pages 71–96 *in* A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. Camera trap in animal ecology: methods and analyses. Springer, New York, New York, USA.

Oppenheimer, E. C., and J. R. Oppenheimer. 1975. Certain behavioral features in the pariah dog (*Canis familiaris*) in west Bengal. Applied Animal Ethology 2:81–92.

Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martínez-Abraín. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16:1501–1514.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:1–135.

Pal, S. K., B. Ghosh, and S. Roy. 1998. Dispersal behaviour of free-ranging dogs (*Canis familiaris*) in relation to age, sex, season and dispersal distance. Applied Animal Behaviour Science 61:123–132.

Pal, S. K. 2015. Factors influencing intergroup agonistic behaviour in free-ranging domestic dogs (*Canis familiaris*). Acta Ethologica 18:209–220.

Parker, I. M., et al. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1:3–19.

Paschoal, A. M. O., R. L. Massara, J. L. Santos, and A. G. Chiarello. 2012. Is the domestic dog becoming an abundant species in the Atlantic forest? A study case in southeastern Brazil. Mammalia 76:67–76.

Pita, R., A. Mira, F. Moreira, R. Morgado, and P. Beja. 2009. Influence of landscape characteristics on carnivore diversity and abundance in Mediterranean farmland. Agriculture, Ecosystems and Environment 132:57–65.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52:137–154.

Reece, J. F. 2005. Dogs and dog control in developing countries. Pages 55–64 *in* D. J. Salem and A. N. Rowa, editors. The state of the animals III. Humane Society Press, Washington, D.C., USA.

Ribeiro, M. C., J. P. Metzger, A. C. Martensen, F. J. Ponzoni, and M. M. Hirota. 2009. The Brazilian Atlantic forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142:1141–1153.

Ripple, W. J., et al. 2014. Status and ecological effects of the world's largest carnivores. Science 343:1241484.

Ritchie, E. G., C. R. Dickman, M. Letnic, and A. T. Vanak. 2014. Dogs as predators and trophic regulators. Pages 55–65 *in* M. E. Gompper, editor. Free-ranging dogs and wildlife conservation. Oxford University Press, Oxford, UK.

Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982–998.

Ruiz-Izaguirre, E., A. Woersem, K. Eilers, S. Wieren, G. Bosch, A. Zijpp, and I. Boer. 2014. Roaming characteristics and feeding practices of village dogs scavenging sea-turtle nests. Animal Conservation. http://dx.doi.org/10.1111/acv.12143

Sakai, A. K., et al. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32:305–332.

Sampaio, A. B., and I. B. Schmidt. 2013. Espécies Exóticas Invasoras em Unidades de Conservação Federais do Brasil. Biodiversidade Brasileira 3: 32–49.

Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of open-model capture recapture experiments. Biometrics 52: 860–873.

Schwarz, C. J., and W. T. Stobo. 1997. Estimating temporary migration using the robust design. Biometrics 53:178–194.

Sepúlveda, M. A., K. Pelican, P. Cross, A. Eguren, and R. S. Singer. 2015. Fine-scale movements of rural free-ranging dogs in conservation areas in the temperate rainforest of the coastal range of southern Chile. Mammalian Biology-Zeitschrift für Säugetierkunde 80:290–297.

Silva-Rodríguez, E. A., and K. E. Sieving. 2012. Domestic dogs shape the landscape-scale distribution of a threatened forest ungulate. Biological Conservation 150:103–110.

Simberloff, D. 2001. Biological invasions – How are they affecting us, and what can we do about them? Western North American Naturalist 61:308–315.

SNUC [Sistema Nacional de Unidades de conservação]. 2000. Texto da Lei 9.985 de 18 de julho de 2000 e vetos da presidência da República ao PL aprovado pelo congresso Nacional e Decreto Nº 4.340, de 22 de agosto de 2002. Second edition. Conselho Nacional da Reserva da Biosfera da Mata Atlântica, São Paulo, São Paulo, Brazil.

Soisalo, M. K., and S. M. C. Cavalcanti. 2006. Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. Biological Conservation 129: 487–496.

SOS Mata Atlântica. 2014. Atlas dos remanescentes florestais da Mata Atlântica (período 2008–2010). http://mapas.sosma.org.br

Sparkes, J., G. Körtner, G. Ballard, P. J. Fleming, and W. Y. Brown. 2014. Effects of sex and reproductive

state on interactions between free-roaming domestic dogs. PLoS One 9:e116053.

Spotte, S. 2012. Societies of wolves and free-ranging dogs. Cambridge University Press, Cambridge, UK.

Srbek-Araujo, A. C., and A. G. Chiarello. 2008. Domestic dogs in Atlantic forest protected areas of southeastern Brazil: a camera-trapping study on patterns of entrance and site occupancy rates. Brazilian Journal of Biology 68:771–779.

Terborgh, J., and C. Peres. 2002. The problem of people in parks. Pages 307–319 *in* M. Rao, editor. Making parks work: strategies for preserving tropical nature. Island Press, Washington, D.C., USA.

Torres, P. C., and P. I. Prado. 2010. Domestic dogs in a fragmented landscape in the Brazilian Atlantic Forest: abundance, habitat use and caring by owners. Brazilian Journal of Biology 70:987–994.

Vanak, A. T., and M. E. Gompper. 2009. Dogs *Canis familiaris* as carnivores: their role and function in intraguild competition. Mammal Review 39:265–283.

Vanak, A. T., and M. E. Gompper. 2010. Interference competition at the landscape level: the effect of free-ranging dogs on a native mesocarnivore. Journal of Applied Ecology 47:1225–1232.

Vázquez, D. P., C. J. Melián, N. M. Williams, N. Blüthgen, B. R. Krasnov, and R. Poulin. 2007. Species abundance and asymmetric interaction strength in ecological networks. Oikos 116:1120–1127.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmánek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. New Zealand Journal of Ecology 21:1–16.

Wallach, A. D., W. J. Ripple, and S. P. Carroll. 2015. Novel trophic cascades: Apex predators enable coexistence. Trends in Ecology and Evolution 30:146–153.

Wandeler, A. I., H. C. Matter, A. Kappeler, and A. Budde. 1993. The ecology of canine rabies: a selective review. Revue Scientifique el Techinique de I'Office International des Epizooties 12:51–71.

White, G. C., and K. P. Burnham. 1999. Program Mark: survival estimation from populations of marked animals. Bird Study 46:120–139.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

Wittemyer, G., P. Elsen, W. T. Bean, A. C. O. Burton, and J. S. Brashares. 2008. Accelerated human population growth at protected area edges. Science 321:123–126.

Woodroffe, R., and C. A. Donnelly. 2011. Risk of contact between endangered African wild dogs *Lycaon pictus* and domestic dogs: opportunities for pathogen transmission. Journal of Applied Ecology. http://dx.doi.org/10.1111/j.1365-2664.2011.02059.x

Young, J. K., K. A. Olson, R. R. Reading, S. Amgalanbaatar, and J. Berger. 2011. Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. BioScience 61:125–132.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1480/full