



Dog activity in protected areas: behavioral effects on mesocarnivores and the impacts of a top predator

Rita de Cassia Bianchi^{1,2} · Natalie Olifiers³ · Letícia Lutke Riski⁴ · Jéssica Abonízio Gouvea^{1,2} · Clarice Silva Cesário^{1,2} · Larissa Fornitano^{1,2} · Gisele Lamberti Zanirato^{1,2} · Mateus Yan de Oliveira¹ · Kimberly Danielle Rodrigues de Moraes¹ · Renan Lieto Alves Ribeiro¹ · Paulo Sergio D'Andrea⁵ · Matthew E. Gompper^{6,7}

Received: 20 October 2019 / Revised: 4 March 2020 / Accepted: 20 March 2020 / Published online: 6 April 2020
© Springer-Verlag GmbH Germany, part of Springer Nature 2020

Abstract

Free-ranging dogs (*Canis familiaris*) negatively impact wildlife worldwide. Yet despite being members of the order Carnivora, we have relatively little information on the role that dogs play in carnivore communities. To evaluate if activity patterns of wild carnivores are influenced by the activity of dogs and if the latter is influenced by the activity of pumas (*Puma concolor*), we placed camera traps in eight protected areas in São Paulo State and in six in Rio de Janeiro State, Brazil, from 2011 to 2017. We obtained 551 photo-captures of dogs in 20,524 trap nights in 11 of the 14 protected areas. Dogs were active primarily during the day and therefore overlapped mainly with diurnal carnivores, such as tayras (*Eira barbara*) and coatis (*Nasua nasua*). Mesocarnivore temporal activity did not appear affected by the activity of dogs, since the activity patterns of tayras, coatis, maned wolves (*Chrysocyon brachyurus*), and ocelots (*Leopardus pardalis*) were similar (from 67 to 82% of overlap) in areas with and without dogs. Further, the activity of dogs was not influenced by puma activity; dog activity patterns in areas with pumas and without pumas overlapped by 84%, with minimal differences. While mesocarnivores might alter their spatial behavior to avoid overlap with dogs, it appears that dog use of protected areas does not result in shifts in the temporal activity of mesocarnivores. Further, we hypothesize that dogs that use protected areas are mostly provisioned by humans (owners), and therefore, their activity patterns may be more related to that of their owners than to the presence of native carnivore species.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10344-020-01376-z>) contains supplementary material, which is available to authorized users.

✉ Rita de Cassia Bianchi
ritacbianchi@gmail.com

Keywords Alien species · Activity patterns · *Canis familiaris* · *Eira barbara* · *Nasua nasua* · *Puma concolor* · Invasive predator

Introduction

The dog (*Canis familiaris*) was the first domestic animal species, with the transition to domestication occurring at a time when human subsistence still depended on hunting and gathering (Clutton-Brock 2017). Today, although the majority of humans no longer interact with dogs during hunting or foraging, the global dog population has increased along with the human population to an estimated one billion animals (Gompper 2014a). While the level of association between humans and dogs varies widely, most dogs depend on human-derived food sources (Ritchie et al. 2014). Therefore, the majority of dog populations can be considered subsidized predators, that is, populations of predators whose densities are above what one might normally expect if human-derived resources were unavailable (Gompper 2014b). These predators

- ¹ Departamento de Biologia Aplicada à Agropecuária, Faculdade de Ciências Agrárias e Veterinárias, Universidade Estadual Paulista-Unesp, Jaboticabal, SP, Brazil
- ² Programa de Pós-Graduação em Biologia Animal, Universidade Estadual Paulista-Unesp, São José do Rio Preto, SP, Brazil
- ³ Universidade Veiga de Almeida, Rio de Janeiro, RJ, Brazil
- ⁴ Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil
- ⁵ Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Rio de Janeiro, RJ, Brazil
- ⁶ School of Natural Resources, University of Missouri, Columbia, MO, USA
- ⁷ Department of Fish, Wildlife and Conservation Ecology, New Mexico State University, Las Cruces, NM, USA

might have strong direct and indirect impacts on natural communities through predation, disturbance, pathogen transmission, competition, and hybridization (Hughes and Macdonald 2013; Doherty et al. 2017; Hughes et al. 2017). These interactions have contributed to 11 vertebrate extinctions and are also a known risk to 188 threatened species worldwide (Doherty et al. 2017). Among vertebrates, the most common interactions involving dogs are with other mammals (54 of 69 studies; Hughes et al. 2017).

The way dogs interact with wildlife depends on dog population density, the extent to which these dogs are constrained and cared for by humans (fed, sheltered, or vaccinated, for instance), and how other species perceive dogs. Vertebrate wildlife species likely perceive dogs as potential predators (Gompper 2014b), which triggers strong and diverse responses, particularly among prey species (Ritchie et al. 2014). For mammalian carnivores, the presence of dogs can also elicit responses, as dogs may be seen as potential predators, competitors, or even as prey (Vanak et al. 2014). For example, over the past 15 years, dogs have been the primary prey for a population of leopards (*Panthera pardus*) in Sanjay Gandhi National Park, which borders the city of Mumbai, India (Braczkowski et al. 2018). In the New World, jaguar (*Panthera onca*) and puma (*Puma concolor*) also prey on dogs (Butler et al. 2014).

Cross-cultural differences in human attitudes towards dogs may play an important role on how dogs interact with wildlife (Serpell 2017). For example, while in some places dog populations strongly impact wildlife (Vanak and Gompper 2010; Johnson et al. 2010; Phillips et al. 2012), in protected areas of the eastern USA, dogs were not perceived as a threat by wildlife despite being the most common non-human mammal detected in the region (Parsons et al. 2016). Further, in some regions of the world, dogs typically interact with wildlife while accompanying their owners in natural habitats (Weston et al. 2014), but in other areas, dogs are less likely to be restrained and enter protected areas in the absence of humans, probably to look for food (Campos et al. 2007; Vanak and Gompper 2010).

To date, Red List assessments generally do not contain information on the non-consumptive effects (i.e., predation risk and fear) of dogs on wildlife behavior and demographics. These risk effects could be substantial but appear understudied or underreported, thus impeding evidence-based management (Doherty et al. 2017). Risk effects arise when prey alters its behavior in response to perceived predators, and these responses carry costs (Creel 2001; Creel et al. 2005; Dröge et al. 2017; Gallagher et al. 2017). Studies of dog roles in vertebrate conservation and management usually consider only the effects of direct predation. Yet non-consumptive effects can be larger than direct effects and can occur even when the direct rate of predation is zero. Further, when risk effects reduce reproduction rather than survival, they are easily

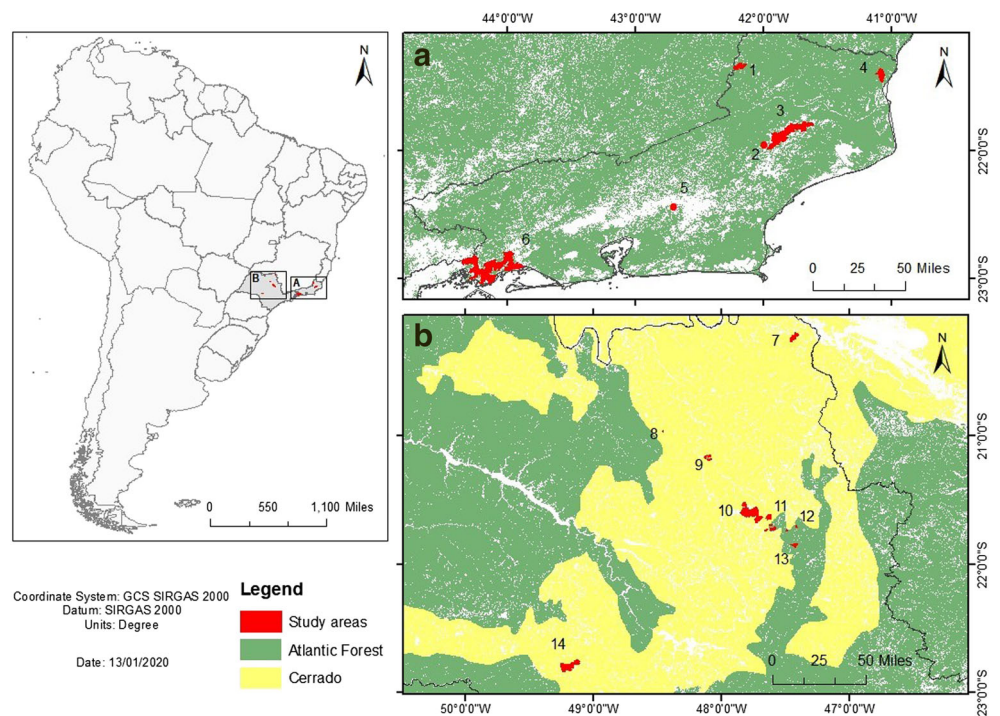
mistaken for limitation of food supply (Creel and Christianson 2008). For example, activity during suboptimal times of higher predation risk, increased energy demand, or lower prey availability may incur fitness costs. Some carnivores show an altered activity pattern in the presence of other carnivores to avoid intraguild predation (Palomares and Caro 1999), and experimental studies have revealed altered vigilance and foraging patterns when dogs are detected by mesocarnivores (Vanak et al. 2009). For instance, *Galidia elegans* and *Eupleres goudotii*, endemic carnivores from Madagascar, shifted from preferred activity periods in the presence of dogs (Gerber et al. 2012; Farris et al. 2015), and spectacled bear (*Tremarctos ornatus*) altered activity patterns where feral dogs were present (Zapata-Ríos and Branch 2016).

Camera-trap data offer an opportunity to identify the potential for altered species interactions, such as altered activity patterns and partitioning along the temporal niche axis. Recognizing these interactions not only is valuable from an ecological perspective but also provides insight into human-driven changes in species behaviors and habitat use and the resulting impacts on niche partitioning and community structure (Frey et al. 2017). Here we investigate the behavior of native carnivores in the presence of invasive competitors by (1) documenting the activity patterns of free-ranging dogs inside and outside protected areas in Cerrado and Atlantic Rainforest biomes, (2) evaluating if temporal segregation occurs between free-ranging dogs and carnivore species in each studied area and if there is a difference in native carnivore activity patterns in areas with and without dogs, and (3) assessing if puma occurrence results in alterations in the activity patterns of free-ranging dogs. Based on assumptions that mesocarnivores perceive dogs as members of the carnivore community that represent a direct or indirect risk and that dogs perceive puma as a direct risk, we hypothesize that (1) native carnivore activity patterns will differ as a function of dog presence and (2) dogs will alter their activity patterns as a function of puma presence.

Material and methods

Study area Field surveys were carried out in forested areas in the south and northeast regions of the state of São Paulo and throughout the state of Rio de Janeiro, Brazil, where the landscapes of native vegetation have become fragmented (Kronka et al. 2005). We sampled eight protected areas in São Paulo State and seven in Rio de Janeiro State (including one site examined across multiple years); for some of these, we also sampled adjacent, non-protected areas. Additionally, six regions without protected areas were sampled (Fig. 1; see [Supplementary Material](#)). Due to intense land exploitation, the broader landscapes were composed of an heterogeneous

Fig. 1 Areas sampled with camera traps from July 2011 to December 2017 in the states of Rio de Janeiro (right top) and São Paulo (bottom right), Brazil



anthropogenic matrix dominated by sugarcane plantations and other crops (e.g., *Pinus*, *Eucalyptus*, and *Coffea*), in addition to pastures, water bodies, and developed or urban areas (Shida and Pivello 2002; Mendes et al. 2009; Melo and Durigan 2011). Commonly detected native carnivore species of these surveyed landscapes include tayra (*Eira barbara*), ocelot (*Leopardus pardalis*), jaguarundi (*Herpailurus yagouaroundi*), puma, coati (*Nasua nasua*), crab-eating raccoon (*Procyon cancrivorus*), crab-eating fox (*Cerdocyon thous*), and maned wolf (*Chrysocyon brachyurus*).

Data collection and analysis From July 2011 to December 2017, we used camera traps (Bushnell® Trophy Cam 6.0 Mpxl and Scoutguard® SG 550) to record the occurrence of mammals in protected and unprotected areas in São Paulo State and Rio de Janeiro State. Sampling design differed between São Paulo and Rio de Janeiro areas (see [Supplementary Material](#)—areas description and sampling design). In brief, in São Paulo State, an unbaited camera trap was placed at each intersection of 1 km² quadrats of a grid in each site. In Rio de Janeiro, camera traps were baited (bacon and bobcat, *Lynx rufus*, urine) on the setting day and distributed across the landscape (forest fragments and altered matrix) with a 500-m minimum linear distance between cameras.

Cameras were affixed to tree trunks approximately 30–40 cm above ground and programmed for continuous operation (24 h/day), capturing three photos every 10 s when triggered. Across the areas, the number of camera traps and the total time they remained active varied (Table 1). In São Paulo, cameras were continuously operating during the

sampling period and inspections were carried out every 15–20 days. In Rio de Janeiro, traps remained uninspected in the field for a month in the dry season and a month in the wet season and others regions without protected areas were sampled with 186 dog records. Cameras recorded the date and time of each image, and pictures taken ≥ 60 min apart by the same camera were considered independent records. We used the non-parametric kernel density estimation procedure (Ridout and Linkie 2009; Meredith and Ridout 2017) to estimate the overlap of activity time between dogs and carnivore species in different areas. We compared the coefficient of overlap between dogs and native carnivore species in areas with sufficient sample sizes (≥ 6 pictures of each species) to investigate the extent of overlap with dogs.

We compared dog activities inside and outside protected areas, subdividing the analyses by biome (Cerrado and Atlantic Forest). We calculated the relative abundance index (RAI) of dogs in all areas by dividing the number of dog pictures by the sample effort. We compared whether frequently recorded carnivores (tayra, ocelot, coati, and maned wolf) altered their temporal activities in areas with high dog activity (≥ 0.2 RAI) and low dog activity (≤ 0.1 RAI). We also compared dog activity in areas with and without recorded puma activity. We first converted all times to radians and used kernel density estimation to generate a probability density distribution of each species' activity pattern in areas with and without dogs (Ridout and Linkie 2009). Next, we calculated the overlap coefficient (Δ), a value ranging from 0 to 1, which is defined as the area under the curve formed by taking the smaller of two density functions at each time point (Ridout

Table 1 Protected areas sampled in São Paulo (Cerrado) and Rio de Janeiro (Atlantic Forest) States from July 2011 to December 2017

Locale	ID	State, biome	Area (ha)	Number of camera traps	Naïve occupancy (%)	Camera trap-nights	Dog RAI	Sampling period
Furnas 2011	7	Cerrado	2069	29	6.9	1189	0.2	07/2011 to 12/2011
Furnas 2013	7	Cerrado	2069	15	20.0	1385	0.4	07/2013 to 11/2013
Furnas 2017*	7	Cerrado	2069	60	46.6	4770	1.8	01/2017 to 08/2017
Santa Rita	12	Cerrado	96	5	60.0	390	3.6	03/2016 to 06/2016
Santa Bárbara	14	Cerrado	2712	70	42.8	4210	1.6	01/2013 to 06/2015
Augusto Ruschi	9	Cerrado	720	15	13.3	562	0.5	10/2012 to 05/2013
Jataí	10	Cerrado	10,735	44	2.3	2798	0.04	01/2014 to 01/2015
Bebedouro	8	Cerrado	99	4	50.0	183	2.2	10/2014 to 12/2014
Vassununga	11	Cerrado	2071	25	0	1538	0	01/2015 to 04/2016
Porto Ferreira	13	Cerrado	611	9	0	608	0	07/2015 to 10/2015
PE do Cunhambebe*	6	Atlantic Rainforest	38,053	19	31.6	471	1.7	08/2015 to 09/2015 and 02/2016 to 03/2016
RPPN REGUA*	5	Atlantic Rainforest	368	20	40.0	459	7.4	07/2017 to 08/2017 and 11/2017 to 12/2017
PE do Desengano*	3	Atlantic Rainforest	22,400	18	44.4	576	1.9	02/2014 to 03/2014 and 07/2014 to 08/2014
RPPN Verbicaro*	2	Atlantic Rainforest	48	2	100	70	10.0	02/2014 to 03/2014 and 07/2014 to 08/2014
Refúgio da Vida Silvestre Municipal Ventania*	1	Atlantic Rainforest	2176	19	52.6	698	8.3	10/2013 to 11/2013 and 05/2014 to 07/2014
Estação Ecológica Estadual de Guaxindiba*	4	Atlantic Rainforest	3260	20	50.0	617	10.7	04/2014 to 05/2014 and 09/2014 to 10/2014

Locale protected area sampled, *ID* number identification in Fig. 1, *naïve occupancy* the proportion of cameras with dog detections, *camera trap-nights* number of cameras \times number days, *dog RAI* relative abundance index of the dog (number of pictures by sample effort)

*Protected areas and their adjacent unprotected natural areas sampled

and Linkie 2009). If species did not change their temporal activity patterns in the presence of dogs, we expected a higher Δ ; the same applies to activity of dogs in the presence of pumas. As recommended by Ridout and Linkie (2009), we used the estimator $\hat{\Delta}_1$, which performs best when the smaller sample size (number of pictures) is < 50 , and $\hat{\Delta}_4$, which performs better when the sample size is > 75 . For those areas with sample sizes of > 50 and < 75 pictures, we used the estimator $\hat{\Delta}_1$. Finally, we obtained 95% confidence intervals for these estimates from 1000 bootstrap samples. All statistics were analyzed using the Overlap package (Meredith and Ridout 2017) in R (R Development Core Team, 2013).

To test whether the time lag after a dog record in a camera trap differed among native carnivore species, we calculated how long (in hours) a species of native carnivore took to be recorded after a previous dog record on a given camera trap. The same approach was repeated to investigate whether dogs tended to avoid places with puma records on cameras, by comparing it with the time other carnivores took to be recorded on a camera trap after a puma. In addition, we compared those values (that is, the time lag for dogs after a puma record and the time lag for native carnivores after dogs) with the time

native carnivore species took to be recorded after another species of native carnivore was recorded by a camera trap. All tests used one-way ANOVA after normalizing the data using Box-Cox and a post hoc Tukey test in R software.

Results

Surveys resulted in a total of 20,524 trap nights and 2189 photographic captures of carnivores (1542 records of 16 native carnivore species and 551 captures of free-ranging dogs). Dogs were detected in 11 of the 14 protected areas investigated. In the largest protected area in São Paulo State (10,735 ha), we recorded only one picture of a dog while in the smallest one (96 ha) we recorded 14 pictures. All protected areas in Rio de Janeiro State had dogs. Free-ranging dogs were essentially diurnal in all areas, with diurnal captures of dogs in the various protected areas ranging from 74 to 100% of total dog capture events. Virtually all ($> 99\%$ of captures) dogs were not accompanied by people. In São Paulo, we detected dogs accompanying people in two areas at least three times; in Rio de Janeiro, we detected six events of dogs with people in three

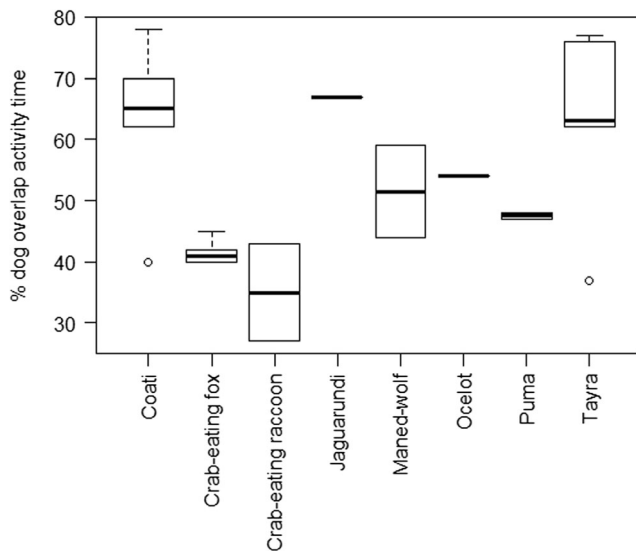


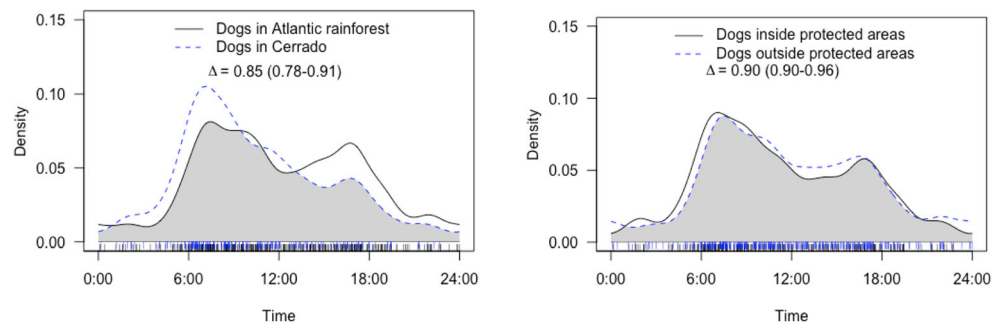
Fig. 2 Coefficient of overlap in activity patterns between dogs and native carnivores in two protected areas in São Paulo State and six in Rio de Janeiro State from July 2011 to December 2017. Intraspecific variance in overlap is a function of the number of sites examined and differences in the extent of overlap between sites

different areas. Dogs with collars were recorded 61 times (11% of all records).

Eight protected areas (two in São Paulo and six in Rio de Janeiro) had sufficient records of dogs and a subset of native carnivores to allow within-site comparisons of their activity. The highest recorded dog overlap was with jaguarundi (mean percent of overlap = 67%; $n = 1$ protected area), coati (65%; $n = 6$), and tayra (63%; $n = 5$) (Fig. 2). The lowest overlap was with the nocturnal/crepuscular carnivores, including crab-eating raccoon (35%; $n = 2$), crab-eating fox (41%; $n = 6$), puma (47%; $n = 2$), maned wolf (51%; $n = 2$), and ocelot (54%; $n = 1$) (Fig. 2).

Activity patterns of dogs were similar between biomes (Cerrado and Atlantic Forest; $\hat{\Delta}_4 = 0.85$; 95% CI = 0.78–0.91) (Fig. 3). In addition, dog activities inside protected areas (one in São Paulo State and six in Rio de Janeiro State; Table 1) and outside protected areas were similar ($\hat{\Delta}_4 = 0.90$; 95% CI = 0.90–0.96) (Fig. 3).

Fig. 3 Overlap between activity patterns of dogs in areas (left) in Cerrado and Atlantic Rainforest biomes in 14 protected areas in São Paulo and Rio de Janeiro States and in areas (right) within and outside protected areas



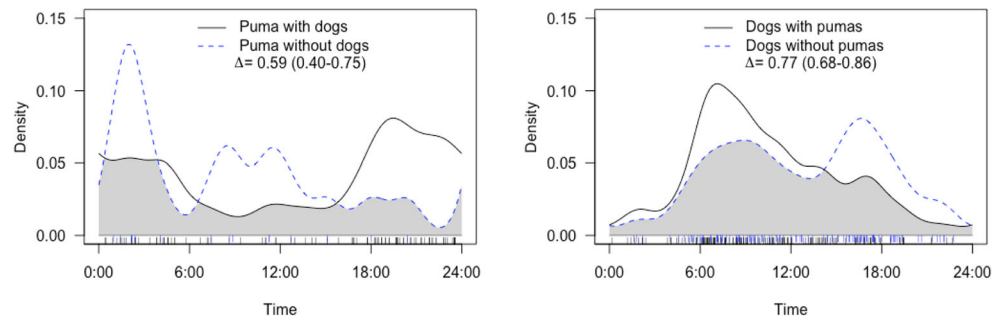
Dogs visiting areas inhabited by puma focused their activity on the morning hours and thereafter showed a decline in their activity. In contrast, dogs in areas that lacked puma records presented two peaks of activity (morning and evening); otherwise, their activity in areas with or without pumas highly overlapped ($\hat{\Delta}_4 = 0.77$; 95% CI = 0.68–0.86) (Fig. 4). Similarly, the activities of pumas in areas without dogs concentrated after 18 h and throughout the evening hours, whereas in areas with dogs, puma were particularly active in the late evening hours until around 6 h, after which there was a period of inactivity before animals became active again throughout much of the day ($\hat{\Delta}_4 = 0.59$; 95% CI = 0.40–0.76). Nevertheless, the lag in time for dogs recorded after detection of pumas ($\bar{x} = 95$ h, 9–581) was similar to that of wild carnivore species recorded after pumas ($\bar{x} = 105$ h, 5–1590, $p = 0.96$) and also similar to that of dogs after any carnivore species ($\bar{x} = 53$ h, 0.5–703, $p = 0.64$) ($F_{4,442} = 7.065$, $p = 0.16$) (Fig. 5).

The activities of some carnivore species in areas with dogs were very similar to that of areas without dogs, and for almost all species evaluated, the intraspecific overlap was approx. $\geq 70\%$ (Fig. 6). The activity patterns of tayra in areas with and without dog were comparable ($\hat{\Delta}_1 = 0.82$; 95% CI = 0.83–0.96). Ocelots ($\hat{\Delta}_1 = 0.75$; 95% CI = 0.67–0.89), maned wolves ($\hat{\Delta}_1 = 0.68$; 95% CI = 0.57–0.87), coatis ($\hat{\Delta}_1 = 0.66$; 95% CI = 0.46–0.87), and jaguarundis ($\hat{\Delta}_1 = 0.57$; 95% CI = 0.26–0.82) also do not seem to differ in activity patterns as a function of dog co-occurrence on the landscape (Fig. 6). Further, the time passed until detection after dog records on camera traps did not differ between native carnivores (Fig. 7, $F_{6,134} = 1.731$, $p = 0.118$) and the mean time lag following dog capture records ($\bar{x} = 79$ h, 0.88–1319) was less than half the lag that occurred after capture of any native carnivore species ($\bar{x} = 161$ h, 0.16–1276, $p = 0.0178$) (Fig. 5).

Discussion

Free-ranging dogs were widely distributed in most of the areas investigated. Dog occurrence in Brazilian protected

Fig. 4 Overlap between activity patterns of dogs in areas with and without pumas and activity of pumas in areas with and without dogs in 14 protected areas in São Paulo and Rio de Janeiro States based on data collected by camera traps from July 2011 to December 2017



areas is not unusual; dogs were, for instance, the most frequently detected species in six protected areas in Minas Gerais State (Paschoal et al. 2016), and the presence of human residents and hunters in protected areas were the factors most often considered to promote dog occurrence (Lessa et al. 2016). In our study, the protected areas investigated did not have human residents, although surrounding landscapes had variable levels of development. Illegal poaching in the majority of the areas is common and can be an important reason for the presence of dogs. Thus, the spatial scope and scale of adjacent settlements may be more important than the size of a protected area in determining the extent of dog visitation. For example, both Furnas State Park and Santa Bárbara Ecological Station are protected areas with restricted human access. Nonetheless, they showed the largest number of free-ranging dogs, which was likely a function of the proximity of nearby cities and large numbers of nearby country homes and farmsteads. In contrast, Jataí is the largest protected area (10,735 ha) in São Paulo and is near the city of Luiz Antônio, but its boundaries are surrounded by large

commercial sugarcane or eucalyptus plantations, buffering the area from human homes and therefore possibly underpinning the low frequency of dogs in the area.

In general, dogs were diurnal, a pattern that has been reported elsewhere in Brazil (Srbek-Araújo and Chiarello 2007; Silva et al. 2018) and in other countries such as Madagascar (Farris et al. 2015) and Chile (Sepúlveda et al. 2015). Although free-ranging dogs can be active across a wide range of times, their diurnal activity may be strongly influenced by human activities and provisioning, as the activity time of owned free-ranging dogs has been described as more diurnal (Gerber et al. 2012; Farris et al. 2015; Silva et al. 2018), while feral dogs are generally more nocturnal (Zapata-Ríos and Branch 2016). The ownership status of dogs that are accessing protected areas in São Paulo and Rio de Janeiro is uncertain. Nevertheless, like most free-ranging dog populations (Vanak and Gompfer 2009a, 2009b; Ritchie et al. 2014), they probably depend greatly on localized human resources such as food directly or indirectly provided by households to meet nutritional requirements. These food sources are likely more available during the day. Such links to human activities may explain more diurnal activities in a variety of commensal species. For instance, unowned cats tend to be more nocturnal than owned cats, and the care a cat owner provides may influence the impact a cat has on its environment (Horn et al. 2011). Indeed, the more food an owned dog or cat receives, the less likely it is to prey on wild vertebrates, perhaps because it is less driven by hunger (Kays and DeWan 2004; Silva-Rodríguez and Sieving 2011). In this way, hunger may be seen as a potentiator of a predatory tendency (Adamec 1976), although domestic cats (owned and feral), and probably dogs, may hunt even when their hunger is satiated (Jessup 2004; Baker et al. 2005). Presumably, as a consequence, fewer of these animals invade protected areas. In contrast, where dogs depend less on human resources, they are more nocturnal and might be more affected by their prey activities (Zapata-Ríos and Branch 2016). The observation that the vast majority of photographs of dogs occurred during the day further suggests that these dog populations are principally relying on human-derived resources, although the extent of this resource subsidy is uncertain.

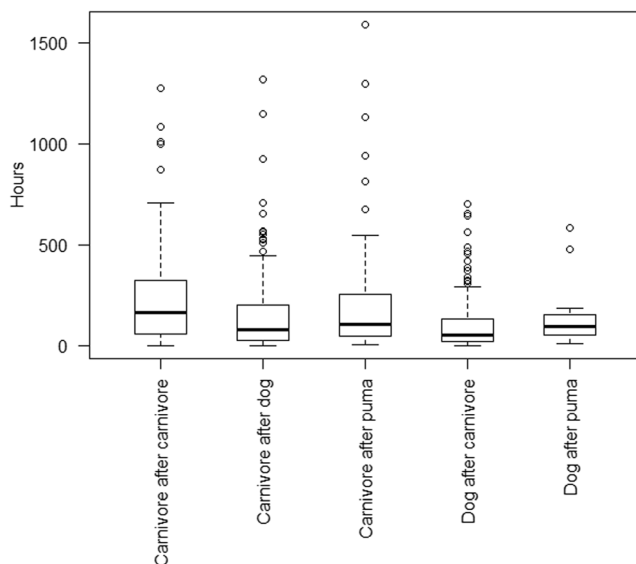


Fig. 5 Hours passed after each carnivore record obtained on camera trap from July 2011 to December 2017 in 14 protected areas in São Paulo and Rio de Janeiro States

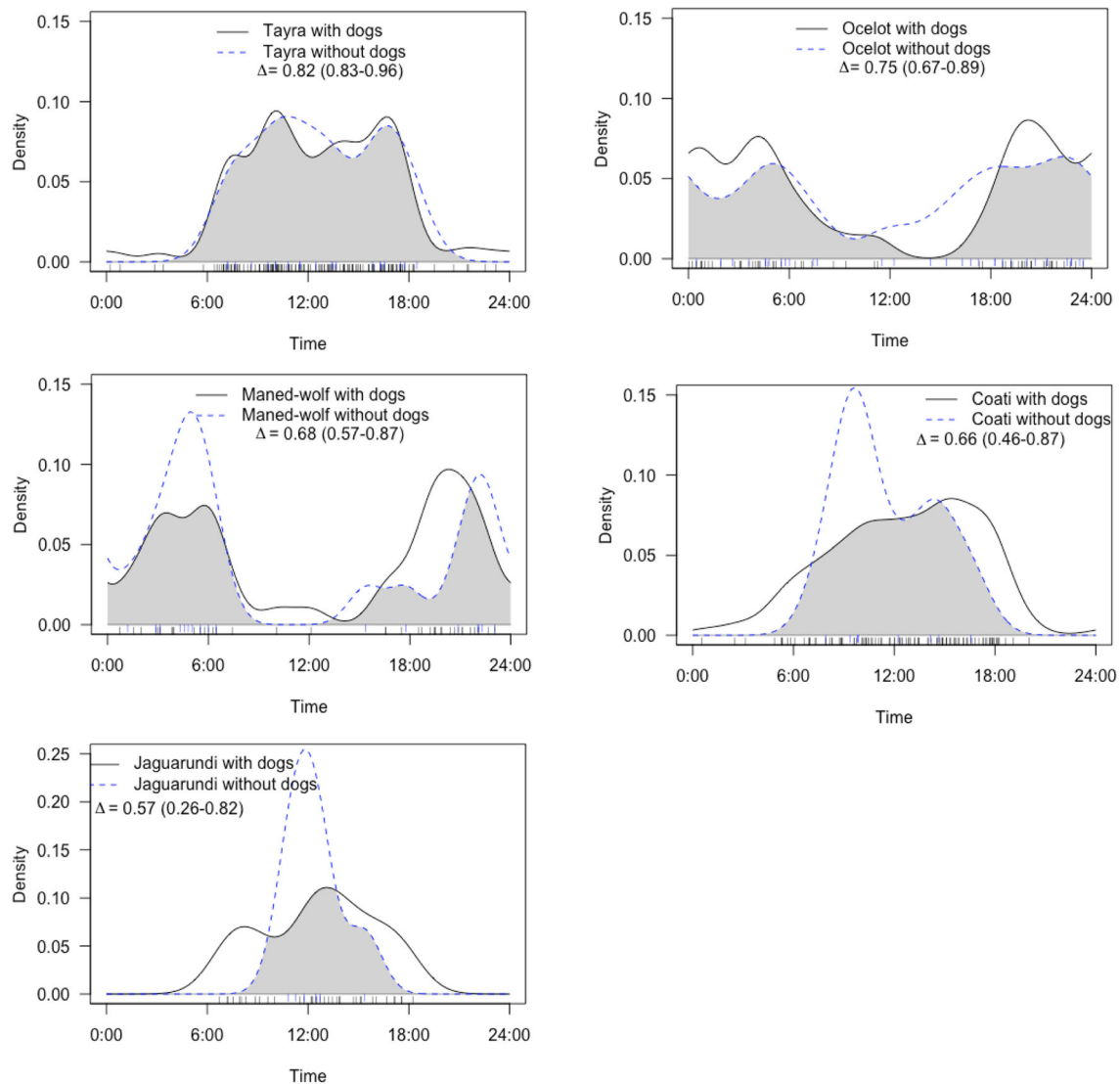


Fig. 6 Activity density overlap of carnivores in areas with ($n = 11$) and without ($n = 3$) dogs in protected areas in São Paulo and Rio de Janeiro based on data collected using camera traps from July 2011 to December 2017

Dogs are a primary mammalian predator in some areas, and as such, they might have an important impact on other carnivores through interference competition (Vanak and Gompper 2009b; Vanak et al. 2014). Yet despite the fact that some carnivores change their activity in response to dogs (Gerber et al. 2012; Farris et al. 2015; Zapata-Ríos and Branch 2016), we did not detect differences in the activity patterns that were attributable to the presence of dogs. Both tayras and coatis are primarily diurnal (Gómez et al. 2005; Blake et al. 2012; Bianchi et al. 2016), and these species did not differ in activity in locations with and without dogs. The lower overlap between jaguarundi in areas with and without dogs seems more an artifact of the small sample size ($n = 6$ pictures in areas without dogs). In fact, these species showed activity patterns similar to that observed in more pristine areas or in areas with very low dog activity, such as in the Pantanal (Bianchi et al. 2016). A similar result was observed for ocelots and maned

wolves; these species showed similar activity patterns in areas with and without dogs, and these were similar to those observed in other areas of their distribution (Bianchi et al. 2016; Castelló 2018). Since interference competition and intraguild killing should be more intense between members of the same family (Donadio and Buskirk 2006), we would expect native canids to show stronger responses to dogs than to other carnivores; however, our understanding of how South American canids (and other Carnivora) interact with domestic dogs is poorly developed. While dogs are known to attack maned wolves (Lacerda et al. 2009), and kill or harass native species such as chilla foxes (*Lycalopex griseus*) (Silva-Rodríguez and Sieving 2012), other studies have not shown evidence of negative effects of dogs upon native canids (e.g., Espartosa 2009).

We also could expect that smaller species (e.g., coati and tayra) should be more affected by dogs, as intraguild predation is expected to occur between species with larger differences in

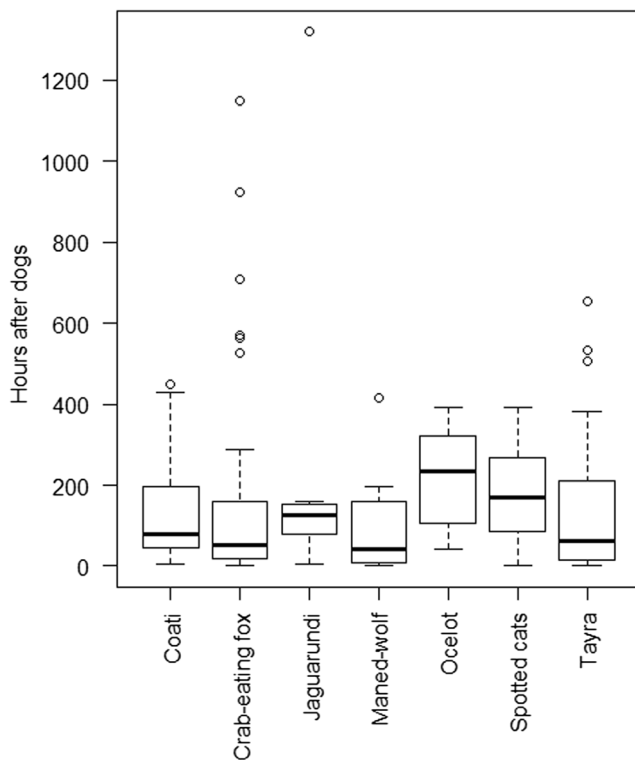


Fig. 7 Hours passed until native carnivore species detection after dog records in camera traps for 14 protected areas in São Paulo and Rio de Janeiro States sampled from July 2011 to December 2017. Spotted cats = *Leopardus guttulus* and *Leopardus wiedii*

size (Palomares and Caro 1999). Two non-exclusive hypotheses might explain the apparent lack of response, as measured by activity patterns, to dogs by native carnivores. First, the absence of altered activity in the presence of dogs might result from an internal control (Hut et al. 2012; Kronfeld-Schor et al. 2017) or morphological limitation such as relatively poor vision in tayras (Defler 1980; Presley 2000) that limits the animal's activity to particular periods. Second, neotropical carnivores might simply perceive dogs as a low-risk predator or competitor whose presence is of insufficient importance to trigger a dramatic change in temporal activity patterns. Given that the majority of native carnivores in our study are able to use trees as a way to escape perceived danger and some species use trees to forage, rest, or nest (Bianchi et al. 2016; Olifiers et al. 2009), there may be limited apparent risk effects (Creel and Christianson 2008) within the carnivore community due to dog presence. Nonetheless, it is important to recognize that perceived risk and true risk are not equivalent. If the true risk is greater than the perceived risk, a lack of altered activity in the presence of dogs might result in (1) higher chance of agonistic encounters and, as a consequence, higher chances of intraguild predation or pathogen transmission and (2) less time spent in vigilance with potential negative impacts on fitness. Such consequences can negatively impact carnivore populations but are difficult to record and quantify.

Intraguild predation can be an important force shaping natural communities. Species can respond to this pressure by changing their pattern of activities to avoid agonistic encounters (Vanak and Gompfer 2009b; Kennedy et al. 2012; Kays et al. 2015; Ramesh et al. 2017). While much of the thinking regarding dog-carnivore interactions focuses on how dogs negatively influence other carnivores, it is important to recognize that larger predators may also influence dog activity or, where dog presence influences larger carnivore activity, that change may be a function of larger carnivores hunting dogs (Butler et al. 2014). Although we can expect some modifications on dog activity in the presence of pumas because pumas can prey upon dogs (Torres et al. 1996; Mazzolli 2009), at the scale of this study, a response of dogs to the presence of pumas was not detected. Such a finding may occur because rates of dog-puma interactions are insufficient to result in altered dog behavior or because dogs are naïve prey with respect to puma-associated risks (Berger et al. 2001).

Acknowledgments We are grateful to the trainees and Furnas do Bom Jesus State Park workers for their assistance with fieldwork. We are also grateful to São Paulo State University (Campus Jaboticabal) for logistic support and Coordination for the Improvement of Higher Education Personnel and National Council for Scientific and Technological Development for graduate scholarships.

Funding information This study was funded by São Paulo Research Foundation (Proc. n°. 2013/18526-9; Internships Abroad scholarship Proc. n°. 2018/07886-6; undergraduate student scholarships Proc. n°. 2017/06060-6, 2017/03501-1, 2018/15793-0) and Rio de Janeiro Research Foundation (Proc. n°. E26/112.115/2013; Programa Jovens Talentos Processo Proc. n°. 23,038.009833/2012-56).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

References

- Adamec RE (1976) The interaction of hunger and preying in the domestic cat (*Felis catus*): an adaptive hierarchy? *Behav Biol* 18:263–272. [https://doi.org/10.1016/S0091-6773\(76\)92166-0](https://doi.org/10.1016/S0091-6773(76)92166-0)
- Baker PJ, Bentley AJ, Ansell RJ, Harris S (2005) Impact of predation by domestic cats *Felis catus* in an urban area. *Mammal Rev* 35:302–312. <https://doi.org/10.1111/j.1365-2907.2005.00071.x>
- Berger J, Swenson JE, Persson IL (2001) Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. *Science* 291:1036–1039. <https://doi.org/10.1126/science.1056466>
- Bianchi RDC, Olifiers N, Gompfer ME, Mourão G (2016) Niche partitioning among mesocarnivores in a Brazilian wetland. *PLoS One* 11:e0162893. <https://doi.org/10.1371/journal.pone.0162893>
- Blake JG, Mosquera D, Loiselle BA et al (2012) Temporal activity patterns of terrestrial mammals in lowland rainforest of Eastern Ecuador. *Ecotropica* 18:137–146

- Braczkowski AR, O'Bryan CJ, Stringer MJ et al (2018) Leopards provide public health benefits in Mumbai, India. *Front Ecol Environ* 16: 176–182. <https://doi.org/10.1002/fee.1776>
- Butler JRA, Linnell JDC, Marrant D et al (2014) Dog eat dog, cat eat dog: social-ecological dimensions of dog predation by wild carnivores. In: Gompper ME (ed) *Free-ranging dogs and wildlife conservation*. Oxford University Press, pp 55–65
- Campos CB, Esteves CF, Ferraz KMPMB et al (2007) Diet of free-ranging cats and dogs in a suburban and rural environment, south-eastern Brazil. *J Zool* 273:14–20. <https://doi.org/10.1111/j.1469-7998.2007.00291.x>
- Castelló JR (2018) *Canids of the world. Wolves, wild dogs, foxes, jackals, coyotes, and their relatives*. Princeton University Press, Princeton, p 332
- Clutton-Brock J (2017) Origins of the dog: the archaeological evidence. In: Serpell J (ed) *The domestic dog: its evolution, behavior and interactions with people*, 2nd edn. Cambridge University Press, Cambridge, pp 15–29
- Creel S (2001) Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conserv Biol* 15:271–274. <https://doi.org/10.1046/j.1523-1739.2001.99534.x>
- Creel S, Christianson D (2008) Relationships between direct predation and risk effects. *Trends Ecol Evol* 23:194–201. <https://doi.org/10.1016/j.tree.2007.12.004>
- Creel S, Winnie J, Maxwell B, et al (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387–3397. <https://doi.org/10.1890/05-0032>
- Defler TR (1980) Notes on interactions between the tayra (*Eira barbara*) and the white-fronted capuchin. *J Mammal* 61:156
- Doherty TS, Dickman CR, Glen AS et al (2017) The global impacts of domestic dogs on threatened vertebrates. *Biol Conserv* 210:56–59. <https://doi.org/10.1016/j.biocon.2017.04.007>
- Donadio, Buskirk (2006) Diet, morphology, and interspecific killing in Carnivora. *Am Nat* 167(4):526–536. <https://doi.org/10.2307/3844707>
- Dröge E, Creel S, Becker MS, M'soka J (2017) Spatial and temporal avoidance of risk within a large carnivore guild. *Ecol Evol* 7:189–199. <https://doi.org/10.1002/ece3.2616>
- Espartosa KD (2009) Mamíferos terrestres de maior porte e a invasão de cães domésticos em remanescentes de uma paisagem fragmentada de Mata Atlântica: avaliação da eficiência de métodos de amostragem e da importância de múltiplos fatores sobre a distribuição das espécies. Universidade de São Paulo
- Farris ZJ, Gerber BD, Karpanty S et al (2015) When carnivores roam: temporal patterns and overlap among Madagascar's native and exotic carnivores. *J Zool* 296:45–57. <https://doi.org/10.1111/jzo.12216>
- Frey S, Fisher JT, Burton AC, Volpe JP (2017) Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sens Ecol Conserv* 3: 123–132. <https://doi.org/10.1002/rse2.60>
- Gallagher AJ, Creel S, Wilson RP, Cooke SJ (2017) Energy Landscapes and the Landscape of Fear. *Trends Ecol Evol* 32:88–96. <https://doi.org/10.1016/j.tree.2016.10.010>
- Gerber BD, Karpanty SM, Randrianantenaina J (2012) Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. *J Mammal* 93:667–676. <https://doi.org/10.1644/11-MAMM-A-265.1>
- Gómez H, Wallace RB, Ayala G et al (2005) Dry season activity periods of some Amazonian mammals. *Stud Neotrop Fauna Environ* 40:91–95. <https://doi.org/10.1080/01650520500129638>
- Gompper, ME (2014a) The dog-human-wildlife interface: Assessing the scope of the problem. In: Gompper ME (ed) *Free-ranging dogs and wildlife conservation*. Oxford University Press, Oxford, pp 9–54
- Gompper ME (2014b) Introduction: outlining the ecological influences of a subsidized, domesticated predator. In: Gompper ME (ed) *Free-ranging dogs and wildlife conservation*. Oxford University Press, Oxford, pp 1–8
- Horn JA, Mateus-Pinilla N, Warner RE, Heske EJ (2011) Home range, habitat use, and activity patterns of free-roaming domestic cats. *J Wildl Manag* 75:1177–1185. <https://doi.org/10.1002/jwmg.145>
- Hughes J, Macdonald DW (2013) A review of the interactions between free-roaming domestic dogs and wildlife. *Biol Conserv* 157:341–351. <https://doi.org/10.1016/j.biocon.2012.07.005>
- Hughes J, MacDonald DW, Boitani L (2017) Roaming free in the rural idyll: dogs and their connections with wildlife. In: Serpell J (ed) *The domestic dog: its evolution, behavior and interactions with people*, 2nd edn. Cambridge University Press, Cambridge, pp 377–392
- Hut RA, Kronfeld-Schor N, van der Vinne V, De la Iglesia H (2012) In search of a temporal niche: Environmental factors. *Prog Brain Res* 199:281–304. <https://doi.org/10.1016/B978-0-444-59427-3.00017-4>
- Jessup DA (2004) The welfare of feral cats and wildlife. *J Am Vet Med Assoc* 225(9):1377–1383
- Johnson N, Mansfield KL, Marston DA, Wilson C, Goddard T, Selden D, Hemson G, Edea L, van Kesteren F, Shiferaw F, Stewart AE, Sillero-Zubiri C, Fooks AR (2010) A new outbreak of rabies in rare Ethiopian wolves (*Canis simensis*). *Arch Virol* 155:1175–1177. <https://doi.org/10.1007/s00705-010-0689-x>
- Kays RW, DeWan AA (2004) Ecological impact of inside/outside house cats around a suburban nature preserve. *Anim Conserv* 7:273–283. <https://doi.org/10.1017/S1367943004001489>
- Kays R, Costello R, Forrester T et al (2015) Cats are rare where coyotes roam. *J Mammal* 96:981–987. <https://doi.org/10.1093/jmammal/gyv100>
- Kennedy M, Phillips BL, Legge S et al (2012) Do dingoes suppress the activity of feral cats in northern Australia? *Austral Ecol* 37:134–139. <https://doi.org/10.1111/j.1442-9993.2011.02256.x>
- Kronfeld-Schor N, Visser ME, Salis L, van Gils JA (2017) Chronobiology of interspecific interactions in a changing world. *Philos Trans R Soc B Biol Sci* 372:201660248. <https://doi.org/10.1098/rstb.2016.0248>
- Kronka FJN, Nalon MA, Matsukuma CK et al (2005) Inventário florestal da vegetação natural do Estado de São Paulo. Secretaria do Meio Ambiente, Instituto Florestal, Imprensa Oficial, São Paulo
- Lacerda ACR, Tomas WM, Marinho-Filho J (2009) Domestic dogs as an edge effect in the Brasília National Park, Brazil: interactions with native mammals. *Anim Conserv* 12:477–487. <https://doi.org/10.1111/j.1469-1795.2009.00277.x>
- Lessa I, Corrêa Seabra Guimarães T, de Godoy Bergallo H et al (2016) Domestic dogs in protected areas: a threat to Brazilian mammals? *Nat Conserv* 14:46–56. <https://doi.org/10.1016/j.ncon.2016.05.001>
- Mazzolli M (2009) Mountain lion *Puma concolor* attacks on a maned wolf *Chrysocyon brachyurus* and a domestic dog in a forestry system. *Mastozoología Neotrop* 16:465–470
- Melo ACG, Durigan G (2011) Plano de manejo da Estação Ecológica de Santa Bárbara. Instituto Florestal/Secretaria do Meio Ambiente, São Paulo
- Mendes AF, Mendes AF, Igari AT et al (2009) Plano de manejo do Parque Estadual de Vassununga. Governo do Estado de São Paulo, Secretaria do Meio Ambiente, Instituto Florestal, Fundação Florestal, São Paulo
- Meredith M, Ridout M (2017) Overview of the overlap package. *R Proj* 1–9. <https://doi.org/10.1016/j.contraception.2006.09.005>
- Olifiers N, Bianchi RDC, Mourão GDM, Gompper ME (2009) Construction of arboreal nests by brown-nosed coatis, *Nasua nasua* (Carnivora: Procyonidae) in the Brazilian Pantanal. *Zoologia* 26: 571–574. <https://doi.org/10.1590/S1984-46702009000300023>
- Palomares, Caro (1999) Interspecific killing among mammalian carnivores. *Am Nat* 153:492–508. <https://doi.org/10.2307/2463664>
- Parsons AW, Bland C, Forrester T et al (2016) The ecological impact of humans and dogs on wildlife in protected areas in eastern North

- America. *Biol Conserv* 203:75–88. <https://doi.org/10.1016/j.biocon.2016.09.001>
- Paschoal AMO, Massara RL, Bailey LL et al (2016) Use of Atlantic Forest protected areas by free-ranging dogs: estimating abundance and persistence of use. *Ecosphere* 7:1–15. <https://doi.org/10.1002/ecs2.1480>
- Phillips RB, Wiedenfeld DA, Snell HL (2012) Current status of alien vertebrates in the Galápagos Islands: invasion history, distribution, and potential impacts. *Biol Invasions* 14:461–480. <https://doi.org/10.1007/s10530-011-0090-z>
- Presley SJ (2000) *Eira barbara*. *Mamm Species* 636:1–6. [https://doi.org/10.1644/1545-1410\(2000\)636<0001:eb>2.0.co;2](https://doi.org/10.1644/1545-1410(2000)636<0001:eb>2.0.co;2)
- Ramesh T, Kalle R, Downs CT (2017) Staying safe from top predators: patterns of co-occurrence and inter-predator interactions. *Behav Ecol Sociobiol* 71:1–14. <https://doi.org/10.1007/s00265-017-2271-y>
- Ridout MS, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. *J Agric Biol Environ Stat* 14:322–337. <https://doi.org/10.1198/jabes.2009.08038>
- Ritchie EG, Dickman CR, Letnic M, Vanak AT (2014) Dogs as a predators and trophic regulators. In: Gompper ME (ed) *Free-ranging dogs and wildlife conservation*. Oxford University Press, Oxford, pp 55–68
- Sepúlveda M, Pelican K, Cross P, Eguren A, Singer R (2015) Fine-scale movements of rural free-ranging dogs in conservation areas in the temperate rainforest of the coastal range of southern Chile. *Mamm Biol* 80:290–297. <https://doi.org/10.1016/j.mambio.2015.03.001>
- Serpell J (2017) From paragon to pariah: cross-cultural perspectives on attitudes to dogs. In: Serpell J (ed) *The domestic dog: its evolution, behavior and interactions with people*, 2nd ed. Cambridge University Press, Cambridge, pp 300–316
- Shida CN, Pivello VR (2002) Caracterização fisiográfica e de uso das terras da região de Luiz Antônio e Santa Rita do Passa Quatro, SP, com o uso de sensoriamento remoto e SIG. *Investig Geográficas, Bol Del Inst Geogr* 49:27–42
- Silva KVKA, Kenup CF, Kreischer C et al (2018) Who let the dogs out? Occurrence, population size and daily activity of domestic dogs in an urban Atlantic Forest reserve. *Perspect Ecol Conserv* 16:228–233. <https://doi.org/10.1016/j.pecon.2018.09.001>
- Silva-Rodríguez EA, Sieving KE (2011) Influence of care of domestic carnivores on their predation on vertebrates. *Conserv Biol* 25:808–815. <https://doi.org/10.1111/j.1523-1739.2011.01690.x>
- Silva-Rodríguez EA, Sieving KE (2012) Domestic dogs shape the landscape-scale distribution of a threatened forest ungulate. *Biol Conserv* 150:103–110. <https://doi.org/10.1016/j.biocon.2012.03.008>
- Srbek-Araujo AC, Chiarello AG (2007) Armadilhas fotográficas na amostragem de mamíferos: considerações metodológicas e comparação de equipamentos. *Rev Bras Zool* 24:647–656. <https://doi.org/10.1590/S0101-81752007000300016>
- Torres SG, Mansfield TM, Foley JE, Lupo T (1996) Mountain lion and human activity in California: testing speculations. *Wildl Soc Bull* 24:451–460
- Vanak AT, Gompper ME (2009a) Dietary niche separation between sympatric free-ranging domestic dogs and Indian foxes in Central India. *J Mammal* 90:1058–1065. <https://doi.org/10.1644/09-MAMM-A-107.1>
- Vanak AT, Gompper MEME (2009b) Dogs *Canis familiaris* as carnivores: their role and function in intraguild competition. *Mammal Rev* 39:265–283. <https://doi.org/10.1111/j.1365-2907.2009.00148.x>
- Vanak AT, Gompper ME (2010) Interference competition at the landscape level the effect of free-ranging dogs on a native mesocarnivore. *J Appl Ecol* 47:1225–1232. <https://doi.org/10.1111/j.1365-2664.2010.01870.x>
- Vanak AT, Thaker M, Gompper ME (2009) Experimental examination of behavioural interactions between free-ranging wild and domestic canids. *Behav Ecol Sociobiol* 64:279–287. <https://doi.org/10.1007/s00265-009-0845-z>
- Vanak AT, Dickman CR, Silva-Rodríguez EA et al (2014) Top-dogs and under-dogs: competition between dogs and sympatric carnivores. In: Gompper ME (ed) *Free-ranging dogs and wildlife conservation*. Oxford University Press, Oxford, pp 69–93
- Weston MA, Fitzsimons JA, Wescott G, Miller KK, Ekanayake KB, Schneider T (2014) Bark in the park: a review of domestic dogs in parks. *Environ Manag* 54:373–382. <https://doi.org/10.1007/s00267-014-0311-1>
- Zapata-Ríos G, Branch LC (2016) Altered activity patterns and reduced abundance of native mammals in sites with feral dogs in the high Andes. *Biol Conserv* 193:9–16. <https://doi.org/10.1016/j.biocon.2015.10.016>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.