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Puma in check: How domestic dogs influence the behavior of a top predator

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ABSTRACT

Domestic dogs (*Canis familiaris*) occur widely in protected areas, yet their effects on native carnivores remain poorly quantified. We used camera traps and two-species occupancy models to investigate dog impacts on puma (*Puma concolor*) space use and activity patterns in Atlantic Forest protected areas of São Paulo, Brazil. Across 67 systematically positioned camera stations, we found that dogs were associated with changes in puma temporal behavior but not spatial occupancy. Pumas exhibited temporal avoidance of dog activity, taking approximately 74 h to return to camera sites after dog detections, compared to shorter intervals following other species. Natural vegetation positively influenced puma occupancy, but this effect was reduced when dogs were present. Dogs did not spatially exclude pumas, suggesting context-dependent behavioral responses rather than competitive displacement. These patterns are consistent with the hypothesis that pumas perceive dogs as a localized disturbance to avoid temporally rather than as territorial competitors. Given the potential for cascading effects on prey and mesopredator communities, our results emphasize the need for improved dog management in protected areas. Recommended actions include responsible pet ownership programs, spay/neuter initiatives, and enforcement of access restrictions. Effective implementation requires collaboration among protected area managers, local communities, and regional authorities to balance conservation goals with human livelihoods in Neotropical landscapes.

1. Introduction

Large carnivores play fundamental roles in shaping the structure and functioning of ecosystems worldwide (Hoeks et al., 2020; Wolf and Ripple, 2018). Occupying the highest trophic level, these species exert significant influence over ecological communities through trophic cascades (Ritchie et al., 2012; Ripple et al., 2014). Despite existing at naturally low densities, apex predators can generate ecological effects of remarkable magnitude, with huge documented impacts in prey abundance, plant biomass, and associated ecosystem processes (Hunter, 2018; Ripple et al., 2014; Borer et al., 2005). However, large carnivores face alarming population declines and severe contractions in their geographic ranges worldwide (Borrvall and Ebenman, 2006; Bleyhl et al., 2021; Hunter, 2018), driven by multiple synergistic threats largely associated with human activities (Bleyhl et al., 2021; Marshall and Quental, 2016). These threats affect large carnivores differently depending on species traits such as body size, home-range requirements, and tolerance to human presence (Ordiz et al., 2021; König et al., 2020). In many regions, habitat fragmentation forces large carnivores to move through human-dominated landscapes, increasing interactions with livestock and people and often leading to retaliatory persecution (Estes and Carswell, 2020; Ordiz et al., 2021).

This increasing overlap between large carnivores and human-dominated landscapes also intensifies interactions with free-ranging domestic dogs (*Canis familiaris*), which can assume dual and contrasting ecological roles. While dogs can represent an important prey source for some large carnivores in urban settings, as documented for leopards (*Panthera pardus*) in Mumbai, India, where predation on stray dogs provides food subsidies and generates significant public health benefits (Braczkowski et al., 2018), free-ranging dogs more commonly function as a major threat to native wildlife. Although many of these animals are pets, at least 60% are estimated to live freely, roaming without direct human supervision in both rural areas and protected regions (Gompper, 2014). Their remarkable abundance, estimated in one billion (Gompper, 2014), makes free-ranging dogs the most numerous terrestrial carnivore on the planet, often reaching population densities several orders of magnitude higher than those of native carnivores occupying similar ecological niches (Doherty et al., 2017; Zapata-Ríos, 2018). Dogs can

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directly affect wildlife through predation, competition, disease transmission, and hybridization with native carnivores (Young et al., 2011; Gompper, 2014; Doherty et al., 2017; Manzo et al., 2025), or indirectly through alterations in activity patterns, habitat use, and antipredator behavior (Vanak et al., 2009; Merson et al., 2019; Yen et al., 2019; Manzo et al., 2025), which can have cascading consequences on individual fitness and population dynamics (Mark Elbroch et al., 2010; Dobrovolski et al., 2013).

Interactions between sympatric carnivores are complex and often antagonistic, dominated by intraguild competition and intraguild predation (Palomares and Caro, 1999; Linnell and Strand, 2000; Prugh and Sivy, 2020). In these processes, dogs can act as aggressors, competitors, or prey depending on the species involved (Vanak and Gompper, 2010; Hughes and Macdonald, 2013; Butler et al., 2014; Athreya et al., 2016). To reduce encounters with dogs and other dominant or potentially threatening species, native species may adopt behavioral strategies that facilitate coexistence (Ritchie and Johnson, 2009; Gaynor et al., 2021), such as altering their activity periods to minimize temporal overlap (Broekhuis et al., 2013; Swanson et al., 2014; Manzo et al., 2025; Rafiq et al., 2023), avoiding areas where dogs are present (Yen et al., 2019; Gálvez et al., 2021; Zuercher et al., 2022), or restricting their activities to refuge habitats (Elbroch et al., 2015; Zapata-Ríos and Branch, 2016; Gálvez et al., 2021; Manzo et al., 2025). On the temporal dimension, evidence suggests that native carnivores adjust their daily activity patterns in response to dog presence (Vanak and Gompper, 2010; Farris et al., 2016; Zapata-Ríos and Branch, 2016; Gálvez et al., 2021), with some species reducing temporal overlap particularly during reproductive periods—possibly to reduce the risk of predation on offspring (Swanson et al., 2014; Yen et al., 2019). Understanding these behavioral avoidance dynamics is crucial for predicting how the high densities of domestic dogs in increasingly human-modified landscapes may affect the persistence of native large carnivores (Vanak and Gompper, 2009; Prugh et al., 2019, 2023; Gaynor et al., 2021).

For pumas specifically, most studies examining interactions with domestic dogs have focused on limited geographic areas and single behavioral dimensions. In North America, pumas exhibited minimal responses to playbacks of dog vocalizations (Suraci et al., 2019) but pumas and bobcats spatially avoided areas with higher dog activity at fine scales and adjusted temporal activity patterns, becoming more nocturnal where dogs had access (Granados et al., 2024). In South America, fewer studies exist and most have relied on observational camera trap data without experimental manipulation. Studies in the Andes have documented reduced carnivore occupancy in areas with dogs (Zapata-Ríos and Branch, 2016; Zapata-Ríos et al., 2018; Moreira-Arce et al., 2015), and Azevedo et al. (2018) reported higher temporal overlap between female pumas and domestic dogs in fragmented Brazilian landscapes, apparently showing no temporal segregation or avoidance.

Despite these advances, most studies have examined either spatial or temporal dimensions in isolation. Importantly, dog-puma interactions can be bidirectional, sometimes resulting in intraguild predation. Pumas are known to prey on domestic dogs, which constitute part of their diverse diet that includes at least 232 prey species (Karandikar et al., 2022). Yet, pumas can also be vulnerable to dog attacks, particularly when confronted by packs. Anecdotal reports document pumas being harassed, injured, or even killed by dog packs in both rural and protected areas (e.g., G1 Paraná, 2025; CBS Los Angeles, 2024). These bidirectional interactions suggest that the nature of dog-puma encounters may be context-dependent, varying with dog characteristics, pack size, and landscape characteristics. Consequently, substantial knowledge gaps persist regarding how pumas behaviorally respond to free-ranging dogs across multiple spatiotemporal scales, particularly in human-dominated Neotropical landscapes where both species extensively co-occur.

This study investigates the behavioral responses of pumas to free-ranging domestic dogs in two protected areas located in the Cerrado–Atlantic Forest ecotone of São Paulo State, Brazil. Using camera-trap data, we evaluated: (1) diel activity patterns and temporal overlap between the two species; (2) fine-scale temporal avoidance by quantifying time intervals between consecutive detections at the same locations; and (3) spatial co-occurrence patterns using two-species occupancy models. We hypothesized that domestic dog presence influences puma spatial and temporal activity patterns, potentially leading pumas to adjust their behavior in response to dog activity.

2. Methods

2.1. Study area

Data were collected in two protected areas in the state of São Paulo, Brazil: the Santa Bárbara Ecological Station (2872 ha) and the Águas de Santa Bárbara State Forest (1659.97 ha), both located in the municipality of Águas de Santa Bárbara (22°48′59“ S, 49°14’12” W) (Fig. 1). The study areas are situated in a contact zone between two globally recognized biodiversity hotspots: the Cerrado (Brazilian savanna) and the Atlantic Forest (Myers et al., 2000). Although the vegetation is predominantly Cerrado, this ecotonal position confers additional conservation value to the area. The regional climate is classified as Cwa (Köppen), characterized by dry winters and wet summers, with mean temperatures ranging from approximately 17 °C in the coldest months (June–July) to 24 °C in the hottest months (January–February), and mean annual rainfall of approximately 1400 mm, peaking in December (ca. 206 mm) and reaching its minimum in August (ca. 44 mm) (Melo and Durigan, 2011). The Santa Bárbara Ecological Station (IUCN Category Ia) is classified as a fully protected area, while the Águas de Santa Bárbara State Forest (IUCN Category VI) allows limited sustainable use under strict regulations. The land cover consists of a mosaic predominantly composed of Cerrado, with vegetation types ranging from open savannah fields to dense woodland (cerradão), followed by areas of seasonal semideciduous forest and plantations of pine and eucalyptus. The surrounding landscape includes pasture, agricultural areas, an urban center, and two highways cutting through both areas: the SP-280 (Castelo Branco) and the SP-261, an unpaved road connecting Avaré to Lençóis Paulista (Melo and Durigan, 2011).

2.2. Sampling design

We obtained records of pumas and domestic dogs through systematically placed camera traps (Bushnell® Trophy Cam 6.0 Mpxl, Scoutguard® SG 550) at 67 sampling points spaced approximately one kilometer apart, with adjustments made according to local conditions. Following Gompper (2014), domestic dogs recorded in this study are characterized as rural free-ranging dogs: individuals owned or peripherally associated with human habitations in the surrounding rural properties, but not confined to a prescribed area, allowing them to range into the protected areas sampled in this study. Due to equipment limitations, cameras were rotated among sampling points throughout the study period. Although this rotation resulted in some spatially proximate points being included in the design, no two neighboring points were ever active simultaneously, deployment scheduling ensured that spatially proximate points always operated in different sampling periods, thereby maintaining spatial independence among concurrently active sampling units. The location of the cameras was carefully selected to capture varying environmental contexts: some were positioned along roads and trails in open areas, while others were placed within dense forest fragments to assess the differences in species detection across these contrasting habitats. Each camera operated continuously, 24 h a day, for an average period of 60 consecutive days at each sampling point. Whenever the sensor was activated, each camera triggered three photos with a 10-s interval. We secured the equipment on tree trunks at approximately 30–40 cm above the ground to detect ground-level activity. The overall sampling effort extended from August 2014 to June

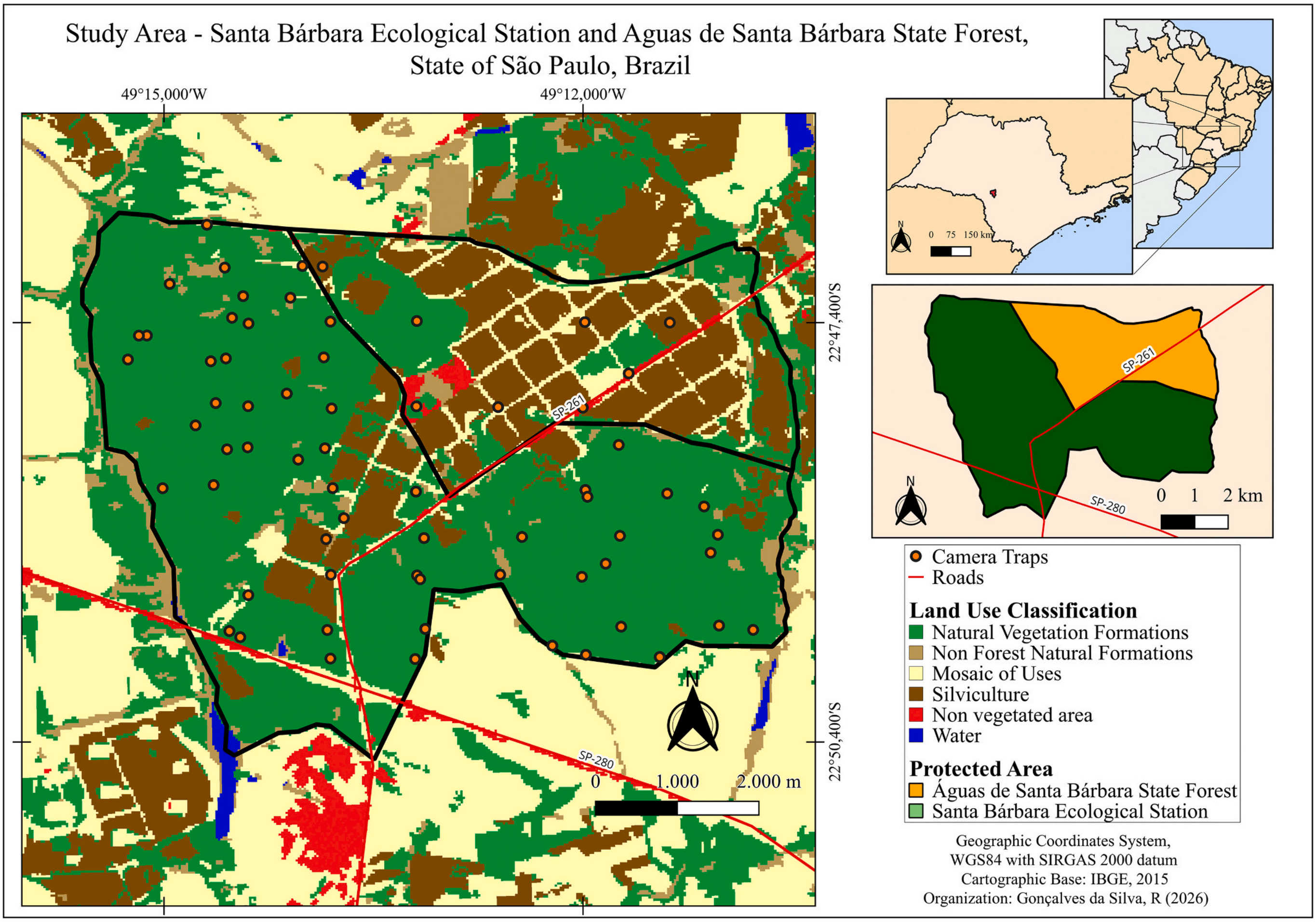

Fig. 1. Map of the study area showing the sampling points at Santa Bárbara Ecological Station and Águas de Santa Bárbara State Forest, located in the municipality of Águas de Santa Bárbara/SP.

2015, spanning both dry and wet seasons in this climatically seasonal region (Cwa, Köppen). To account for potential seasonal variation in detection probability, daily temperature, precipitation, and humidity were included as covariates in the detection component of the occupancy models.

2.3. *Data analysis*

2.3.1. *Activity patterns*

To assess whether pumas modify their activity patterns in the presence of domestic dogs, we compared activity patterns between species and between presence/absence contexts using circular statistics and temporal overlap analyses. Specifically, we converted all times into radians and used kernel density estimation, generating a probability density distribution of the activity pattern (Meredith et al., 2021). We included only independent photographic records, those with a minimum interval of 30 min between records of the same species at the same station (Ridout and Linkie, 2009). To assess the overlap of the activity times between species, we compared the kernel density curves and calculated the overlap coefficient (Δ) using the Dhat4 estimator (recommended for sample sizes >75), implemented in the Overlap package in R (Ridout and Linkie, 2009; Meredith et al., 2021). Additionally, we compared the activity pattern of one species at sampling points in the presence and absence of the second species. Furthermore, we performed a Watson-Wheeler test (W) (Batschelet, 1981) to compare activity distribution and assess whether the frequency distributions of activity times were significantly different.

2.3.2. *Temporal avoidance*

To evaluate potential mutual temporal avoidance between pumas and domestic dogs, we compared the time intervals between sequential detections of each focal species and the subsequent detection of the other species against baseline intervals involving prey or neutral species. Prey species were defined as those recorded in the study area and documented in the diet of pumas or domestic dogs based on Karandikar et al. (2022). Species recorded in the area but not identified as prey in that review were treated as neutral for the purposes of this analysis. A complete list of species and their classifications is provided in Supplementary Data SD1. This approach follows Bianchi et al. (2020) and is based on the rationale that if a species actively avoids a recently detected individual of another species, the time interval before its detection should be longer than that observed for species with no reason to avoid the focal species. Specifically, we calculated the time interval (in hours) between the initial passage of a puma and the subsequent passage of a domestic dog, comparing it with intervals recorded for prey and neutral species after puma passage. Similarly, we calculated the time interval between the initial passage of a domestic dog and the subsequent passage of a puma, comparing it with intervals recorded for prey and neutral species after dog passage. All interval data were transformed using the Box-Cox transformation to improve normality and analyzed through ANOVA tests, followed by Tukey's post hoc test. The ANOVA analyses were conducted to evaluate whether there were significant differences in the time intervals between the passages of pumas and domestic dogs, compared to the passages of prey or neutral species. This allowed for testing the hypothesis that the presence of one species influences the temporal behavior of the other. All analyses were performed in the R environment.

To assess whether the observed differences in return times could arise from chance variation in baseline detection frequencies, we conducted a permutation test with 10,000 iterations. In each iteration, species identities were randomly reassigned among detections while maintaining the observed number of detections per species and preserving the temporal sequence and camera-station structure of the dataset, thereby generating a null distribution of expected return intervals under no species-specific temporal response. The observed mean interval for pumas following dog detections was then compared with this null distribution. *P*-values were calculated as the proportion of permutations yielding mean intervals equal to or greater than the observed mean interval (Niedballa et al., 2019).

To assess the directionality and temporal dynamics of the interaction between domestic dogs and pumas, we used piecewise exponential additive mixed models (PAMMs; Ferry et al., 2024) within a recurrent event framework. PAMMs estimate non-linear temporal dynamics of visitation rates while using all available detections, including recurrent observations. We fitted two separate models: (i) the effect of domestic dogs on puma visitation rate, and (ii) the effect of pumas on domestic dog visitation rate. Surveys were initiated upon detection of the primary species and ended when another detection of the primary species or a non-focal species occurred, the camera was removed, or the maximum survey duration (30 days) was reached; detections of the secondary species within each survey were treated as recurrent events. Data were structured using the ctrecurrent package in R, and PAMMs were fitted following Ferry et al. (2024), with camera station included as a random effect to account for repeated observations within sites.

2.4. Spatial assessment

To assess spatial overlap and habitat use patterns of pumas and domestic dogs, we used single-species and two-species single-season occupancy models, which estimate site occupancy probability (ψ) while accounting for imperfect detection.

2.4.1. Predictor variables

We selected predictor variables based on their biological relevance to puma and domestic dog ecology and their expected influence on detection probability and occupancy probability. Environmental variables (temperature, rainfall, and humidity) were used as predictors of detection probability, as weather conditions can affect both species activity levels and camera trap performance. These data were obtained through the Integrated Center for Agrometeorological Information (http://www.ciiagro.sp.gov.br/). Additionally, we included camera location type (roads/trails vs. forest fragments) as a detection covariate, given that detection rates often differ between open and closed habitats due to differences in animal movement patterns and camera visibility (Mann et al., 2015; Kolowski and Forrester, 2017). Lunar illumination was also evaluated as a detection covariate, as moonlight is known to influence mammalian activity patterns and detectability (Bischof et al., 2024; Ladine and Settles, 2020); the mean illuminated fraction of the moon for each sampling occasion was calculated using the suncalc package in R (Thieurmel et al., 2019).

For occupancy probability, we selected landscape-scale variables representing gradients of anthropogenic modification and human disturbance exposure — such as proximity to roads and urban areas, agricultural mosaic, silviculture, non-vegetated areas, and domestic dog activity — known to influence the spatial patterns of large carnivores (Basille et al., 2013; McClure et al., 2017; Milanesi et al., 2022; Barceló et al., 2025). We extracted landscape variables (Natural Vegetation Formations, Non-Forest Natural Formations, Mosaic of Uses — areas of mixed agricultural and pastoral land use where distinction between pasture and cropland was not possible — Silviculture, Non-vegetated Area, and Water) from land use and cover maps from the MapBiomas Project of 2015, collection 7 (http://mapbiomas.org) using QGIS 3.18.3 with GRASS 7.8.5. These variables were calculated as percentages within buffer radii of 100, 200, 300, 400, 500, 800, and 1000 m around each sampling point. For each variable, we fitted single-covariate occupancy models across all buffer sizes and selected the scale with the lowest AICc, retaining only models in which the confidence interval of the β coefficient did not overlap zero. We also calculated distances from sampling points to the nearest highways, water bodies, and urban areas using the "point to line distance" and "point to polygon distance" tools in the SAGA package of QGIS. Distance to water bodies was included because both species require water resources; distance to urban areas reflects potential human disturbance and domestic dog source populations; and distance to highways captures edge effects and human access. Natural vegetation formations represent core habitat for pumas, while mosaic of uses and silviculture reflect habitat modification that may differentially affect both species. A complete description of all predictor variables and their selected buffer sizes is provided in Supplementary Data SD2.

2.4.2. Occupancy modeling approach

Sampling occurrences were defined as 5-day periods, generating encounter histories for each species at each camera, considering both detections and non-detections. This duration was selected to strike a balance between maintaining model stability and ensuring an adequate number of repeat visits to each site (Burton et al., 2015; Brittain et al., 2022).

To assess the spatial overlap of species in the landscape, we used occupancy models in a three-step approach: (1) probabilities of individual species detection (p), (2) landscape use for pumas and domestic dogs (single species), and (3) patterns of use for two species (i.e., co-occurrence) of puma-dog using the variables from the best-ranked models among single species models. Given the limited number of detections relative to potential parameters, we adopted a parsimonious modeling approach. For detection probability models, we tested a maximum of four covariates (temperature, rainfall, humidity, and camera location type). For occupancy models, we focused on a reduced set of ecologically meaningful variables to avoid model overfitting, testing no more than three covariates simultaneously (following general guidelines for logistic regression with limited sample sizes; Agresti, 2007). We prioritized variables with the strongest theoretical support and tested single-covariate models before considering additive combinations.

For the single-species models (step 2), we first identified the best detection probability structure for each species, then held detection covariates constant while modeling occupancy. For the two-species co-occurrence model (step 3), we used the occupancy covariates from the best-supported single-species models to assess whether the presence of one species influenced the occupancy probability of the other, while accounting for detection differences. Variable selection for the co-occurrence model was based on: (1) performance in single-species models, retaining only covariates whose 85% confidence interval of the β coefficient did not overlap zero; (2) biological plausibility, prioritizing variables representing habitat gradients most likely to mediate behavioral interactions between wild carnivores and domestic species; and (3) parsimony, including only the most influential variables from single-species models.

We used the Unmarked package (Fiske and Chandler, 2011) in the R language (R Core Team, 2020) for all analyses and ranked models based on the Akaike Information Criterion adjusted for small sample size (AICc) and model weights (Wt) (MacKenzie and Hines, 2018). We considered models with a cumulative 0.90Wt (i.e., the 90% confidence set). We used 85% confidence intervals (CI) rather than the conventional 95% CI for the beta (β) coefficients to provide a more exploratory assessment of potentially important variables while acknowledging the limited statistical power inherent in our sample size (Arnold, 2010). This approach allowed us to identify variables warranting further investigation in future studies with larger sample sizes, while still maintaining a conservative interpretation of our results. Covariates with confidence intervals of the beta (β) coefficient of 85% that did not overlap with zero were considered to have potential biological importance (Arnold, 2010). Correlated covariates were not used in the same model (Spearman rank correlation $|>0.60|$). All continuous covariates were standardized (mean = 0, SD = 1) prior to analysis to facilitate model convergence and parameter comparison.

3. Results

With a total sampling effort of 3860 camera-days across 67 sampling points, we obtained 194 independent records and 100 occurrences of pumas, detected at 37 of the 67 sampling points, and 300 independent records and 79 occurrences of domestic dogs, detected at 30 of the 67 sampling points. Both species were detected together at 23 sampling points.

Pumas exhibited crepuscular-nocturnal activity, with the highest peak of activity around 7:00 PM and a frequent occurrence between 1:00 AM and 7:00 AM (Fig. 2). Domestic dogs were predominantly diurnal, showing three detection peaks at 6:00 AM, 12:00 PM, and 6:00 PM (Fig. 2). The analysis revealed that there was a 47% overlap in activity time between pumas and domestic dogs ($\Delta 4 = 0.47$, 95% CI = 0.37–0.51) with a significant difference ($W = 183.36$, $p < 0.001$) in the frequency of activity times between the two species considering all records (Fig. 2). However, this overlap decreased to 38% ($\Delta 4 = 0.38$, 95% CI = 0.26–0.46, $W = 81.48$, $p < 0.001$) when considering only spatial overlap points (Fig. 2). This reduction represents a decrease of approximately 19% in the overlap, equivalent to a reduction to about 1.24 times the initial value. The activity pattern of pumas in points with and without domestic dog records was similar, with an 83% overlap ($\Delta 1 = 0.83$, 95% CI = 0.79–0.94, $W = 1.4678$, $p = 0.48$) (Fig. 2). In contrast, domestic dogs seemed to modify their activity in points with pumas ($\Delta 4 = 0.49$, 95% CI = 0.33–0.52, $W = 66.951$, $p < 0.001$), concentrating activity at 7:00 AM in points with puma presence (Fig. 2).

To evaluate mutual temporal avoidance between pumas and domestic dogs, we compared time intervals between sequential detections of each focal species and subsequent detections of other species. After puma detections, we obtained seven domestic dog records, three neutral species records, and 75 prey records. There was no significant difference in the time intervals recorded for domestic dogs (mean = 40 h), neutral species (mean = 52 h), and prey (mean = 48 h) following puma passage ($F = 0.176$, $p = 0.839$) (Fig. 3). Following domestic dog detections, we obtained seven neutral species records, 54 prey records, and 10 puma records. The time intervals differed significantly among species following domestic dog detections ($F = 4.146$, $p = 0.02$) (Fig. 4).

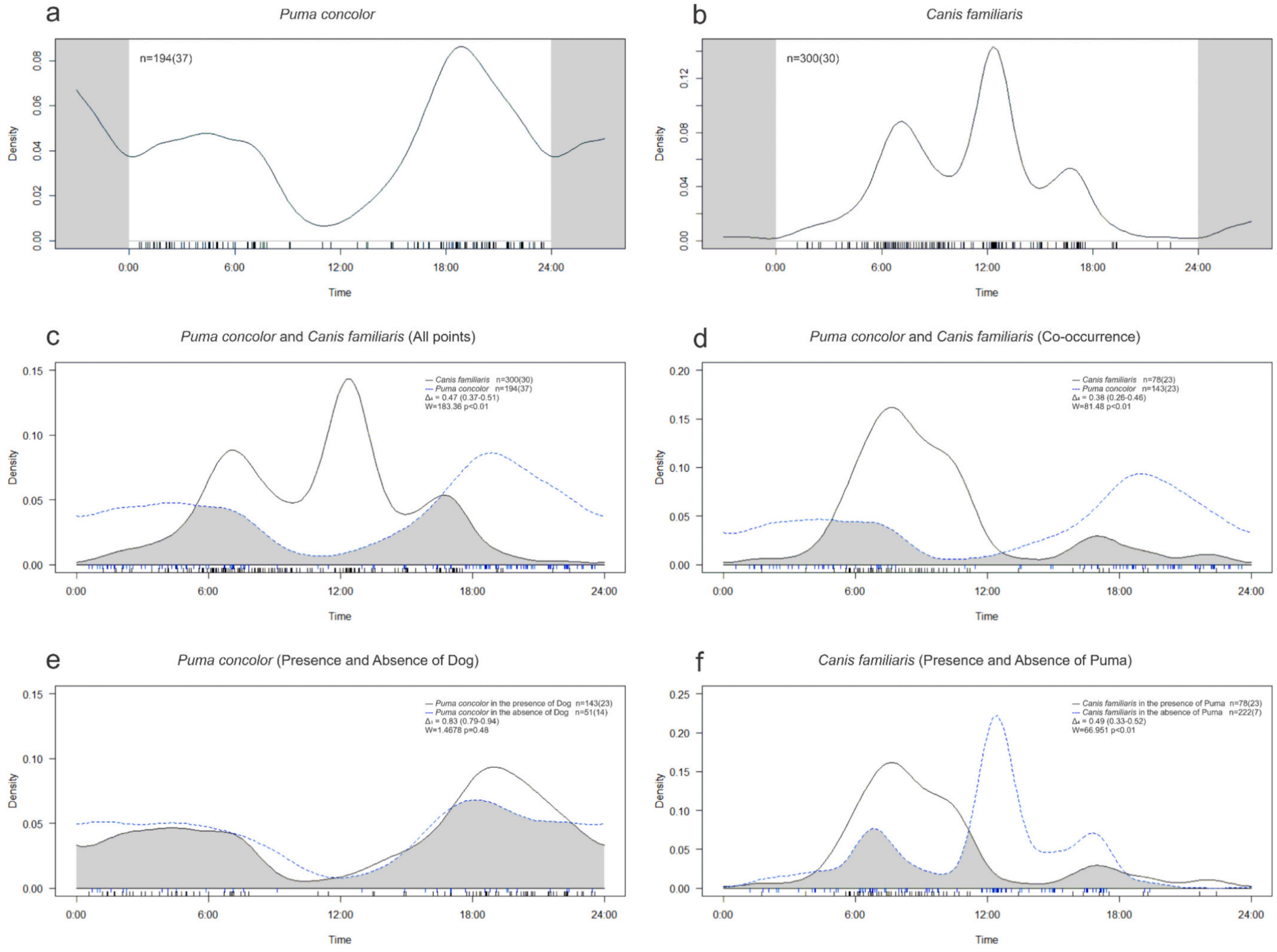

Fig. 2. Activity patterns and temporal overlap between pumas (*Puma concolor*) and domestic dogs (*Canis familiaris*), recorded from August 2014 to June 2015 at Santa Bárbara Ecological Station and Águas de Santa Bárbara State Forest, São Paulo State, Brazil. Panels represent: (a) puma activity pattern ($n = 194$, sites = 37); (b) domestic dog activity pattern ($n = 300$, sites = 30); (c) overlap between both species across all sampling points; (d) overlap at co-occurrence points only (dogs: $n = 78$, sites = 23; pumas: $n = 143$, sites = 23); (e) overlap in puma activity pattern at points with (n = 143, sites = 23) and without ($n = 51$, sites = 14) domestic dog detection; (f) overlap in domestic dog activity pattern at points with (n = 78, sites = 23) and without ($n = 222$, sites = 7) puma detection.

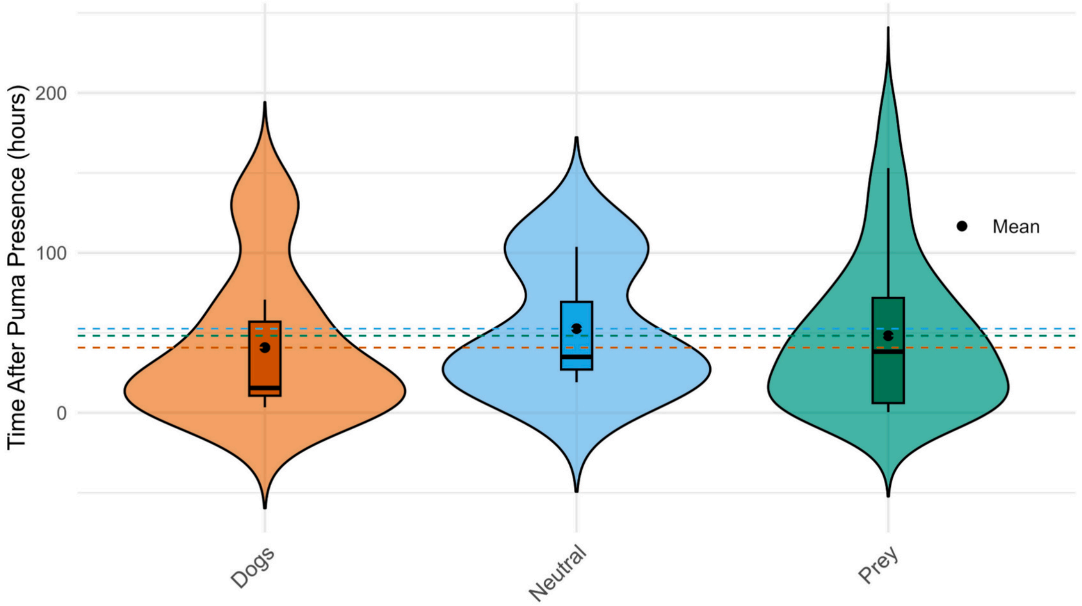

Fig. 3. Time interval (in hours) between detection of domestic dog (*Canis familiaris*), neutral species, and prey species following pumas (*Puma concolor*) passage at camera trap stations. Violin plots show density distributions, boxplots indicate median and interquartile ranges, and black dots and dashed lines represent group means. Santa Bárbara Ecological Station, São Paulo, Brazil.

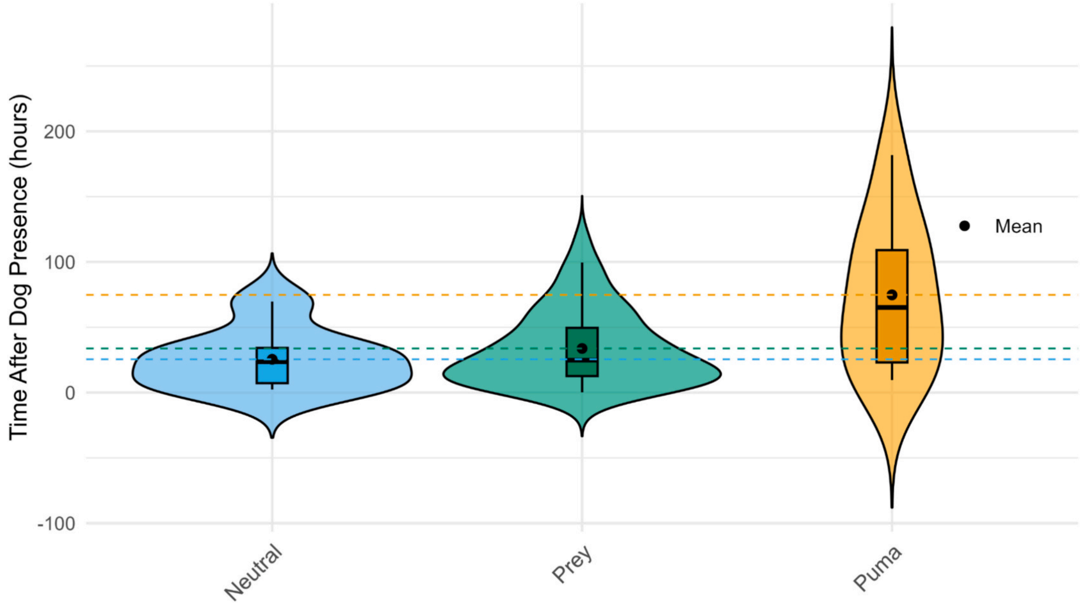

Fig. 4. Time interval (in hours) between detection of pumas (*Puma concolor*), neutral species, and prey species following domestic dog (*Canis familiaris*) passage at camera trap stations. Violin plots show density distributions, boxplots indicate median and interquartile ranges, and black dots and dashed lines represent group means. Santa Bárbara Ecological Station, São Paulo, Brazil.

Specifically, pumas took significantly longer to be detected after domestic dog records (mean = 74 h) compared to both neutral species (mean = 25 h; Tukey HSD, $p = 0.04$) and prey species (mean = 33 h; Tukey HSD, $p = 0.02$). Although pumas were less frequently detected than most prey species, and differences in abundance, home-range size, or detection probability may influence re-detection intervals, the observed mean delay of approximately 74 h for pumas following dog detections suggests a temporal pattern that is not readily explained by diel segregation alone, which would primarily operate within a 24-h cycle. A permutation test indicated that this delay was longer than expected under the null model used here ($p = 0.005$). To further assess temporal dynamics while accounting for recurrent detections, we applied piecewise exponential additive mixed models (PAMMs), which revealed an asymmetric interaction (Figs. 5 and 6): pumas exhibited reduced visitation rates for approximately 5–6 days following dog detections ($p = 0.02$), whereas dogs showed increased occurrence immediately after puma detections (OR = 11.32, $p = 0.02$), with this effect lasting approximately one day.

Puma detection was positively related to camera locations on roads within the protected area ($\beta = 1.96$, 85% CI: 1.32, 2.59) and showed a negative trend with high temperatures, although the confidence interval marginally overlapped zero ($\beta = -0.15$, 85% CI: -0.33, 0.02) (Table 1). For pumas, we selected the model including both road and temperature as the top model, as it substantially improved model performance

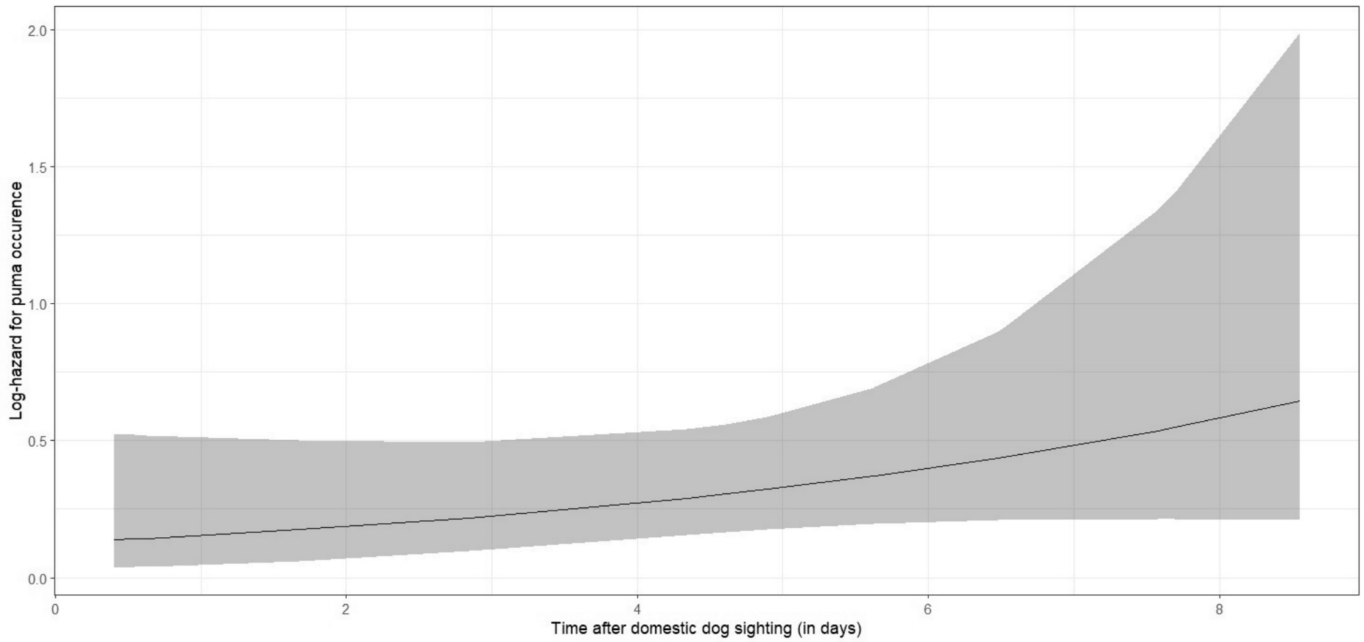

Fig. 5. Estimated temporal change in puma visitation rates following domestic dog detections based on piecewise exponential additive mixed models (PAMMs). The solid line shows the fitted log-hazard, and the shaded area represents 95% confidence intervals. Lower visitation rates during the first days after dog detections, followed by a gradual increase, are consistent with delayed puma site revisitation lasting approximately 5–6 days.

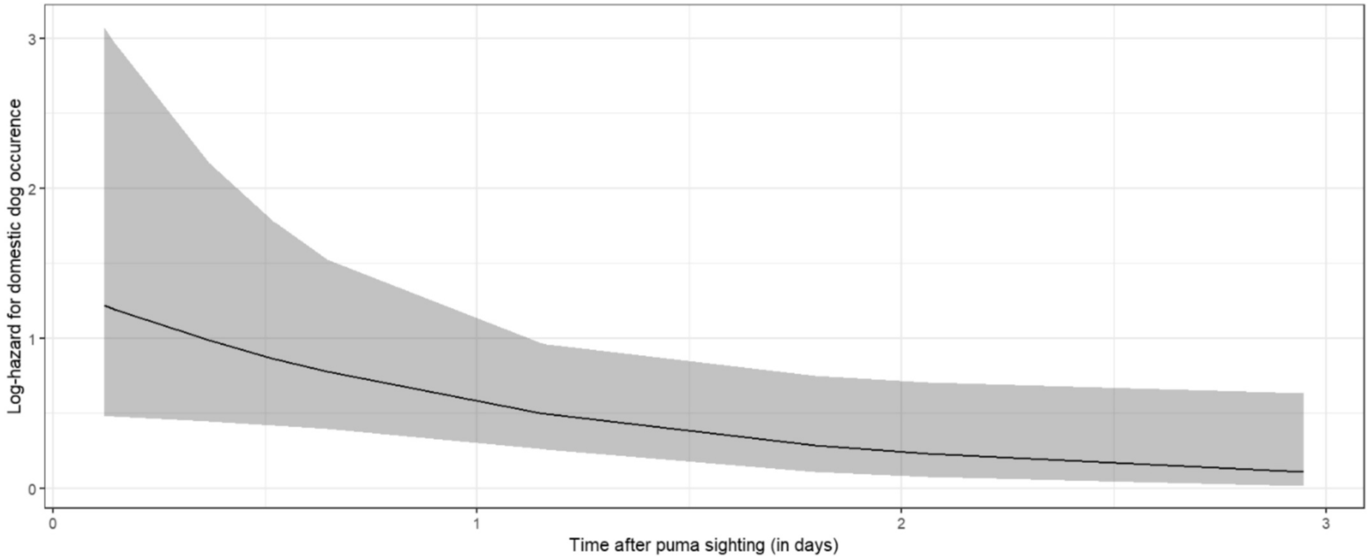

Fig. 6. Estimated temporal change in domestic dog visitation rates following puma detections based on piecewise exponential additive mixed models (PAMMs). The solid line shows the fitted log-hazard, and the shaded area represents 95% confidence intervals. Higher visitation rates immediately after puma detections, followed by a gradual decrease, are consistent with increased dog occurrence at sites recently visited by pumas.

(cumulative model weight = 1.00) compared to the road-only model (model weight = 0.56; ΔAICc = 0.48). In contrast, for domestic dogs, camera location on roads was the primary driver of detection probability (β = 2.75, 85% CI: 1.85, 3.64), and we selected the road-only model (model weight = 0.72) as the addition of temperature contributed minimally to model performance (ΔAICc = 1.90; additional weight = 0.28) (Table 1).

3.1. Occupancy models

For pumas, four models had substantial support (ΔAICc <2), collectively accounting for 98% of the model weight (Table 2a). Given the uncertainty among competing models, we employed model averaging to obtain robust parameter estimates (Burnham and Anderson, 2002). Model-averaged estimates revealed that natural vegetation formations had the strongest positive effect on puma occupancy (β = 1.96, 85% CI: 0.76, 3.15), while mosaic of agricultural uses (β = −1.51, 85% CI: −2.74, −0.28) and forest plantation (β = −1.14, 85% CI: −2.20, −0.09) (Fig. 7) negatively influenced occupancy. These results indicate that natural vegetation formations positively influenced puma occupancy, while mosaic of agricultural uses and forest plantation showed negative effects.

For domestic dogs, the model including only distance to roads was clearly the best-supported (model weight = 0.81, ΔAICc >4 from the

Table 1
Single-species detection models for puma (*Puma concolor*) and domestic dog (*Canis familiaris*) at Santa Bárbara Ecological Station and Águas de Santa Bárbara State Forest, São Paulo State, Brazil. Models are ranked by ΔAICc (difference from the best model). Road = camera location type (road vs. forest interior); Temperature = daily average temperature during sampling; Precipitation = daily average precipitation; Humidity = daily average humidity; Lunar = mean lunar illumination fraction during sampling occasion; p = detection probability; ψ = occupancy probability; nPars = number of parameters; AICwt = Akaike weight; Cumulative Wt = cumulative Akaike weight; (.) = constant parameter.

Models	K	ΔAICc	AICc	logLik	AICwt	cumltvWt
Puma (*Puma concolor*)						
p(Road) ψ(.)	3	0.00	566.27	−296.00	0.56	0.56
p(Road + Temp) ψ(.)	4	0.48	566.75	−295.52	0.44	1
p(Temp) ψ(.)	3	22.19	588.46	−291.23	0.00	1
p(Lunar) ψ(.)	3	26.99	593.26	−295.63	0.00	1
p(.) ψ(.)	2	29.72	595.90	−280.14	0.00	1
p(Prec) ψ(.)	3	30.76	597.03	−279.38	0.00	1
p(Umid) ψ(.)	3	30.99	597.27	−293.63	0.00	1
Domestic Dogs (*Canis familiaris*)						
p(Road) ψ(.)	3	0.00	466.80	−239.27	0.72	0.72
p(Road + Temp) ψ(.)	4	1.90	468.71	−239.18	0.27	1
p(.) ψ(.)	2	15.74	482.54	−238.99	0.00	1
p(Temp) ψ(.)	3	17.17	483.97	−239.13	0.00	1
p(Umid) ψ(.)	3	17.45	484.26	−230.40	0.00	1
p(Prec) ψ(.)	3	17.56	484.37	−230.35	0.00	1
p(Lunar) ψ(.)	3	17.70	484.50	−239.25	0.00	1

Table 2
Top-ranked single-species and multi-species occupancy and detection models for *Puma concolor* and *Canis familiaris* at Santa Bárbara Ecological Station and Águas de Santa Bárbara State Forest, Municipality of Águas de Santa Bárbara, São Paulo State, Brazil.

Models	K	ΔAICc	AICc	logLik	AICwt	cumltvWt
a - Puma (*Puma concolor*)						
p(Road + Temp) ψ(Forest_500)	5	0.00	559.65	−274.83	0.36	0.36
p(Road + Temp) ψ(Mosaic.of.Uses_100)	5	0.48	560.14	−275.07	0.29	0.65
p(Road + Temp) ψ(Mosaic.of.Uses_100 + Forest.Plantation_500)	6	1.51	561.16	−274.58	0.17	0.82
p(Road + Temp) ψ(Forest.Plantation_500)	5	1.63	561.28	−275.64	0.16	0.98
p(Road) ψ()	3	6.62	566.27	−280.14	0.01	0.99
p(Road + Temp) ψ()	4	7.10	566.75	−279.38	0.00	1.00
p(Temp) ψ()	3	28.81	588.46	−291.23	0.00	1.00
p() ψ()	2	36.34	595.99	−296.00	0.00	1.00
b- Domestic Dogs (*Canis familiaris*)						
p(Road) ψ (D_Highway)	4	0.00	462.25	−227.12	0.81	0.81
p(Road) ψ (Mosaic.of.Uses_100)	4	4.06	466.31	−229.15	0.11	0.92
p(Road) ψ ()	3	4.55	466.80	−233.40	0.08	1.00
p() ψ ()	2	20.29	482.54	−239.27	0.00	1.00
c - Co-Occurrence Puma and Domestic Dogs						
pPuma(Temp + Road) pDogs (Road) ψPuma (Forest.Plantation_500) ψDogs (D_Highway) ψPuma-Dogs (Forest.Plantation_500)	11	0.00	1021.43	−499.71	0.80	0.80
pPuma(Temp + Road) pDogs (Road) ψPuma (Forest_500) ψDogs()	8	5.03	1026.46	−505.23	0.07	0.87
pPuma(Temp + Road) pDogs (Road) ψPuma (Mosaic.of.Uses_100) ψDogs()	8	5.51	1026.94	−505.47	0.05	0.92
pPuma(Temp + Road) pDogs (Road) ψPuma (Mosaic.of.Uses_100 + Forest.Plantation_500) ψDogs()	9	6.54	1027.96	−504.98	0.03	0.95
pPuma(Temp + Road) pDogs (Road) ψPuma (Forest.Plantation_500) ψDogs()	8	6.66	1028.09	−506.04	0.03	0.98

(*continued on next page*)

next model) (Table 2b). Proximity to roads strongly increased dog occupancy ($\beta = -1.02$, 85% CI: −1.63, −0.40) (Fig. 8), with the negative coefficient indicating that occupancy probability decreased with increasing distance from roads. This pattern reinforces the strong association between domestic dogs and human infrastructure.

3.2. *Co-occurrence models*

We constructed two-species occupancy models to assess spatial overlap between pumas and domestic dogs. The best-supported co-occurrence model (model weight = 0.80) included forest plantation as a predictor for puma occupancy, distance to roads for dog occupancy, and forest plantation as an interaction term affecting co-occurrence probability (Table 2c). The co-occurrence model revealed that forest plantation negatively affected puma occupancy ($\beta = -1.93$, 85% CI: −3.20, −0.84), consistent with single-species models. Forest plantation also reduced the probability of co-occurrence between pumas and dogs ($\beta = -0.84$, SE = 0.79, $p = 0.29$). The Species Interaction Factor (SIF) was 0.43 (85% CI: 0.14, 1.34), indicating spatial independence between the two species.

4. Discussion

Pumas took approximately 74 h to be detected at camera stations following domestic dog detections — roughly three times longer than neutral species and more than twice the interval observed for prey species — while simultaneously showing reduced occupancy in human-modified landscapes, particularly in areas with higher mosaic agricultural uses and silviculture. Domestic dogs, in contrast, were strongly associated with roads and human infrastructure. Together, these patterns suggest that free-ranging domestic dogs may function as ecological stressors for pumas in human-modified Neotropical landscapes by inducing spatial displacement, temporal activity shifts, and reduced site occupancy (Granados et al., 2024; Zapata Ríos, 2014), potentially influencing their behavior and space use across multiple spatiotemporal scales, although broader generalizations will require replication across additional landscapes and predator species.

Table 2 (*continued*)

Models	K	ΔAICc	AICc	logLik	AICwt	cumltvWt
pPuma(Temp + Road) pDogs (Road) ψPuma() ψDogs (D_Highway)	8	7.58	1029.00	−506.50	0.02	1.00
pPuma(Temp + Road) pDogs (Road) ψPuma() ψDogs(Mosaic.of.Uses_800)	8	11.63	1033.06	−508.53	0.00	1.00

The directional PAMM analysis revealed an asymmetric temporal interaction between the two species. While intervals recorded after puma passage did not differ significantly among species groups (F = 0.176, p = 0.839), the PAMM models—which leverage all available detections and account for recurrent observations—demonstrated that dogs exhibited increased occurrence immediately following puma detections (OR = 11.32, p = 0.02), suggesting attraction rather than avoidance. In contrast, pumas showed reduced visitation rates at sites recently visited by dogs, with this avoidance lasting approximately 5–6 days ($p = 0.02$). These results suggest that the observed temporal displacement is more consistent with puma avoidance of dogs than with mutual temporal exclusion, although differences in baseline detectability should still be considered when interpreting this pattern. This asymmetric pattern, where pumas avoid dogs but dogs show increased occurrence after puma detections, contrasts with typical apex predator-mesopredator dynamics in which apex predators suppress mesopredators through predation and fear (Ritchie and Johnson, 2009; Prugh et al., 2009). Instead, our results suggest that dog–puma interactions in human-modified landscapes may not follow classical apex predator–mesopredator expectations, consistent with experimental evidence from North America showing that pumas exhibit minimal immediate

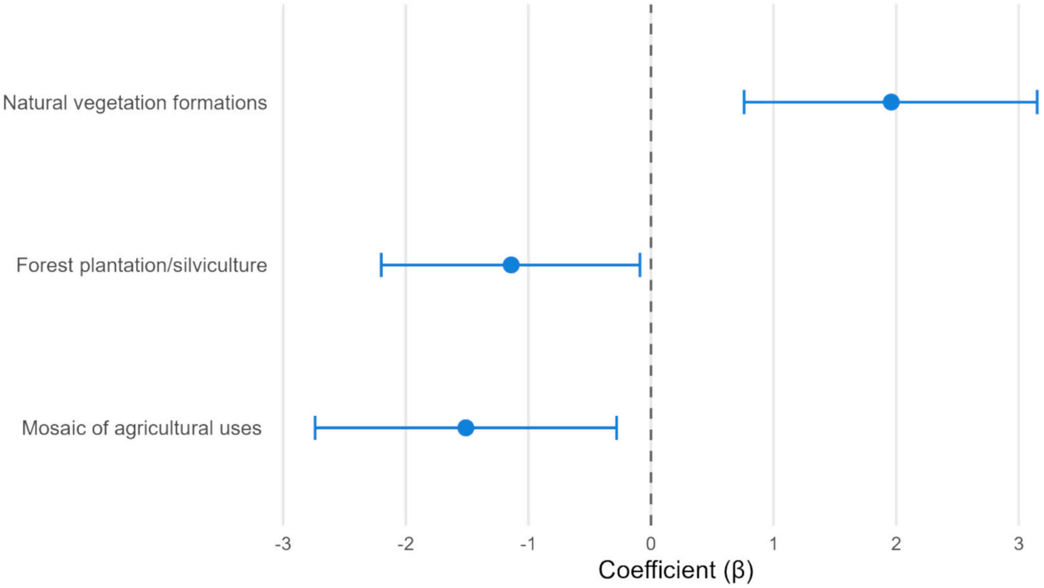

Fig. 7. Model-averaged effects of landscape covariates on puma (*Puma concolor*) occupancy. Points represent the model-averaged coefficients (β) and horizontal bars show 85% confidence intervals. Positive values indicate an increase in occupancy probability with increasing covariate values, while negative values indicate a decrease. Data collected between August 2014 and June 2015 at the Santa Bárbara Ecological Station and the Águas de Santa Bárbara State Forest, São Paulo State, Brazil.

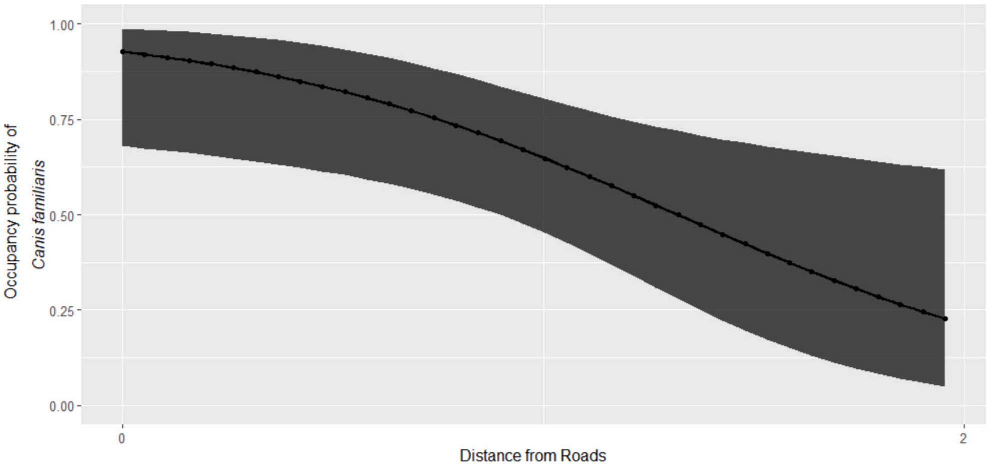

Fig. 8. Effect of distance to roads (km) on domestic dog (*Canis familiaris*) occupancy probability based on the best-supported single-species model. Shaded area represents 85% confidence intervals. Data collected from August 2014 to June 2015 at Santa Bárbara Ecological Station and Águas de Santa Bárbara State Forest, São Paulo State, Brazil.

behavioral responses to dog vocalizations at kill sites, responding no more strongly to dogs than to non-threatening controls, while exhibiting strong behavioral responses to human cues (Suraci et al., 2019).

Our observed pattern of pronounced temporal avoidance by pumas contrasts with experimental evidence showing minimal immediate behavioral responses to dog vocalizations at kill sites (Suraci et al., 2019), suggesting that free-ranging dogs may function more as indicators of anthropogenic disturbance rather than triggering typical apex predator-mesopredator suppression dynamics. Although an alternative explanation is that pumas avoid sites recently used by dogs to optimize foraging efficiency rather than responding to perceived risk, this would imply that dog detections primarily indicate reduced prey availability or lower foraging returns. However, the prolonged delay in puma re-detection after dog records, the PAMM-estimated reduction in puma visitation rates for approximately 5–6 days following dog detections, and the reduced puma occupancy in areas with higher agricultural use and dog activity suggest a broader spatiotemporal pattern consistent with avoidance of dog-associated disturbance. Therefore, while foraging-related mechanisms cannot be excluded, the observed pattern appears more consistent with a behavioral response to perceived risk or disturbance than with simple foraging-driven site selection. These results align with growing recognition that domestic dogs, unlike wild mesopredators in intact ecosystems, occupy an ecological role that does not fit traditional trophic frameworks given their association with human activities and subsidized populations (Doherty et al., 2017; Gompper, 2014).

Spatial occupancy analysis revealed that pumas strongly selected natural vegetation formations while avoiding human-modified landscapes, particularly areas with mosaic agricultural uses and silviculture. Model-averaged results consistently demonstrated that natural vegetation formations positively influenced puma occupancy. These patterns align with broader evidence that pumas, despite their adaptability to diverse habitats, fundamentally depend on native vegetation and areas with reduced human activity (Zeller et al., 2017; Craighead et al., 2022; Zanón Martínez et al., 2022). In Panama, puma occupancy increased proportionally with primary forest extent (Craighead et al., 2022). In Argentina, occupancy was higher near natural reserves in central regions (Zanón Martínez et al., 2022) and increased with woody cover in the Dry Chaco (Nanni et al., 2023). This consistent preference for forested environments across geographic contexts emphasizes the critical importance of protecting forests and native vegetation for large felid conservation, even for generalist species capable of persisting in human-modified landscapes (Krishnamurthy et al., 2016; Alvarenga et al., 2021).

In contrast, domestic dogs showed strong spatial association with roads and human infrastructure. The proximity to highways, whether paved or not, and the percentage of Mosaic of Use were the variables that best explained the utilization of space by dogs. These results corroborate previous studies that demonstrated a strong association between domestic dogs and human activities, especially in areas near roads (Bianchi et al., 2021; Gompper, 2014; Sepúlveda et al., 2015). Roads are places of intense human activity, with a higher probability of dog abandonment or escape, as well as the availability of food and the presence of people who can feed them (Sepúlveda et al., 2015; Paschoal et al., 2018). Moreover, the association between domestic dogs and roads underscores the importance of considering human influence on the ecology and behavior of these animals. Roads often act as facilitators for the introduction of exotic species, increasing habitat fragmentation, and providing access for fire, hunters, and stray dogs (Mulero-Pázmány et al., 2022; Ruiz-Capillas et al., 2021).

The co-occurrence analysis indicates that pumas and domestic dogs exhibit largely independent spatial distributions. It is important to note that statistical independence in this context does not imply the absence of spatial overlap, as both species were detected at the same 23 sampling points. Rather, independence indicates that the presence of one species did not significantly predict the presence of the other across the landscape. Thus, co-occurrence at shared sampling points likely reflects overlap in habitat use rather than direct spatial association between species. Although the point estimate of the Species Interaction Factor was below 1, suggesting a tendency toward spatial avoidance, the confidence interval overlapped 1, indicating that the data are also consistent with spatial independence. Forest plantations, representing highly modified habitats, negatively affected puma occupancy and were also associated with reduced probability of co-occurrence. Together with the temporal avoidance patterns observed in this study, these results are consistent with the hypothesis that pumas may reduce overlap with domestic dogs across temporal and spatial dimensions, although the evidence for spatial interaction remains inconclusive. Domestic dogs have been reported to influence space use patterns in several species (Vanak et al., 2009), including large carnivores such as spectacled bears (Zapata-Ríos and Branch, 2016). These findings suggest that anthropogenic influences mediated through free-ranging dog populations may alter habitat use patterns of native carnivores, even in adaptable species such as pumas.

The mechanisms through which domestic dogs influence puma space use likely operate through multiple pathways. First, the strong spatial association between dogs and human infrastructure means that dog presence serves as a reliable indicator of anthropogenic disturbance — a factor known to negatively affect puma occupancy (Zeller et al., 2017). Second, the temporal avoidance we documented indicates that pumas adjust their space use in response to dog presence, which may cumulatively reduce their effective occupancy in areas with high dog activity. Third, the association between dogs and human-modified landscapes may create spatially structured gradients of disturbance that extend beyond sites of direct encounters (Suraci et al., 2019). These combined effects result in the observed spatial segregation, where pumas concentrate in natural vegetation away from roads and human-modified areas where dog activity is highest.

Beyond the spatial segregation described above, differences in daily activity patterns provide an additional temporal dimension to the interaction between pumas and domestic dogs. Pumas exhibited crepuscular-nocturnal activity patterns consistent with observations across their geographic range, though considerable variation exists among studies reflecting the species' behavioral plasticity in response to local conditions (Azevedo et al., 2018; Di Bitetti et al., 2010; Bianchi et al., 2020). Domestic dogs displayed predominantly diurnal activity, typical of free-ranging dogs whose activity patterns closely track human routines and resource provisioning (Bianchi et al., 2020; Frigeri et al., 2014; Guedes et al., 2021). This contrast suggests that temporal partitioning may complement spatial avoidance, although differences in activity schedules alone are unlikely to explain the longer site-revisitation intervals observed for pumas after dog detections.

Together, these results indicate that behavioral responses between the two species may operate at different temporal scales: dogs appear to adjust their circadian activity patterns in areas with puma presence, whereas pumas exhibit delayed site revisitation following dog detections, consistent with avoidance over longer temporal intervals. However, whether these responses represent a truly symmetric or asymmetric interaction remains uncertain given the limited sample size of the site revisitation analysis.

Our study has limitations that should be acknowledged. Our study areas in protected forests surrounded by a matrix of rural properties captured subsets of puma home ranges given these felids' large spatial requirements. Based on published home-range estimates for pumas in Brazilian Cerrado habitats (approximately 2.5–61 km^2; Silveira, 2004), our ~45 km^2 study area likely encompassed portions of the home ranges of only a few individuals. Given the large spatial requirements of pumas and the typical overlap between male and female territories, the camera grid probably sampled movements of a small number of adults using the surrounding landscape. However, this design allowed us to assess fine-scale behavioral responses at sites where species co-occur, precisely where management interventions are most needed. We could not assess individual-level variation in behavioral responses, which may vary with sex, age, reproductive status, or prior experience with dogs. Furthermore, as individual pumas could not be identified from camera-trap images, repeated detections of the same individual at multiple sampling points cannot be ruled out. This represents a common limitation of camera-trap studies without individual identification. Because domestic dogs are strongly associated with human-modified landscapes, their effects may be difficult to disentangle from other anthropogenic stressors such as habitat degradation, prey depletion, and human disturbance. The reduced puma occupancy observed in these areas likely reflects the combined influence of multiple factors, including the presence of free-ranging dogs. We acknowledge that inter-event times may be influenced by multiple factors beyond behavioral avoidance, including baseline detection frequency, home-range size, detection probability, diel activity, microhabitat preferences, and prey distribution (Karanth et al., 2017). We addressed these concerns through multiple analytical approaches: permutation tests helped account for variation in baseline detection frequency, and the PAMM framework explicitly modeled temporal dynamics while accounting for recurrent observations and site-level variation. The convergence of results across these complementary approaches strengthens support for the temporal avoidance interpretation, though these results should still be interpreted cautiously given the complexity of factors influencing camera-trap detection patterns. Future studies combining camera-trap data with GPS telemetry would allow for a more direct assessment of movement patterns and space use following dog encounters.

Our results suggest that the presence of domestic dogs in areas where pumas occur may negatively affect their activity patterns and occupancy, potentially contributing to additional pressures on puma populations, which are considered Vulnerable in the state of São Paulo (São Paulo, 2018). Beyond the behavioral effects documented here, competition and disease transmission represent potential additional consequences of coexistence with dogs in areas close to human activities, though these processes were not directly evaluated in this study. These findings highlight the importance of considering free-ranging dog management in the conservation planning and management of protected areas and their surrounding landscapes, particularly in regions where dogs and large carnivores co-occur. Potential measures may include responsible ownership programs, control of dog circulation near natural areas, and community engagement strategies, though the effectiveness of such interventions requires direct evaluation in future studies.

CRediT authorship contribution statement

Rodolpho Gonçalves da Silva: Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Formal analysis, Conceptualization. **Isabele Aparecida Manzo:** Writing – review & editing, Software, Methodology, Formal analysis. **Rita Bianchi:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111916.

Data availability

Data will be made available on request.

References

Agresti, A., 2007. An Introduction to Categorical Data Analysis, second ed. John Wiley & Sons, Hoboken, NJ.

Alvarenga, G.C., Chiaverini, L., Cushman, S.A., Dröge, E., Macdonald, D.W., Kantek, D.L. Z., Kaszta, Ż., 2021. Multi-scale path-level analysis of jaguar habitat use in the Pantanal ecosystem. Biol. Conserv. 253, 108900.

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's Information Criterion. J. Wildl. Manag. 74 (6), 1175–1178.

Athreya, V., Odden, M., Linnell, J.D., Krishnaswamy, J., Karanth, K.U., 2016. A cat among the dogs: leopard *Panthera pardus* diet in a human-dominated landscape in western Maharashtra, India. Oryx 50 (1), 156–162.

Azevedo, F.C., Lemos, F.G., Freitas-Junior, M.C., Rocha, D.G., Azevedo, F.C.C., 2018. Puma activity patterns and temporal overlap with prey in a human-modified landscape at southeastern Brazil. J. Zool. 305 (4), 246–255.

Barceló, G., Benavent-Corai, J., Peris, S., Santos, X., 2025. Human disturbance alters the foraging and spatiotemporal activity of a large carnivore. Oecologia 207, 112.

Basille, M., Herfindal, I., Santin-Janin, H., Linnell, J.D.C., Odden, J., Andersen, R., Høgda, K.A., Gaillard, J.-M., 2013. Selecting habitat to survive: the impact of road density on survival in a large carnivore. PloS One 8, e65493.

Batschelet, E., 1981. Circular Statistics in Biology. Academic Press, London.

Bianchi, R., Olifiers, N., Riski, L.L., Gouvea, J.A., Cesário, C.S., Fornitano, L., Gompper, M.E., 2020. Dog activity in protected areas: behavioral effects on mesocarnivores and the impacts of a top predator. Eur. J. Wildl. Res. 66 (3), 36.

Bianchi, R., Jenkins, J.M., Lesmeister, D.B., Gouvea, J.A., Cesário, C.S., Fornitano, L., Gompper, M.E., 2021. Tayra (Eira barbara) landscape use as a function of cover types, forest protection, and the presence of puma and free-ranging dogs. Biotropica 53 (6), 1569–1581.

Bischof, R., Hameed, S., Ali, H., Kabir, M., Younas, M., Shah, K.A., Din, J.U., Nawaz, M. A., 2024. The moon's influence on the activity of tropical forest mammals. Proc. R. Soc. B Biol. Sci. 291, 20241479.

Bleyhl, B., Ghoddousi, A., Askerov, E., Bocedi, G., Breitenmoser, U., Manvelyan, K., Kuemmerle, T., 2021. Reducing persecution is more effective for restoring large carnivores than restoring their prey. Ecol. Appl. 31 (5), e02338.

Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Halpern, B.S., 2005. What determines the strength of a trophic cascade? Ecology 86 (2), 528–537.

Borrvall, C., Ebenman, B., 2006. Early onset of secondary extinctions in ecological communities following the loss of top predators. Ecol. Lett. 9 (4), 435–442.

Braczkowski, A.R., O'Bryan, C.J., Stringer, M.J., Watson, J.E., Possingham, H.P., Beyer, H.L., 2018. Leopards provide public health benefits in Mumbai, India. Front. Ecol. Environ. 16 (3), 176–182.

Brittain, S., Rowcliffe, M.J., Kentatchime, F., Tudge, S.J., Kamogne-Tagne, C.T., Milner-Gulland, E.J., 2022. Comparing interview methods with camera trap data to inform occupancy models of hunted mammals in forest habitats. Conservation Science and Practice 4 (4), e12637.

Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J.W., Macdonald, D.W., 2013. Risk avoidance in sympatric large carnivores: reactive or predictive? J. Anim. Ecol. 82 (5), 1098–1105.

Burnham, K.P., Anderson, D.R. (Eds.), 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer New York, New York, NY.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Boutin, S., 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. J. Appl. Ecol. 52 (3), 675–685.

Butler, J.R., Linnell, J.D., Morrant, D., Athreya, V., Lescureux, N., McKeown, A., 2014. Dog eat dog, cat eat dog: social-ecological dimensions of dog predation by wild carnivores. In: Free-ranging dogs and wildlife conservation, pp. 117–143.

CBS Los Angeles, 2024. Mountain Lion Captured By Wildlife Officials After Getting Scared Up Tree By Dog in Tustin. https://www.cbsnews.com/losangeles/news/mountain-lion-captured-by-wildlife-officials-after-getting-scared-up-tree-by-dog-in-tustin/. (Accessed 29 November 2024).

Craighead, K., Yacelga, M., Wan, H.Y., Vogt, R., Cushman, S.A., 2022. Scale-dependent seasonal habitat selection by jaguars (Panthera onca) and pumas (Puma concolor) in Panama. Landsc. Ecol. 37 (1), 129–146.

Di Bitetti, M.S., De Angelo, C.D., Di Blanco, Y.E., Paviolo, A., 2010. Niche partitioning and species coexistence in a Neotropical felid assemblage. Acta Oecol. 36 (4), 403–412.

Dobrovolski, R., Loyola, R.D., Guilhaumon, F., Gouveia, S.F., Diniz-Filho, J.A.F., 2013. Global agricultural expansion and carnivore conservation biogeography. Biol. Conserv. 165, 162–170.

Doherty, T.S., Dickman, C.R., Glen, A.S., Newsome, T.M., Nimmo, D.G., Ritchie, E.G., Wirsing, A.J., 2017. The global impacts of domestic dogs on threatened vertebrates. Biol. Conserv. 210, 56–59.

Elbroch, L.M., Lendrum, P.E., Allen, M.L., Wittmer, H.U., 2015. Nowhere to hide: pumas, black bears, and competition refuges. Behav. Ecol. 26 (1), 247–254.

Estes, J.A., Carswell, L.P., 2020. Costs and benefits of living with predators. Science 368 (6496), 1178–1180.

Farris, Z.J., Kelly, M.J., Karpanty, S., Ratelolahy, F., 2016. Patterns of spatial co-occurrence among native and exotic carnivores in north-eastern M adagascar. Anim. Conserv. 19 (2), 189–198.

Ferry, N., Dupont, P., Bender, A., Heurich, M., 2024. Introducing recurrent event analyses to assess species interactions based on camera-trap data: a comparison with time-to-first-event approaches. Methods Ecol. Evol. 15 (7), 1233–1246.

Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1–23.

Frigeri, E., Cassano, C.R., Pardini, R., 2014. Domestic dog invasion in an agroforestry mosaic in southern Bahia, Brazil. Trop. Conserv. Sci. 7 (3), 508–528.

G1 Paraná, 2025. Vídeo: considerado culpado de sumir com galinhas, vira-lata 'prova inocência' botando onças para correr em sítio do PR. https://g1.globo.com/pr/norte-noroeste/noticia/2025/10/24/cachorro-espanta-oncas-pr.ghtml. (Accessed 29 November 2024).

Gálvez, N., Infante, J., Fernandez, A., Díaz, J., Petracca, L., 2021. Land use intensification coupled with free-roaming dogs as potential defaunation drivers of mesocarnivores in agricultural landscapes. J. Appl. Ecol. 58 (12), 2962–2974.

Gaynor, K.M., Cherry, M.J., Gilbert, S.L., Kohl, M.T., Larson, C.L., Newsome, T.M., Smith, J.A., 2021. An applied ecology of fear framework: linking theory to conservation practice. Anim. Conserv. 24 (3), 308–321.

Gompper, M.E. (Ed.), 2014. Free-Ranging Dogs and Wildlife Conservation. Oxford University Press, USA.

Granados, A., McDonald, Z., McPherson, K., Stoner, D., 2024. Unraveling the impact of dog-friendly spaces on urban–wildland pumas and other wildlife. Wildl. Biol., e01290

Guedes, J.J.M., Assis, C.L., Feio, R.N., Quintela, F.M., 2021. The impacts of domestic dogs (Canis familiaris) on wildlife in two Brazilian hotspots and implications for conservation. Anim. Biodivers. Conserv. 44 (1), 45–58.

Hoeks, S., Huijbregts, M.A., Busana, M., Harfoot, M.B., Svenning, J.C., Santini, L., 2020. Mechanistic insights into the role of large carnivores for ecosystem structure and functioning. Ecography 43 (12), 1752–1763.

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

Hunter, L., 2018. Carnivores of the World, 117. Princeton University Press.

Karandikar, H., Serota, M.W., Sherman, W.C., Green, J.R., Verta, G., Kremen, C., Middleton, A.D., 2022. Dietary patterns of a versatile large carnivore, the puma (Puma concolor). Ecol. Evol. 12 (6), e9002.

Karanth, K.U., Srivathsa, A., Vasudev, D., Puri, M., Parameshwaran, R., Kumar, N., 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proc. R. Soc. B Biol. Sci. 284 (1848).

Kolowski, J.M., Forrester, T.D., 2017. Camera trap placement and the potential for bias due to trails and other features. PloS One 12, e0186679.

König, H.J., Kiffner, C., Kramer-Schadt, S., Fürst, C., Keuling, O., Ford, A.T., 2020. Human–wildlife coexistence in a changing world. Conserv. Biol. 34 (4), 786–794.

Krishnamurthy, R., Cushman, S.A., Sarkar, M.S., Malviya, M., Naveen, M., Johnson, J.A., Sen, S., 2016. Multi-scale prediction of landscape resistance for tiger dispersal in Central India. Landsc. Ecol. 31 (6), 1355–1368.

Ladine, T.A., Settles, L., 2020. Response in nighttime activity of white-tailed deer (Odocoileus virginiaus) to lunar cycle and cloud cover. Southeast. Nat. 19, 325–332.

Linnell, J.D., Strand, O., 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Divers. Distrib. 6 (4), 169–176.

MacKenzie, D., Hines, J., 2018. RPresence: R interface for program PRESENCE. R package version 2 (9).

Mann, G.K.H., O'Riain, M.J., Parker, D.M., 2015. The road less travelled: assessing variation in mammal detection probabilities with camera traps in a semi-arid biodiversity hotspot. Biodivers. Conserv. 24, 531–545.

Manzo, I.A., Gonçalves da Silva, R., Bianchi, R.C., 2025. The influence of domestic dogs on the spatial and temporal distribution of tayra. Wildl. Biol. 2025 (2), e01298.

Mark Elbroch, L., Saucedo, C., Wittmer, H.U., 2010. Swimming by pumas (Puma concolor) in Patagonia: rethinking barriers to puma movement. Stud. Neotropical Fauna Environ. 45 (3), 187–190.

Marshall, C.R., Quental, T.B., 2016. The uncertain role of diversity dependence in species diversification and the need to incorporate time-varying carrying capacities. Philos. Trans. R. Soc. B 371 (1691), 20150217.

McClure, M.L., Dickson, B.G., Nicholson, K.L., 2017. Modeling connectivity to identify current and future anthropogenic barriers to movement of large carnivores: a case study in the American southwest. Ecol. Evol. 7, 3762–3772.

Melo, A.C.G., Durigan, G., 2011. Plano de manejo da Estação Ecológica de Santa Bárbara, 221. Instituto Florestal, São Paulo.

Meredith, M., Ridout, M., Campbell, L.A.D., 2021. Overlap: estimates of coefficient of overlapping for animal activity patterns (version 0.3. 4), 2021-05-17. https://cran.r-project.org/web/packages/overlap.

Merson, S.D., Dollar, L.J., Tan, C.K.W., W Macdonald, D., 2019. Activity patterns of sympatric living exotic and endemic carnivores (the fosa) in Western Madagascar's deciduous forests. J. Zool. 307 (3), 186–194.

Milanesi, P., Puopolo, F., Zellweger, F., 2022. Landscape features, human disturbance or prey availability? What shapes the distribution of large carnivores in Europe? Land 11, 1807.

Moreira-Arce, D., Vergara, P.M., Boutin, S., 2015. Diurnal human activity and introduced species affect occurrence of carnivores in a human-dominated landscape. PloS One 10 (9), e0137854.

Mulero-Pázmány, M., Rollán, L., D`Amico, M., González-Suárez, M., 2022. Road orientation affects the impact of roads on wildlife. Wildl. Res. 50 (1), 39–46.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403 (6772), 853–858.

Nanni, A.S., Regolin, A.L., Fernández, P.D., Giordano, A.J., Martello, F., Bailey, L.L., Lucherini, M., 2023. Woody cover and pasture within the surrounding matrix drive puma (Puma concolor) occupancy in agroecosystems of the argentine dry Chaco. J. Nat. Conserv. 75, 126475.

Niedballa, J., Wilting, A., Sollmann, R., Hofer, H., Courtiol, A., 2019. Assessing analytical methods for detecting spatiotemporal interactions between species from camera trapping data. Remote Sensing in Ecology and Conservation 5 (3), 272–285.

Ordiz, A., Aronsson, M., Persson, J., Støen, O.G., Swenson, J.E., Kindberg, J., 2021. Effects of human disturbance on terrestrial apex predators. Diversity 13 (2), 68.

Palomares, F., Caro, T.M., 1999. Interspecific killing among mammalian carnivores. Am. Nat. 153 (5), 492–508.

Paschoal, A.M., Massara, R.L., Bailey, L.L., Doherty Jr., P.F., Santos, P.M., Paglia, A.P., Chiarello, A.G., 2018. Anthropogenic disturbances drive domestic dog use of Atlantic Forest protected areas. Trop. Conserv. Sci. 11, 1940082918789833.

Prugh, L.R., Sivy, K.J., 2020. Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. Ecol. Lett. 23 (5), 902–918.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S., Brashares, J.S., 2009. The rise of the mesopredator. Bioscience 59 (9), 779–791.

Prugh, L.R., Sivy, K.J., Mahoney, P.J., Ganz, T.R., Ditmer, M.A., van de Kerk, M., Montgomery, R.A., 2019. Designing studies of predation risk for improved inference in carnivore-ungulate systems. Biol. Conserv. 232, 194–207.

Prugh, L.R., Cunningham, C.X., Windell, R.M., Kertson, B.N., Ganz, T.R., Walker, S.L., Wirsing, A.J., 2023. Fear of large carnivores amplifies human-caused mortality for mesopredators. Science 380 (6646), 754–758.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Rafiq, K., Jordan, N.R., Golabek, K., McNutt, J.W., Wilson, A., Abrahms, B., 2023. Increasing ambient temperatures trigger shifts in activity patterns and temporal partitioning in a large carnivore guild. Proc. R. Soc. B 290 (2010), 20231938.

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14 (3), 322–337.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science 343 (6167), 1241484.

Ritchie, E.G., Johnson, C.N., 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecol. Lett. 12 (9), 982–998.

Ritchie, E.G., Elmhagen, B., Glen, A.S., Letnic, M., Ludwig, G., McDonald, R.A., 2012. Ecosystem restoration with teeth: what role for predators? Trends Ecol. Evol. 27 (5), 265–271.

Ruiz-Capillas, P., Mata, C., Fernández, B., Fernandes, C., Malo, J.E., 2021. Do roads alter the trophic behavior of the mesocarnivore community living close to them? Diversity 13 (4), 173.

São Paulo, 2018. Decreto n° 63.853, de 27 de novembro de 2018. Declara as espécies da fauna silvestre no Estado de São Paulo regionalmente extintas, as ameaçadas de extinção, as quase ameaçadas e as com dados insuficientes para avaliação, e dá providências correlatas. Governo do Estado de São Paulo, São Paulo.

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 (4), 290–297.

Silveira, L., 2004. Ecologia comparada e conservação da onça-pintada (Panthera onca) e onça-parda (Puma concolor), no Cerrado e Pantanal. Ph.D. dissertation. Universidade de Brasília, Brasília, Brazil.

Suraci, J.P., Smith, J.A., Clinchy, M., Zanette, L.Y., Wilmers, C.C., 2019. Humans, but not their dogs, displace pumas from their kills: an experimental approach. Sci. Rep. 9 (1), 12214.

Swanson, A., Caro, T., Davies-Mostert, H., Mills, M.G., Macdonald, D.W., Borner, M., Packer, C., 2014. Cheetahs and wild dogs show contrasting patterns of suppression by lions. J. Anim. Ecol. 83 (6), 1418–1427.

Thieurmel, B., Elmarhraoui, A., Thieurmel, M.B., 2019. Package 'suncalc'. R package version 0 (5), 1.

Vanak, A.T., Gompper, M.E., 2009. Dogs *Canis familiaris* as carnivores: their role and function in intraguild competition. Mammal Rev. 39 (4).

Vanak, A.T., Gompper, M.E., 2010. Interference competition at the landscape level: the effect of free-ranging dogs on a native mesocarnivore. J. Appl. Ecol. 47 (6), 1225–1232.

Vanak, A.T., Thaker, M., Gompper, M.E., 2009. Experimental examination of behavioural interactions between free-ranging wild and domestic canids. Behav. Ecol. Sociobiol. 64 (2), 279–287.

Wolf, C., Ripple, W.J., 2018. Rewilding the world's large carnivores. R. Soc. Open Sci. 5 (3), 172235.

Yen, S.C., Ju, Y.T., Shaner, P.J.L., Chen, H.L., 2019. Spatial and temporal relationship between native mammals and free-roaming dogs in a protected area surrounded by a metropolis. Sci. Rep. 9 (1), 8161.

Young, J.K., Olson, K.A., Reading, R.P., Amgalanbaatar, S., Berger, J., 2011. Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. BioScience 61 (2), 125–132.

Zanón Martínez, J.I., Seoane, J., Kelly, M.J., Sarasola, J.H., Travaini, A., 2022. Assessing carnivore spatial co-occurrence and temporal overlap in the face of human interference in a semiarid forest. Ecol. Appl. 32 (1), e02482.

Zapata Ríos, G., 2014. Impacts of Domestic Dogs on the Native Mammalian Fauna of the Ecuadorian Andes.

Zapata-Ríos, G., 2018. Dogs are more than wet kisses and tail wags: domestic dogs as invasive species. Anim. Conserv. 21 (4), 287–288.

Zapata-Ríos, G., Branch, L.C., 2016. Altered activity patterns and reduced abundance of native mammals in sites with feral dogs in the high Andes. Biol. Conserv. 193, 9–16.

Zapata-Ríos, G., Branch, L.C., Kalka, G., Corcoran, M., Zapata-Ríos, A.F., 2018. ¿ Cómo afectan los perros a la fauna silvestre de los Andes? Environmental Science Journal for Teens 1–5. Julio.

Zeller, K.A., Vickers, T.W., Ernest, H.B., Boyce, W.M., 2017. Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: pumas as a case study. PloS One 12 (6), e0179570.

Zuercher, G.L., Owen, R.D., Torres, J., Gipson, P.S., 2022. Mechanisms of coexistence in a diverse Neotropical mammalian carnivore community. J. Mammal. 103 (3), 618–638.