

# Assessing carnivore spatial co-occurrence and temporal overlap in the face of human interference in a semiarid forest

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**Abstract.** Apex predators drive top-down effects in ecosystems and the loss of such species can trigger mesopredator release. This ecological process has been well documented in human-modified small areas, but for management and conservation of ecological communities, it is important to know which human factors affect apex predator occurrence and which mediate mesopredators release at large scales. We hypothesized that mesopredators would avoid spatial and temporal overlap with the apex predator, the puma; but that human perturbations (i.e., cattle raising and trophy hunting) would dampen top-down effects and mediate habitat use. We installed 16 camera traps in each of 45, 10 × 10 km grid cells in the Caldén forest region of central Argentina resulting in 706 total stations covering 61,611 km<sup>2</sup>. We used single-season occupancy and two-species co-occurrence models and calculated the species interaction factor (SIF) to explore the contributions of habitat, biotic, and anthropic variables in explaining co-occurrence between carnivore pairs. We also used kernel density estimation techniques to analyze temporal overlap in activity patterns of the carnivore guild. We found that puma habitat use increased with abundance of large prey and with proximity to protected areas. Geoffroy's cats and skunks spatially avoided pumas and this effect was strong and mediated by distance to protected areas and game reserves, but pumas did not influence pampas fox and pampas cat space use. At medium and low levels of puma occupancy, we found evidence of spatial avoidance between three pairs of mesocarnivores. All predators were mostly nocturnal and crepuscular across seasons and mesopredators showed little consistent evidence of changing activity patterns with varying levels of puma occupancy or human interference. We found potential for mesopredator release at large scale, especially on the spatial niche axis. Our results suggest that a combination of interacting factors, in conjunction with habitat features and intervening human activities, may make mesopredator release unlikely or difficult to discern at broad scales. Overall, we believe that promoting the creation of new protected areas linked by small forest patches would likely lead to increased predator and prey abundances, as well as the interactions among carnivores inside and outside of protected areas.

**Key words:** apex predator; Caldén forest; co-occurrence; habitat use; human interference; intraguild interactions; mesopredator release; occupancy model; puma.

## INTRODUCTION

Apex predators drive top-down effects in community structure and ecosystem dynamics, often recognized only after they have been eliminated from ecosystems (Estes,

2011, Ripple et al. 2013). One consequence of losing an apex predator is the increase in mesopredators (i.e., mesopredator release; Prugh et al. 2009). Larger predators may regulate populations of smaller predators through indirect exploitative competition by feeding on the same resources, or through direct interference competition by harassment and intraguild predation (Polis and Holt 1992) or interspecific killing (Palomares and Caro 1999). However, a number of niche-partitioning mechanisms allow coexistence within a predator guild

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including trophic niche partitioning according to predator body sizes (Palomares and Caro 1999, Donadio and Buskirk 2006) and preferred prey (Rosenzweig 1966), selection of different habitats (Johnson and Franklin 1994), shifts in temporal activity patterns (Grassman et al. 2005, Penteriani 2013), or behavioral avoidance (Wilson et al. 2010). These mechanisms are costly for subordinate predators in terms of suboptimal foraging, which may lead to increased risk of interactions with humans (Rasmussen and MacDonald 2012). When the apex predator is absent, mesopredators are freed from top-down regulation and may increase in abundance and/or expand their spatiotemporal niches, which in turn, can ripple through the trophic chain and lead to overexploitation of their prey and suppression of their subordinate competitors (Soulé et al. 1988, Crooks and Soulé 1999, Ripple et al. 2013, Gordon et al. 2015).

However, habitat loss and modification in a world where human societies demand more land and natural resources for subsistence and development, inexorably affect ecological processes outside wilderness areas and protected areas. In human-dominated landscapes, trophic interactions and mechanisms shaping predator niches can be affected and distorted by habitat management and patterns of human activity (Dorresteijn et al. 2015). First, humans influence species abundances through bottom-up processes, for example, by clearing of land for agricultural production and cattle grazing, which simplifies landscapes. This reduces vegetation complexity and changes food availability, resulting in limited opportunities for smaller predators to partition the habitat and lessen competition by finding refuges to avoid encounters with larger predators (Crooks and Soulé 1999, Ramesh et al. 2012). Second, humans can affect top-down processes, directly or indirectly. Human presence alters distribution and temporal activity patterns of predators potentially impairing niche partitioning. For example, predators can become more nocturnal when human activity is high, increasing the probability of temporal overlap, although the magnitude of this effect differs among species (Wang and Allen 2015, Zanón Martínez et al. 2016b). Some smaller predators are more tolerant of humans and may benefit from using residential areas or other human-modified landscapes (Lewis et al. 2015, Pasanen-Mortensen and Elmhagen 2015, Wang et al. 2015). Thus, habitat alteration (through urbanization and agricultural development) and human activity (interference and direct persecution) blur natural patterns of niche segregation among predators (Ramesh et al. 2012), but when accounted for, may increase understanding of intraguild relationships in the increasingly widespread human-modified landscapes (Brook and Johnson 2012, Núñez-Regueiro et al. 2015).

As predators are frequently secretive and nocturnal, most tests of mesopredator release or temporal or spatial segregation are based on camera-trap surveys, often logistically constrained to small spatial scales and extents (but see Núñez-Regueiro et al. 2015, Rich 2017,

Davis 2018). However, apex predators are typically large bodied and their home ranges span large areas (for example, 151 km<sup>2</sup> for male pumas *Puma concolor*; Sunquist and Sunquist 2002), and thus small-scale surveys may record a limited number of individuals. Ecosystem managers and conservation practitioners would benefit from assessments of whether temporal and spatial shifts registered at small local scales transfer to larger regions, where predator interactions with habitat and humans vary extensively. To contribute knowledge useful to management, we need a better understanding of predator interactions, functional roles, and coexistence over large scales across human-modified landscapes. Occupancy modeling has proven useful for determining factors influencing species distribution while accounting for the imperfect detection that typically hinders studies of elusive predators (MacKenzie et al. 2004b). This is especially important for multispecies studies because detection probabilities are species specific and are highly influenced by detection method.

In this study, we investigate the spatial and temporal activity pattern relationships between the puma and the rest of members of the predator guild (four species, including: Geoffroy's cat, *Leopardus geoffroyi*; pampas cat, *Leopardus colocolo*; pampas fox, *Pseudalopex gymnocercus*; and Molina's hog-nosed skunk, *Conepatus chinga*) in the Caldén (*Prosopis caldenia*) forest biogeographical region. After the jaguar (*Panthera onca*) was extirpated throughout the region at the beginning of the 20th century (Chebez 1994), the puma became the apex predator in the current carnivore assemblages. Caldén forest is one of the more severely transformed ecosystems in Argentina (González-Roglich and Southworth 2012) where knowledge of the effects of predators on ecosystems is lacking, as is the case for the wider South America subcontinent (Ritchie and Johnson 2009). Here we described patterns of predator activity and we use a combination of occupancy and co-occurrence models that considered habitat factors and intensity of human activity. Assuming interference competition is prevailing, we expected to find evidence of competitive interactions and hypothesized that (1) in areas heavily used by pumas, dominant mesopredators (i.e., pampas foxes and wild cats) would avoid those areas whereas the smaller, subordinate mesopredators (i.e., Molina's hog-nosed skunk), would benefit from this suppression of their competitors and release spatially, (2) in areas where pumas are scarce, dominant mesopredators would occur and would diminish occurrence of subordinate mesopredators, (3) predators' daily activity patterns would vary seasonally, and where top predator habitat use is high, temporal activity patterns of mesopredators would change to avoid pumas, and (4) human activities would modify these interactions such that human threats would cause declines primarily in puma occupancy in some areas while species less sensitive to humans (subordinate mesopredators) may benefit from humans as shield from larger predators (the human shield hypothesis; Berger 2007).

STUDY AREA

The study area is in the central region of La Pampa province, Argentina (Fig. 1), comprising 79,993 km<sup>2</sup>. This region corresponds to the Espinal phytogeographic province, mainly occupied by the Caldén forest, but includes interspersed sand grasslands and salt deposits (Cabrera 1976). This forest is a xerophilic forest ecosystem dominated by caldén trees, where tree cover ranges from 30% to 50%, and grasslands predominate over bushes. The topography is characterized by plateaus, valleys, hills, and low-altitude plains (<200 m). Average temperatures reach 23°C in summer and 8°C in winter, and annual mean precipitation is 550 mm.

In this region, most of the land is privately owned and managed for livestock (mainly cattle), hunting, and, to a lesser extent, cultivation; only <1% of forest cover is protected in a local reserve (González-Roglich et al. 2012). Red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) were introduced for sport hunting in 1907, and from 1980, La Pampa Province’s government encouraged game species farming of these introduced ungulates and pumas were hunted. In contrast, the native large ungulates such as guanacos (*Lama guanicoe*) and pampas

deer (*Ozotoceros bezoarticus*) became extinct in the area. Pumas are still often poached as trophy animals in game reserves (see Zanón Martínez et al. 2016a, b for details).

*The carnivore guild under study*

The puma (family Felidae) is the largest predator in the area (≥40 kg, from seven adult individuals, author’s data). Pumas can take large prey and small to medium-sized prey if available (Zanón Martínez et al. 2012, 2016a). Pampas foxes (Canidae: 2.4–8 kg) are common in rural areas and use all available habitats in certain parts of their range and exhibit a generalist diet (García and Kittlein 2005). Geoffroy’s cats (Felidae, ≥2.95 kg) and Pampas cats (Felidae, 2.36–6 kg) have extensively overlapping distribution ranges (Redford and Einseberg 1992, Macdonald and Loveridge 2010). Their diets consists primarily of small rodents (Walker et al. 2007, Bisceglia et al. 2008), but include other species such as birds (Guidobono et al. 2016), the Plains vizcachas (*Lagostomus maximus*; Branch 1995), and the introduced European hares (*Lepus europaeus*) when locally abundant. Geoffroy’s cats are dominant to Pampas cats due to their greater ecological plasticity in diet and

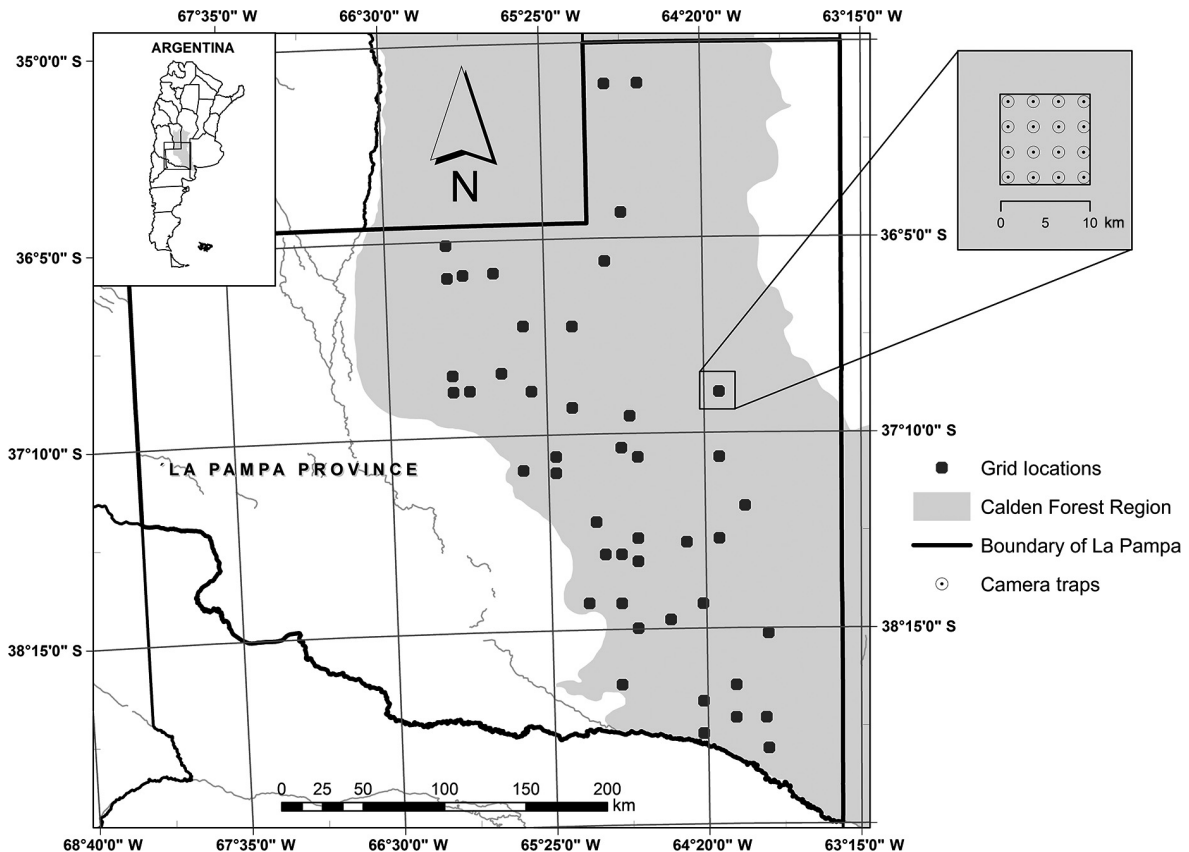


FIG. 1. Map of study area in the Caldén forest represented by gray, within the political boundaries of La Pampa province, Argentina, and the 45 (10 × 10 km) grid square locations marked by black dots. Schematization of sampling design shows a grid with 16 camera traps marked as bull’s eyes.

spatial requirements (Pereira et al. 2006, Pereira and Fracassi 2011). Finally, Molina's hog-nosed skunk (Mephitidae) is the smallest predator (2.3–4.5 kg). It is a mainly nocturnal, solitary, and generalist feeder, with a diet that includes arthropods, vertebrates, and some plant material (Travaini and Delibes 1998).

## METHODS

### *Sampling design*

We divided the study area into a grid of  $10 \times 10$  km cells from which we randomly selected 45 (~8% of the total area, Fig. 1). We installed 16 single, remote cameras (Moultrie Game Spy 4.0 MP DGTL, Moultrie Products, LLC., Alabaster, AL, USA) at regular intervals (2–3 km) in a  $4 \times 4$  array within each selected  $10 \times 10$  km square (Fig. 1) between October 2010 and March 2013, for a total of 720 sites to use in occupancy models. The total number of cameras available allowed us to operate four grids simultaneously. Taking advantage of the distribution and availability of dirt roads inside grids, we installed and georeferenced these cameras along roads and wildlife and cattle trails, following standard practices (Kelly et al. 2008). The cameras operated 24 h/d for 25–30 d, taking a photograph with a minimum 5-minute delay between triggering events. We did not use a shorter delay (e.g., 15–30 s) as in other studies due to the large number of cattle in the area that might cause memory cards to fill.

### *Detection of predators*

We recorded the date, time, camera ID, and species for each photograph taken during our study period. Then we created capture histories for puma, pampas fox, Geoffroy's cat, pampas cat, and Molina's hog-nosed skunk (skunk, henceforward). To describe temporal daily activity patterns, we considered photos of animals of the same species that were not individually distinct as a single capture event if they occurred within 30 minutes of a previous photo (Di Bitetti and Paviolo 2006). To build capture histories, we used daily capture events and recorded the detection or non-detection of each target species at each of the remote camera locations. To reduce the number of zeros in matrixes of capture histories and thus improve model convergence, we joined three daily capture events into each encounter occasion (e.g., 30 d corresponded to 10 occasions).

### *Single-species occupancy modeling*

Single-species occupancy models have been widely used in camera-trap studies to determine wildlife species occurrence and distribution (Mackenzie et al. 2006, Farris et al. 2015, Sunarto et al. 2015). When a species is not detected, the occupancy state is ambiguous: either the site was occupied but the species was not detected

during any visit, or the site was unoccupied and the species was truly absent (Mackenzie et al. 2006). Thus these models estimate the probability of a target species occupying a site or patch from detection–nondetection information while correcting for imperfect species detection (MacKenzie 2002, Mackenzie et al. 2006). We assumed that essential habitat characteristics did not change over the 3 yr of camera-trapping surveys, mostly because vegetation structure in this semi-desert forest remained highly stable. Additionally, during the camera-trapping survey, there were no fires, which could change the vegetation structure completely. There also were no migratory animals in the Caldén region forest that would influence the occurrence of the carnivores and their prey. Finally, we were interested in the factors influencing site use rather than true occupancy, and we used explanatory variables relevant at the camera-station scale. All single-species occupancy models were run in Program Mark (McClintock and White 2012) through the RMark package interface in software R version 3.1.1 (R Development Core Team 2013). Models were ranked using Akaike Information Criterion (AIC) (Burnham and Anderson 2002) and we reported all competing models defined as those within  $\Delta AIC < 2.0$  of the top model.

We used a two-step approach to single-season occupancy modeling for each carnivore species. We first evaluated the effect of covariates on detection probability while holding occupancy constant. We then used the best detection model while exploring the effects of covariates on occupancy (i.e., site use).

*Explanatory variables for single species occupancy.*—We considered three sets of potential explanatory variables for use in occupancy models for each species to test predictions describing the influence of habitat, biotic, and anthropic elements (Appendix S1: Table S1). We used Geographic Information System (GIS), software ArcMap version 10.2.2 (ESRI, Redlands, California, USA), to extract landscape and anthropic variables within a 500-m diameter buffer around each camera station. We acquired data on habitat from the National Forest Administration of Argentina, which used Landsat 5 TM, TERRA-ASTER, and CBERS2-CCDA satellite imagery (Mendez 2007). We identified two habitat categories using the criterion of areas with forest and areas without forest and we extracted the distance from each camera to nearest forest patch (>50 ha; Appendix S1: Table S1).

To account for potential biotic interactions within the assemblage (resource competition and predator–prey interactions), we used the encounter rates of each prey species in camera-trap photos to calculate a relative activity level (or encounter rate) as a continuous variable at each camera station (Appendix S1: Table S1). The encounter rates were built by using the number of photographic events per day obtained per camera divided by the number of days cameras were operative. In contrast to other studies (Kelly and Holub 2008, Monterroso and

Alves 2013, Wang et al. 2015), we counted two individuals of the same species in the same photo as only one record, to be conservative and because they may not be independent events. We choose those prey species that can be appropriately detected by using remote camera technique, considering their behavior and body size. We considered the red deer and wild boar as large prey, while medium-sized prey were armadillos (*ChaetophRACTUS villosus* and *Zaedyus pichiy*) and European hares (*L. europaeus*), and small-sized prey were elegant-crested tinamous (*Eudromia elegans*) and brushland tinamou (*Nothoprocta cinerascens*).

We described the potential effects of anthropic elements using variables that describe human activity and impacts. From photographs of working dogs used by ranchers (there were no free-ranging dogs in our study area), we built a dog encounter rate. We also used an encounter rate of cattle calculated as above to account for the potential influence of ranch practices (Appendix S1: Table S1). Similarly, to describe vulnerability of predators to human interference, we considered the distance from camera station to nearest village, major road, game reserve (where pumas and several introduced game species are hunted), and natural reserves (no hunting allowed), using GIS (the GIS layers were provided by the Department of Statistics and Censuses of La Pampa province).

Finally, we used three covariates on detection probability of carnivore species: a categorical variable based on trail type (CameraSite), and the dog and cattle encounter rates as continuous variables (Appendix S1: Table S1). For CameraSite, we created two categories: (1) closed sites (ClosedTrail), where cameras were installed on trails where animals were forced to pass due to thick vegetation in the surrounding area, and (2) open sites (OpenTrail), where animals could use the trail or another way to pass around the camera station (Appendix S1: Table S1). All continuous variables above were standardized using  $z$  scores.

We tested for correlations between habitat, biotic, and anthropic variables using Pearson's correlation coefficients and found no variables were highly correlated ( $r < 0.61$ , Appendix S1: Table S2), thus we used variables all in occupancy models.

#### *Co-occurrence between carnivore pairs*

We tested for interactions between all carnivore pairs without habitat variables using two-species co-occurrence models, to examine the influence of the dominant (larger) species on the subordinate (smaller) ones. We then included the covariates that entered the top single-species occupancy model for each target species to assess whether habitat variables mediated species interactions. We assumed that the puma, as the largest species in the community, is dominant (A) over all other the smaller carnivores, which are the subordinate (B) species (MacKenzie et al. 2004a, Richmond and Hines 2010).

Also, we built models comparing pairs of subordinate species to each other assuming the larger species would be the dominant of the two. We considered Geoffroy's cat as dominant over Pampa's cat due to its larger size, mass, and wider distribution in the region (Redford and Einseberg 1992). Additionally, we built these models in areas with high, medium, and low puma occupancy (i.e., site use). Low puma site use was defined from zero to the first quartile, medium was from the second quartile to third quartile (we excluded the second quartile because values were dispersed inside the quartile while, in the third quartile, values were more concentrated in that range and thus generated greater contrast between categories), and high was from the third quartile to 1 of the distribution of values of puma site use probability. This categorization resulted in 177 camera stations with low puma site use (i.e., 0.00–0.16), 176 camera stations with medium puma site use (i.e., 0.21–0.26), and 177 camera stations with high puma site use (i.e., 0.27–1.00). We expected that high puma occupancy would decrease the likelihood of negative interactions between subordinate carnivores because pumas would cause low densities of subordinates, while low puma occupancy would result in higher likelihood of negative interactions between smaller predators as their numbers and spatial distribution would increase in the absence of pumas.

We used the second, conditional parameterization of the two-species occupancy model (Richmond et al. 2010), which includes eight parameters (Table 1). The conditional, two-species occupancy model has a priori categorizations of dominant (A) and subordinate (B) species that allows testing whether species B occupancy ( $\psi^B$ ) and detection ( $r^{BA}$ ,  $r^{Ba}$ ) estimates were conditional upon those of species A: when species A is present, capital letters (i.e., <sup>A</sup>), and absent, lowercase letters (i.e., <sup>a</sup>). We formulated several models to determine whether presence of species B is conditional on the presence of species A (i.e.,  $\psi^{BA} \neq \psi^{Ba}$  occupancy for B is not equal when A is present vs. absent), or presence of B is unconditional (i.e.,  $\psi^{BA} = \psi^{Ba}$  occupancy for B is the same with or without A present).

We also compared models without species interactions that only included our best habitat variables from single species modeling to those models with species interactions to determine if model fit improved and to determine whether the interaction between A and B was mediated by biotic, anthropic, or habitat factors. Similarly, we tested if detection (in addition to occupancy) of species B is conditional on the detection of species A, or is unconditional by comparing model performance when  $r^{BA}$  and  $r^{Ba}$  are estimated separately or when they are constant with or without species A ( $r^{BA} = r^{Ba}$ ).

To determine the interaction between two carnivores, we used the formula provided by Richmond et al. (2010) to calculate the species interaction factor (SIF) for each carnivore pairing from parameters derived from occupancy models,  $\psi^A$ ,  $\psi^{BA}$ , and  $\psi^{Ba}$  (Table 1). The SIF measures interaction between two species as independent

TABLE 1. List of parameters and their description used in two-species occupancy models and species interaction factor (SIF) formula.

Parameters and SIF	Description
$\psi^A$	probability that the area is occupied by species A
$\psi^{BA}$	probability that the area is occupied by species B, given species A is present
$\psi^{Ba}$	probability that the area is occupied by species B, given species A is not present
$p^A$	probability of detecting species A, given species B is not present
$p^B$	probability of detecting species B, given species A is not present
$r^A$	probability of detecting species A, given both species are present
$r^{BA}$	probability of detecting species B, given both species are present, and species A was detected
$r^{Ba}$	probability of detecting species B, given both species are present, and species A was not detected
Species interaction factor (SIF)	$\frac{\psi^A \psi^{BA}}{\psi^A \psi^{BA} + (1 - \psi^A) \psi^{Ba}}$

occurrence (SIF = 1.0), or co-occurrence is greater than expected under independence (SIF > 1.0 and CIs do not overlap 1.0), or species co-occur less frequently than expected under independence (SIF < 1.0 and CIs do not overlap 1.0; Steen 2014). The SIF was calculated from the probability of occupancy provided by the top models. We used Program Mark (McClintock and White 2012) through the RMark package interface in software R version 3.1.1 (R Development Core Team 2013) to run all models.

#### Temporal activity patterns

We described species' daily activity patterns throughout four seasons (summer, autumn, winter, and spring, combining data from all study years) except for puma and pampas cat in winter due to low records for this season. We fit kernel density functions to time of animal observations into each season, while accounting for sunrise and sunset times, to describe seasonal daily activities for each carnivore species (Nouvellet et al. 2012). To summarize patterns, activity throughout the day was described as crepuscular (morning [summer 05:45–07:45, autumn 07:05–09:05, winter 07:09–09:09, spring 05:23–07:23] and evening [summer 19:24–21:24, autumn 17:42–19:42, winter 17:45–19:45, spring 19:00–21:00]); diurnal (summer 07:45–19:24, autumn 09:05–17:42, winter 09:09–17:45, spring 07:23–19:00); and nocturnal (summer 21:24–05:45, autumn 19:42–07:05, winter 19:45–07:09, spring 21:00–05:23).

We also examined whether mesopredators shifted their daily activity patterns when co-occurring with pumas. To do so, we split the data according to the first and third quartiles of the distribution of values of

puma habitat use probability from the top single-season occupancy model as above. We fit kernel density functions to time of animal observations to describe activity patterns for overall, high, medium, and low puma site use values, and calculated their temporal co-occurrence with the  $\Delta_1$  overlap term (following Ridout and Linkie [2009]; see Sunarto et al. [2015] for an example). The  $\Delta_1$  version is suggested for small samples of the quantitative index of overlap  $\Delta$ , which ranges from 0 to 1 and is calculated as the area under the curve formed by taking the smaller of two density functions at each time point (Ridout and Linkie 2009). Thus, index values close to 1 indicate large temporal overlap. We expected  $\Delta_1$  to be low for those mesopredators (Geoffroy's cats and pampas cats) that are phylogenetically close species to the pumas and thus are likely to experience negative interactions with the dominant puma (Donadio and Buskirk 2006, de Oliveira and Pereira 2014). Contrary, we expected  $\Delta_1$  to be high for those other species that are not expected to interact with pumas, such as pampas foxes and skunks. Also, we calculated temporal co-occurrence comparing pairs of subordinate species to each other for overall, high, medium, and low puma site use values. We expected that mesopredators might interact negatively in sites where pumas are absent or puma site use is low, and  $\Delta_1$  would be lower than in the sites with high puma use values.

To explore whether human activities influenced predator activity patterns and temporal overlap, we also compared  $\Delta_1$  between low, medium, and high cattle and dog encounter rates for each mesopredator species against pumas. We used the first and third quartile of the distribution of encounter rates of cattle for data splitting, resulting in  $n = 222$  camera stations with zero encounter rates of cattle per day,  $n = 131$  camera stations with medium (>0.00–0.21) encounter rates of cattle per day, and  $n = 177$  camera stations with high (0.81–9.48) encounter rates of cattle per day. Dog records in cameras were rarer and data splitting by quartiles was unsatisfactory, so we resorted to subjective thresholds to define  $n = 608$  camera stations with no dog records,  $n = 55$  camera stations with medium (>0.00–0.05) encounter rates of dogs per day and  $n = 43$  camera stations with high (>0.05–0.25) encounter rates of dogs per day. For these analyses, we first recalculated the time records as time to (or from) sundown and sunset (Nouvellet et al. 2012) and then standardized them to a 24-h day. We expected that puma avoidance by mesopredators might be lower in camera stations with high cattle and dog encounter rates, where potential encounters with a larger dominant predator may be counterbalanced by human persecution of pumas, which would lead to higher  $\Delta_1$  in those areas. We obtained 95% confidence intervals for estimates of  $\Delta_1$  through 10,000 bootstrap simulations.

We conducted the statistical analyses with R 3.1.1 (R Development Core Team 2013) using specialized package *overlap* for analysis of temporal activity (Meredith and Ridout 2014).

## RESULTS

*Camera-trapping survey*

We accumulated 18,987 trap days (excluding days when cameras malfunctioned) across 706 camera-trap locations (mean = 26.89 trap days per camera station; SD = 4.79), covering a total of 52,163 km<sup>2</sup> (crop areas excluded). Only 14 of the 720 camera traps malfunctioned during the sampling period and were disregarded resulting in 706 stations used in analyses. We recorded 4,099 carnivore events including 133 pumas, 2,951 pampas foxes, 624 Geoffroy's cats, 38 pampas cats, and 353 skunks. Occurrence of carnivores across the camera stations ranged from 31 (for pampas cat) to 614 (for pampas fox) of the 706 total traps (Table 2).

*Single species occupancy models*

*Puma*.—Based on the  $\beta$  estimates of the most parsimonious models, puma habitat use increased with closer proximity to nearest natural reserves and also with the encounter rate of large prey (Table 3, Fig. 2). Puma habitat use also increased with proximity to forests and decreased with proximity to game reserves, but these were more ambiguous effects with CIs overlapping 1.0. Probability of detection was higher in closed sites and correlated negatively with encounter rates of cattle (Table 3, Fig. 2).

*Pampas fox*.—The encounter rates of medium-sized prey positively influenced pampas fox habitat use, in particular the encounter rate of European hares, which had a strong relationship in all competing models (Table 3, Fig. 2). Also, pampas fox habitat use increased with distance away from forest patches and the type of site (detection was higher in closed sites) included in all competing models, though with less strong effects (Table 3).

*Geoffroy's cat*.—Four models of Geoffroy's cat habitat-use and probability of detection were similarly plausible. These competing models included anthropic, biotic, and

habitat factors (Table 3). Geoffroy's cat habitat use increased the closer to forest patches and the farther away from natural reserves (Fig. 2). Also, encounter rates of small- and medium-sized prey (tinamous and armadillos) were positively associated with Geoffroy's cat habitat use (Fig. 2). All competing models included the type of site and cattle encounter rates, with closed sites and those with lower encounter rates with cattle having larger probabilities of detection (Fig. 2, Table 3).

*Pampas cat*.—Three models of pampas cat habitat use were competitive. All models suggested that site use increased with distance away from natural reserves (Fig. 2) and decreased (unexpectedly) with the encounter rate of tinamous (Table 3). Pampas cat detection was not affected by any variable, however, photographic records for this species were few.

*Skunk*.—Two models that included only anthropic variables were considered competitive for skunks (Table 3). The models showed that the probability of habitat use increased with the distance away from roads and decreased to the farther away from villages (Fig. 2, Table 3). Detection probability was negatively associated with cattle encounter rate, and, less strongly, to open sites.

*Co-occurrence models*

Puma habitat use did not appear to affect habitat use of either pampas fox or pampas cat: species interaction factors (SIFs)  $\cong 1$ , which indicates spatial independence (Table 4, Appendix S1: Table S3). However, puma habitat use affected Geoffroy's cat and skunk habitat use: SIFs were, respectively, 0.35 and 0.36, which indicates lack of co-occurrence (Table 4, Appendix S1: Table S3). While the top model was unconditional on detection of puma for these last two species ( $r^{BA} = r^{Ba}$  in Appendix S1: Table S3), habitat use was conditional on puma presence in competing models, suggesting species interaction was relevant ( $\psi^{BA} \neq \psi^{Ba}$  in Appendix S1: Table S3).

For Geoffroy's cats, habitat use was higher when pumas were absent and it increased with proximity to nearest forest patch, both with pumas present and

TABLE 2. Summary of survey effort and detection of five carnivore species across 706 camera stations (O, overall), 177 camera stations with high puma occupancy (H, high), 176 camera stations with medium puma occupancy (M, medium), and 177 camera stations with low puma occupancy (L, low) in Caldén forest region, Argentina, from October 2010 to March 2013.

Species	The total number of photos				Camera stations with detections				Naïve occupancy estimate†			
	O	H	M	L	O	H	M	L	O	H	M	L
Puma	133	63	19	16	84	36	19	12	0.12	0.20	0.11	0.08
Pampas fox	2,951	574	480	645	614	156	152	158	0.87	0.90	0.86	0.90
Geoffroy's cat	624	160	107	172	265	74	56	75	0.38	0.42	0.32	0.42
Pampas cat	38	5	6	17	31	5	4	14	0.04	0.03	0.02	0.08
Skunk	353	100	61	66	176	45	38	49	0.25	0.25	0.22	0.28

† Number of camera stations where carnivore species were detected divided by total number of camera stations surveyed.

TABLE 3. Top models ( $\Delta AIC \leq 2$ ) for probability of habitat use ( $\psi$ ) and detection ( $p$ ) of carnivore species across 706 camera stations in Caldén forest region from La Pampa province, Argentina in years 2010–2013.

Species/Model	AIC	$\Delta AIC$	$W$	$K$	-2LL
<i>Puma</i>					
$\psi(-\text{DistNatRes}, +\text{LgPreyER}, -\text{DistForest}, +\text{DistGameRes}); p(+\text{CameraSite}, -\text{DogER}, -\text{CattleER})$	1,115.02	0.00	0.14	9	1,096.76
$\psi(-\text{DistNatRes}, +\text{LgPreyER}); p(+\text{CameraSite}, -\text{DogER}, -\text{CattleER})$	1,115.59	0.58	0.10	7	1,101.43
$\psi(-\text{DistNatRes}, +\text{LgPreyER}, -\text{DistForest}); p(+\text{CameraSite}, -\text{DogER}, -\text{CattleER})$	1,115.66	0.64	0.10	8	1,099.45
$\psi(-\text{DistNatRes}, +\text{LgPreyER}, +\text{DistGameRes}); p(+\text{CameraSite}, -\text{DogER}, -\text{CattleER})$	1,115.75	0.73	0.09	8	1,099.54
$\psi(-\text{DistNatRes}, +\text{LgPreyER}, -\text{DistForest}, +\text{DistGameRes}, +\text{CattleER}); p(+\text{CameraSite}, -\text{DogER}, -\text{CattleER})$	1,116.04	1.03	0.08	10	1,095.73
$\psi(-\text{DistNatRes}, +\text{LgPreyER}, -\text{DistForest}, +\text{DistGameRes}, +\text{DistRoad}); p(+\text{CameraSite}, -\text{DogER}, -\text{CattleER})$	1,116.18	1.16	0.08	10	1,095.86
$\psi(-\text{DistNatRes}, +\text{LgPreyER}, +\text{DistGameRes}, +\text{CattleER}); p(+\text{CameraSite}, -\text{DogER}, -\text{CattleER})$	1,116.60	1.60	0.06	9	1,098.34
$\psi(-\text{DistNatRes}, +\text{LgPreyER}, -\text{DistForest}, +\text{DistGameRes}, -\text{DogER}); p(+\text{CameraSite}, -\text{DogER}, -\text{CattleER})$	1,116.68	1.66	0.06	10	1,096.36
$\psi(-\text{DistNatRes}, +\text{LgPreyER}, +\text{CattleER}); p(+\text{CameraSite}, -\text{DogER}, -\text{CattleER})$	1,116.74	1.73	0.06	8	1,100.54
$\psi(+\text{DistForest}, +\text{HaresER}, +\text{ElegER}, +\text{ArmER}); p(+\text{CameraSite})$	8,166.51	0.00	0.19	7	8,152.35
$\psi(+\text{DistForest}, +\text{HaresER}, +\text{ElegER}, +\text{ArmER}, +\text{DogER}); p(+\text{CameraSite})$	8,166.54	0.03	0.18	8	8,150.33
$\psi(+\text{DistForest}, +\text{HaresER}, +\text{ElegER}, +\text{ArmER}, +\text{CattleER}); p(+\text{CameraSite})$	8,167.55	1.04	0.11	8	8,151.34
$\psi(+\text{DistForest}, +\text{HaresER}, +\text{ElegER}, +\text{ArmER}, +\text{DogER}, +\text{CattleER}); p(+\text{CameraSite})$	8,167.76	1.25	0.10	9	8,149.50
<i>Pampas fox</i>					
$\psi(+\text{DistForest}, +\text{HaresER}, +\text{ElegER}); p(+\text{CameraSite})$	8,167.76	1.26	0.10	6	8,155.64
$\psi(+\text{DistForest}, +\text{HaresER}, +\text{ElegER}, +\text{DogER}); p(+\text{CameraSite})$	8,167.92	1.42	0.09	7	8,153.76
$\psi(+\text{DistForest}, +\text{HaresER}, +\text{ArmER}); p(+\text{CameraSite})$	8,168.14	1.64	0.08	6	8,156.02
$\psi(+\text{DistForest}, +\text{HaresER}, +\text{ArmER}, \text{DogER}); p(+\text{CameraSite})$	8,168.40	1.90	0.07	7	8,154.24
$\psi(-\text{DistForest}, +\text{DistNatRes}, +\text{ArmER}, +\text{NothER}); p(+\text{CameraSite}, -\text{CattleER})$	3,408.77	0.00	0.23	8	3,392.56
<i>Geoffroy's cat</i>					
$\psi(-\text{DistForest}, +\text{DistNatRes}, +\text{ArmER}, +\text{NothER}, +\text{DogER}); p(+\text{CameraSite}, -\text{CattleER})$	3,409.60	0.83	0.39	9	3,391.34
$\psi(-\text{DistForest}, +\text{DistNatRes}, +\text{ArmER}, +\text{NothER}, -\text{CattleER}); p(+\text{CameraSite}, -\text{CattleER})$	3,410.13	1.36	0.11	9	3,391.87
$\psi(-\text{DistForest}, +\text{DistNatRes}, +\text{ArmER}, +\text{NothER}, -\text{DistRoad}); p(+\text{CameraSite}, -\text{CattleER})$	3,410.67	1.90	0.09	9	3,392.41
$\psi(-\text{ElegER}, +\text{DistNatRes}); p(.)$	442.94	0.00	0.22	4	434.88
<i>Pampas cat</i>					
$\psi(-\text{ElegER}); p(.)$	443.85	0.91	0.14	3	437.82
$\psi(+\text{DistNatRes}); p(.)$	444.20	1.26	0.12	3	438.16
$\psi(+\text{DistRoad}, -\text{DistHousing}); p(+\text{CameraSite}, -\text{CattleER})$	2,247.65	0.00	0.53	6	2,235.53
<i>Skunk</i>					
$\psi(+\text{DistRoad}, -\text{DistHousing}, +\text{DistGameRes}); p(+\text{CameraSite}, -\text{CattleER})$	2,248.81	1.15	0.30	7	2,234.65

Notes: Boldface type indicates strong impact for those variables, (i.e., 95% confidence intervals do not overlap 0). Positive (+) and negative (–) signs denote direction of explanatory variables. Variable names refer to distance to nearest forest patch (DistForest), encounter rates of large prey (LgPreyER), armadillos (ArmER), European hares (HaresER), elegant crested tinamou (ElegER), brushland tinamou (NothER), dog (DogER), and cattle (CattleER); distance to nearest village (DistHousing); distance to nearest game reserve (DistGameRes), distance to nearest natural reserve (DistNatRes), distance to nearest major road (DistRoad), and the site (open or closed) where camera trap was set up (TrapSite) in each camera trap (see Appendix S1: Table S1 for more details). AIC is the Akaike information criterion;  $\Delta AIC$  is the relative difference in AIC between the best model and every other model in the set.

absent (Fig. 3). Interestingly, Geoffroy’s cat habitat use was higher when pumas were absent, but habitat use increased (from ~0.4 to ~0.9) with increasing distance away from natural reserves and encounter rate of armadillos, while when pumas were present, habitat use stayed relatively constant (~0.3) with both covariates (Fig. 3). Also, Geoffroy’s cat habitat use increased with increasing encounter rate of brushland tinamou, both with either pumas present or absent; however, in the

presence of pumas, habitat use by Geoffroy’s cat increased exponentially for high encounter rates of brushland tinamou (>1.00), becoming higher than Geoffroy’s cat habitat use when pumas were absent (Fig. 3). The SIF between Geoffroy’s cats and pumas was <1.0 for the most part of the range of variation of our explanatory variables, and indeed declined with the distance away from reserves and with armadillo encounter rate, which overall suggests spatial avoidance.



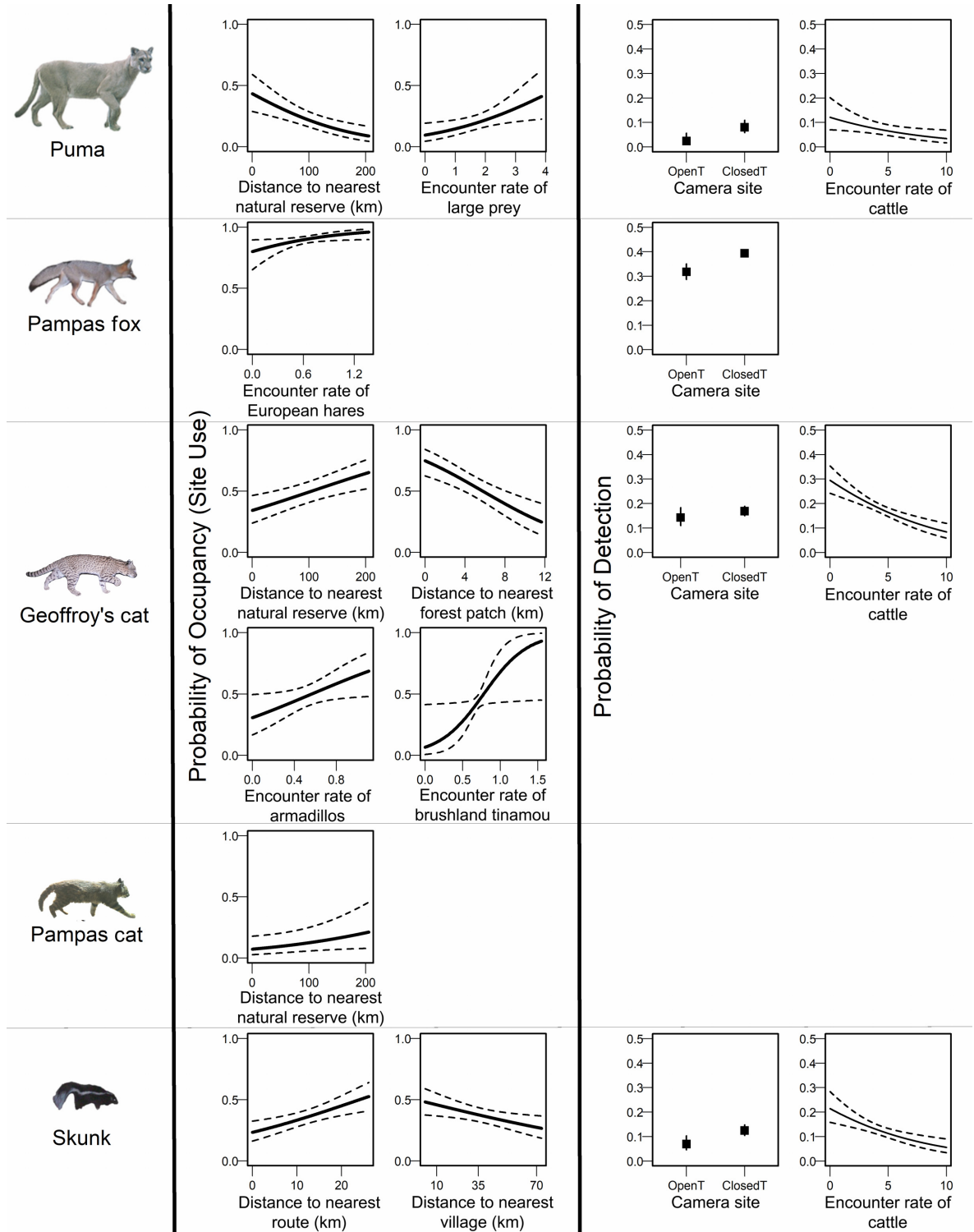


FIG. 2. Relationships between the highly influential continuous covariates based on beta estimates  $\beta$  (solid line) and 95% confident intervals (broken lines) and a categorical covariate ( $\beta$ , black square points, and 95% confident intervals, solid lines) from top single-species-occupancy models and the probability of habitat use and detection of carnivore species across 706 camera traps in Caldén forest region, Argentina, from 2010 to 2013.

TABLE 4. Estimates, standard errors (SE) and 95% confidence intervals for species interaction factors (SIF), between puma (*Puma concolor*) and mesopredators based on their spatial co-occurrence estimated across 706 camera traps, in Caldén forest region, Argentina, from 2010 to 2013.

Species	$\psi^A$ (SE)	$\Psi^{BA}$ (SE)	$\Psi^{Ba}$ (SE)	SIF	CI
Puma and Pampas Fox	0.54 (0.03)	0.97 (0.02)	0.97 (0.02)	1.00	—
Puma and Geoffroy's Cat	0.35 (0.07)	0.29 (0.08)	0.62 (0.08)	0.57	0.29–0.85
Puma and Pampas Cat	0.92 (0.05)	0.99 (0.01)	0.08 (0.15)	1.08	0.97–1.18
Puma and Skunk	0.36 (0.07)	0.18 (0.05)	0.72 (0.14)	0.35	0.16–0.54

Notes: Lack of co-occurrence is denoted by  $SIF < 1.0$  and co-occurrence by  $SIF > 1.0$ . The parameter  $\psi^A$  is the probability that the area is occupied by puma (A);  $\Psi^{BA}$  is probability that the area is occupied by subordinate species (B), given puma (A) is present;  $\Psi^{Ba}$  is probability that the area is occupied by subordinate species (B), given puma (A) is not present.

Nevertheless, the spatial distribution of both feline species might be independent when tinamous encounter rate is high (Fig. 3).

Co-occurrence of skunks and pumas indicated that skunk occupancy in the absence of pumas was higher and increased with distance away from roads (from ~0.5 to 0.9, Fig. 4). When pumas were present, skunk occupancy increased with proximity to villages. The SIFs between skunks and pumas were  $< 1.0$  indicating lack of co-occurrence, and they strongly declined, indicating even stronger avoidance, the farther away from villages and major roads, although the confidence interval was wider for distances closer to major roads (Fig. 4).

Co-occurrence models between pairs of mesocarnivores that consider different categories of puma habitat use (Table 2) showed little evidence that the dominant mesocarnivore species affected habitat use/detection of the subordinate mesocarnivore (Fig. 5, Appendix S1: Table S4). In most cases, the best model was the one with  $SIF \sim 1.0$  (pairs occurred independently). However, some species pairs including Geoffroy's cat showed a lack of co-occurrence according to the presumed hierarchy of dominance. In sites with medium puma occupancy, pampas foxes and Geoffroy's cats co-occurred less frequently than expected under independence ( $SIF = 0.87$ ), where Geoffroy's cat occupancy was lower when pampas fox was present ( $\Psi^{BA} = 0.42$ ) than when this canid was absent ( $\Psi^{Ba} = 1.00$ ; Fig. 5c, Appendix S1: Table S4). Geoffroy's cats and pampas cats also showed lack of co-occurrence in these sites ( $SIF = 0.02$ ), with occurrence of pampas cats conditioned by Geoffroy's cat presence ( $\Psi^{BA} = 0.02$ ), but when Geoffroy's cat was absent, pampas cat was ubiquitous ( $\Psi^{Ba} = 1.00$ ; Fig. 5c, Appendix S1: Table S4). Geoffroy's cat and skunks had  $SIFs < 1$  for overall data (Fig. 5a, Appendix S1: Table S4) and for low puma occupancy (Fig. 5d, Appendix S1: Table S4), such that skunk occupancy was lower when Geoffroy's cats were present.

#### Temporal activity patterns

In general, the activity of the entire predator assemblage was mainly nocturnal and crepuscular throughout the four seasons (Appendix S1: Fig. S1), although there were revealing differences. Pumas had the most

crepuscular activity, both at sunrise and at sunset, and displayed the most diurnal activity, mainly during the spring (Appendix S1: Fig. S1). Pampas foxes were predominately nocturnal but included some activity during the day, being more pronounced during the autumn (Appendix S1: Fig. S1). The smaller cats, Geoffroy's cats and pampas cats, shared a very similar pattern of activity, mainly nocturnal. Skunk activity was almost exclusively nocturnal throughout the four seasons (Appendix S1: Fig. S1).

The overlap in activity patterns between pumas and the rest of mesopredators ranged from a low of 0.70 for pumas and skunks, to a high of 0.89 for pumas and pampas cats (Fig. 6). When splitting the data into categories of puma habitat use from the single-season occupancy model, the overlap in activity patterns between pumas and the rest of mesopredators was slightly higher in sites of high, than in sites of low, puma habitat use.

Overlap in activity patterns between pumas and mesopredators did not differ noticeably with encounter rates of either cattle (ANOVA,  $F_{2,9} = 1.225$ ,  $P = 0.34$ ; Appendix S1: Fig. S2) or dogs (ANOVA,  $F_{2,8} = 1.141$ ,  $P = 0.37$ ; Appendix S1: Fig. S3). However, some differences were striking. The activity of Geoffroy's cats overlapped more with that of pumas in sites with high cattle encounter rates, while the overlap was much higher in areas of low dog encounter rates. Similarly, overlap of pampas cat with puma was highest in sites with low dog encounter rates. Puma activity patterns appeared to be more nocturnal at camera stations with high dog encounter rates and they become more diurnal at low use sites, while Geoffroy's cat behave the opposite (Appendix S1: Fig. S3). Overall, overlap between activity patterns of mesopredators did not differ according to puma site use (ANOVA,  $F_{2,15} = 0.123$ ,  $P = 0.15$ ; Appendix S1: Fig. S4).

#### DISCUSSION

Our study showed strong spatial avoidance of pumas by two of the four mesocarnivores (Geoffroy's cat and skunk). However, in line with previous studies that show context-dependent responses of mesopredators to top predators (Ritchie and Johnson 2009, Pasanen-Mortensen and Elmhagen 2015), outcomes of predator interactions were mediated by human interference (e.g.,

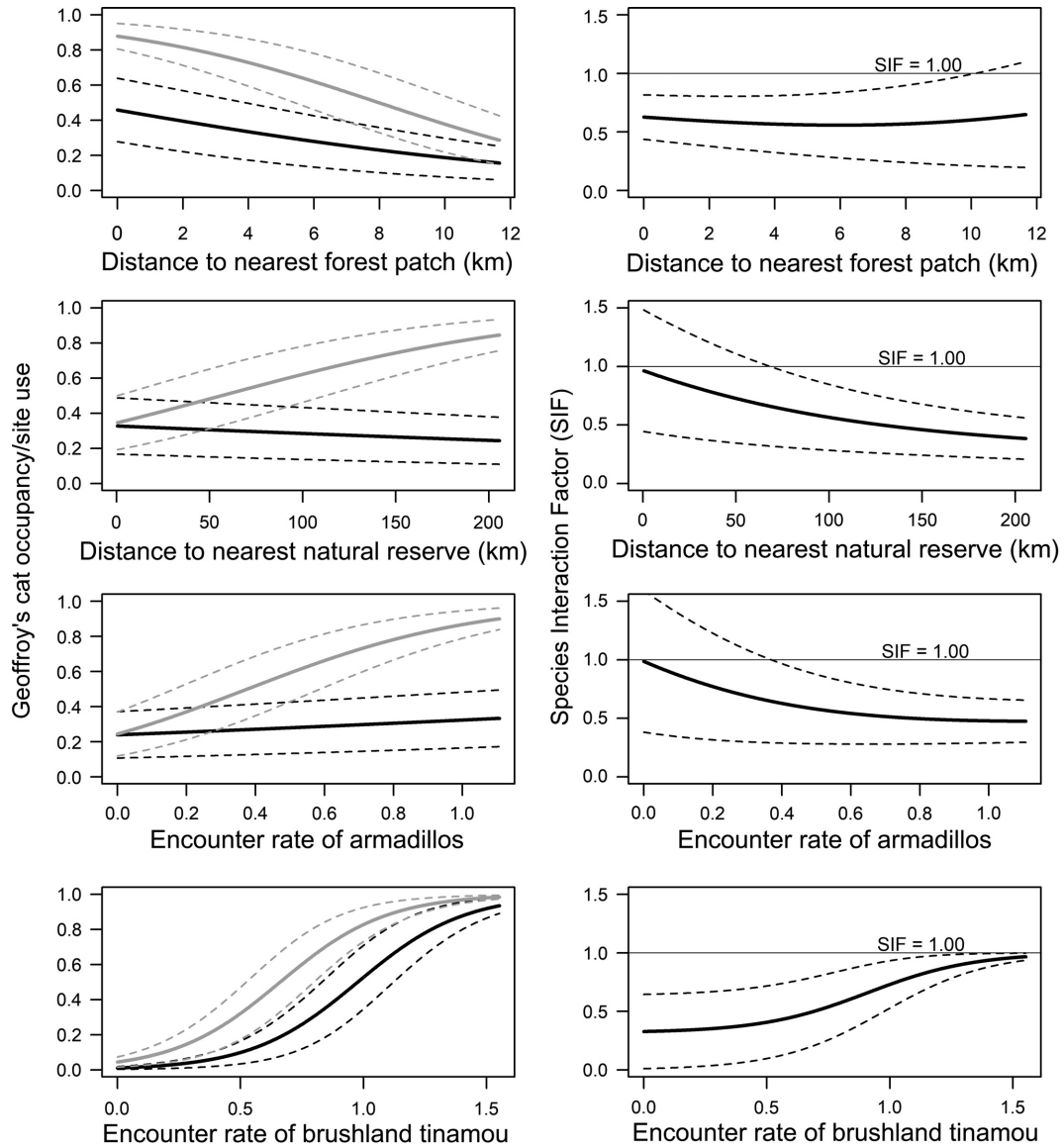


FIG. 3. Co-occurrence models displaying the probability of Geoffroy's cat occupancy (i.e., site use) when pumas are present in black lines ( $\Psi^{BA}$ ) and when pumas are absent in gray lines ( $\Psi^{Ba}$ ) as a function of covariates. The species interaction factor (SIF) between pumas and Geoffroy's cats as a function of covariates. SIF of 1.00 denotes independent occurrence (black horizontal straight lines), while  $SIF < 1.0$  indicates the lack of co-occurrence. Dashed lines show 95% confidence intervals. Data from camera-trapping records from 706 camera stations in the Caldén forest region, Argentina from 2010 to 2013.

distance from game reserves and major roads), resource availability, and habitat complexity. Avoidance of pumas by Geoffroy's cats was stronger the further away from protected natural reserves and with increasing encounter rates of armadillos. Geoffrey's cat occupancy was always higher when pumas were absent, except at extremely high tinamou encounter rates. Skunk occupancy also was higher when pumas were absent, but when present, skunk occupancy increased the closer to villages. Avoidance of pumas by skunks increased the farther away from major roads and the farther away from villages, which suggests that human activities may shield the

smaller carnivores from pumas (i.e., human shield hypothesis; Berger 2007). Contrary, we did not evidence of avoidance of pampas foxes, with highest occupancy, and pampas cats, with lowest occupancy, by pumas in this study.

A number of factors may influence competitive release of smaller predators, where human interference seems to define or modify the species interactions across the wide regional scale of our study. Direct and indirect human-mediated bottom-up and top-down processes can influence species composition and relative abundances within predatory guilds, dramatically altering complete

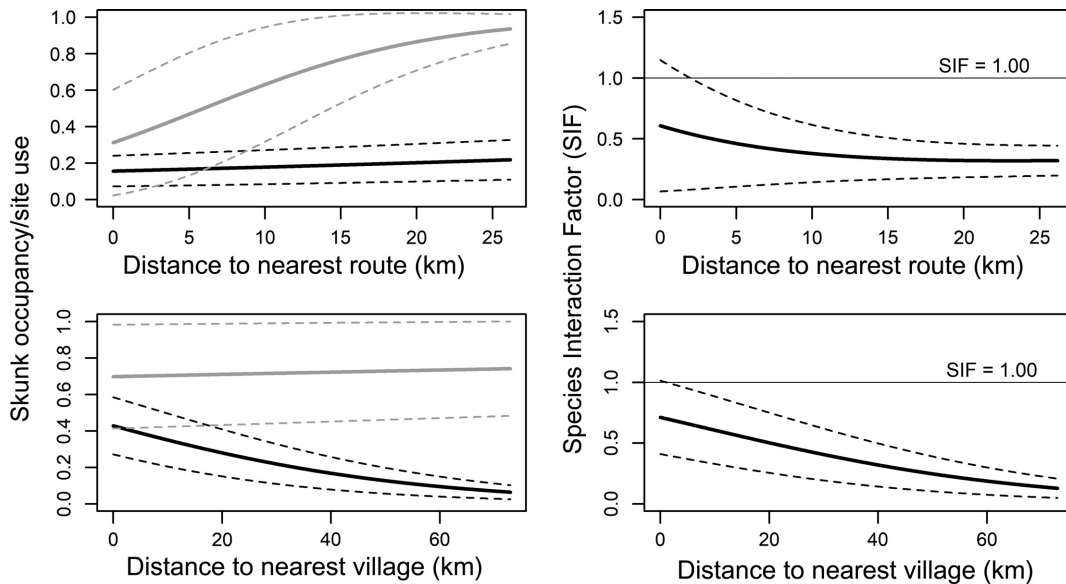


FIG. 4. Co-occurrence models displaying the probability of skunk occupancy (i.e., site use) when pumas are present in black lines ( $\Psi^{BA}$ ) and when pumas are absent in gray lines ( $\Psi^{Ba}$ ) as a function of covariates. The species interaction factor (SIF) between pumas and skunks as a function of covariates. SIF of 1.0 denotes independent occurrence (black horizontal straight lines), while  $SIF < 1.0$  indicates the lack of co-occurrence. Dashed lines show 95% confidence intervals. Data from camera-trapping records from 706 camera stations in the Caldén forest region, Argentina from 2010 to 2013.

ecological networks (Pace et al. 1999, Levi and Wilmers 2012, Dorresteijn et al. 2015, Wang et al. 2015). Human activities associated with livestock raising and poaching can reduce habitat quality, alter interspecific relationships, and distort coexistence among predators, both in space and in time, by decreasing natural abundances of puma, which would dampen controlling effects on mesopredator populations. In addition, hunting pressure on apex predators (i.e., human top-down effect) can affect their spatial and temporal distribution (Prugh et al. 2009). As expected, puma habitat use had a positive relationship with proximity to natural reserves, such that these areas likely function as important sources in a metapopulation structure. Human interference promotes a puma source-sink population dynamic between protected and productive areas (game reserves and cattle ranches), where they are hunted as a trophy (Zanón Martínez et al. 2016a, b) or pest species (Guerisoli et al. 2017). Surplus pumas from natural reserves could be attracted to game reserves by good habitat and high prey (exotic ungulates) availability, where these reserves could act as ecological traps for pumas. This aligns with higher puma densities estimated in the protected area (4.90 pumas/100 km<sup>2</sup>) compared to the game reserve (1.38 pumas/100 km<sup>2</sup>, Zanón Martínez et al. 2016a, b) and cattle ranches (0.88 pumas per 100 km<sup>2</sup>; J. I. Zanón Martínez, unpublished data). However, in all these productive areas (i.e., game reserves and cattle ranches), pumas are heavily hunted, which could lead to increases in Geoffroy's cats and possibly pampas cats (habitat use increased with distance away from natural reserves),

unless pampas cat are suppressed by Geoffroy's cat, which our results indicate could be a possibility.

In undisturbed ecosystems such as protected areas, apex predators are usually abundant and they can also benefit generalist mesopredators that behave as scavengers, frequently taking advantage of carrion provided by apex predators (Allen et al. 2015, Perrig et al. 2017). For example, pumas hunt and kill large prey, providing carrion both to scavengers and generalist mammalian predators (Perrig et al. 2017), such as the pampas foxes and skunks (Travaini et al. 1998, García and Kittlein 2005), which can impact their local density and activity patterns (Perrig et al. 2017). However, our results did not support this scavenging hypothesis, given that pampas foxes did not co-occur with pumas (independent occurrence) and if skunks appear to strongly avoid areas with pumas. One explanation is that human activities could subsidize the region with food through animal carcasses (i.e., human-mediated bottom-up process), either naturally dead cattle or hunted wild ungulates, and thus these species are found closer to human impacted areas. Skunks did follow this pattern with higher occupancy near villages but pampas fox occupancy was 87%, which shows they are ubiquitous, using all available habitats in the Caldén forest region. The fact that skunks, with their much smaller body size and phylogenetic distance, still avoided pumas, could be due to a combination of attraction to human areas and interference competition, since other studies in the same region have documented pumas killing or preying on skunks (Pessino et al. 2001, Zanón Martínez et al. 2016a, b).

On the other hand, in protected areas, where ecological mechanisms are not distorted by humans, the competitive release of smaller predators should be explained by other factors. Past studies have shown that antagonistic behaviors are more frequent and intense the closer species are in phylogeny (Gittleman 1985, Donadio and Buskirk 2006). This may explain the apparent spatial avoidance between pumas and Geoffroy's cats, and Geoffroy's cat and pampas cats, but we did not find such evidence for pumas and pampas cats in our study. Our SIF value for pumas and pampas cats was  $>1.0$  that could occur if pumas suppress Geoffroy's cats causing an indirect positive association. However, these results were inconclusive due to 95% CIs on the SIF overlapping one.

Zanón Martínez et al. (2016a) documented that Geoffroy's cats were often consumed by pumas in a protected area in the same region, and thus intraguild predation may explain spatial avoidance of pumas. In contrast, indirect competition for prey does not seem to explain this pattern. Pumas prey mostly on species of large and medium body size in the Caldén forest (Sarasola et al. 2016, Zanón Martínez et al. 2016a, b), while smaller cats prey mostly on small prey such as rodents and birds (Bisceglia et al. 2008, Santillán and Constán 2014). Indeed, occupancy models for pumas showed a positive relationship with encounter rates of the introduced large ungulate prey: red deer and wild boar, while Geoffroy's cat occupancy increased with medium prey (armadillos and brushland tinamous). Habitat segregation could also explain the pattern of co-occurrence for pumas and Geoffroy's cats. Pumas are known as generalists that occupy many different environments and have the largest habitat range within the felids (Sunquist and Sunquist 2002). Geoffroy's cats tend to use habitats with complex vegetation structure, which matches our finding of increased habitat use with proximity to forest patches, suggesting that they may select more closed habitats, perhaps searching for protective cover (Pereira et al. 2006). However, Geoffroy's cats can also use disturbed and anthropogenic environments (such as croplands), likely tracking small prey availability (Caruso et al. 2016).

While we did document spatial avoidance among many carnivore pairs, we did not find as much evidence of temporal segregation. Subordinate carnivores have been shown to shift their activity patterns to avoid encounters with dominant carnivores. For example, where wolves (*Canis lupus*) are abundant and ecologically effective, coyotes (*Canis latrans*) are absent, occur at low density, or alter their activity patterns to avoid wolves (Ripple et al. 2013). Human activity has also been reported to modify the daily activity patterns of wildlife toward nocturnality, especially outside protected areas where there is poaching pressure on pumas and a high diurnal human activity (Paviolo et al. 2009, Zanón Martínez et al. 2016a, b). We found that all species exhibit mostly nocturnal and crepuscular activity

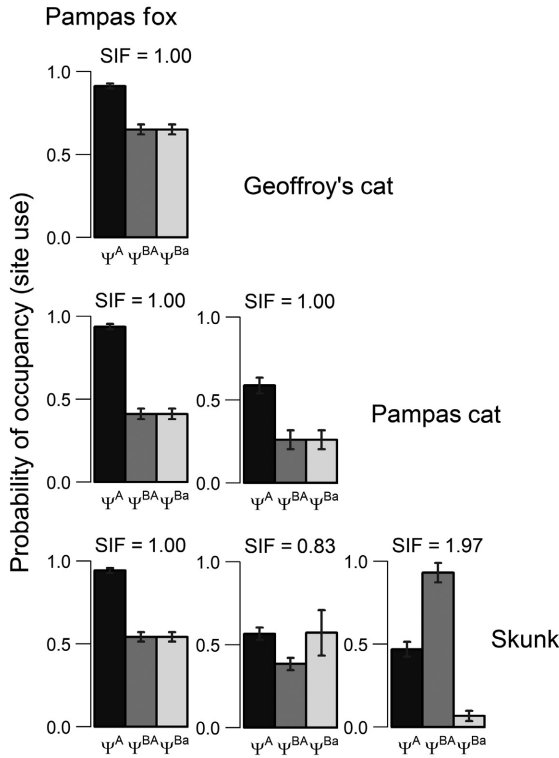
throughout the year, including those seasons with shorter days (i.e., autumn and winter). But we found little evidence that mesopredators change their temporal activity patterns to avoid pumas when they occur at low or even high puma occupancy. We also found some influence of the proxies of human activity on carnivores. Puma activity patterns appeared to be more nocturnal at camera stations with high dog encounter rates and they become more diurnal at low use sites, while Geoffroy's cat follows the opposite trend. Perhaps pumas are more sensitive to dog harassment than Geoffroy's cat. Human activities are ubiquitous in our study area and this may distort the mechanisms of community assemblage in complex ways.

The interactions between mesopredator pairs showed that, at low and intermediate puma occupancy levels, spatial avoidance occurred between three species pairs: pampas foxes and Geoffroy's cats, Geoffroy's cats and pampas cats, and Geoffroy's cats and skunks. Interestingly, at high puma occupancy, all mesopredator interactions were independent, suggesting pumas may suppress negative interactions between mesopredators. For only one pair, pampas cats and skunks, did we find evidence of co-occurrence, and only with all data combined regardless of puma occupancy level. Pampas foxes and Geoffroy's and pampas cats have similar body sizes and are thus expected to use the same prey base (Rosenzweig 1966) and to directly compete for the same type of food (Donadio and Buskirk 2006), which should increase interference competition, in line with our findings of spatial avoidance.

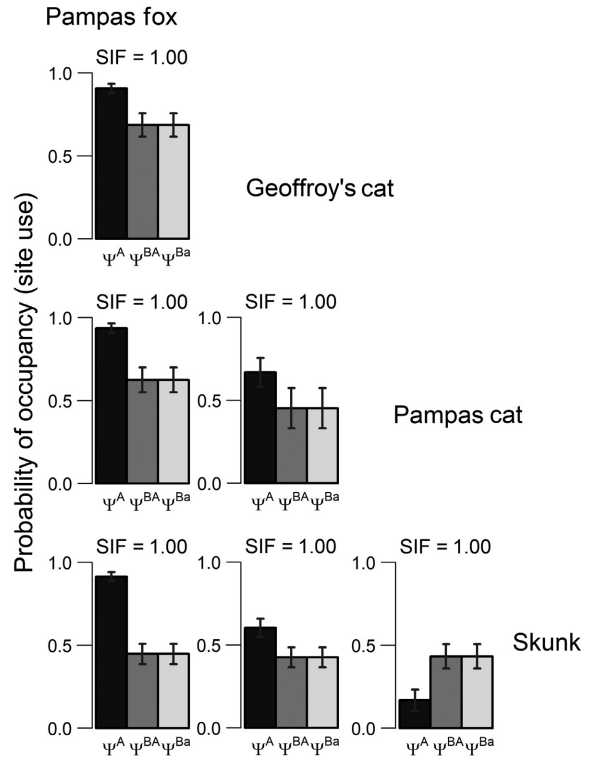
Temporally, overlap in activity patterns of mesopredators was mixed, sometimes higher and sometimes lower at sites with high, medium, and low puma occupancy. But Pampas foxes and Geoffroy's cats increased in temporal overlap as puma site use declined, and Geoffroy's cat and pampas cat had the highest overlap at low puma occupancy. Perhaps low puma habitat use facilitates the release of smaller carnivores to overlap more temporally, in accordance with the mesopredator release hypothesis.

Pumas are widespread in our study area, but occur at low densities in the arid and low-productive environments that are characteristic of the Caldén forest (Zanón Martínez et al. 2016a, b). Smaller predators, such as the pampas cats, may also occur in low numbers in the Caldén forest (Caruso et al. 2012), while Geoffroy's cats may attain high abundances in the region (Pereira et al. 2011, Caruso et al. 2012). But, even at low densities, when the likelihood of direct antagonistic encounters is much reduced, it has been shown that indirect encounters between predators and with their potential prey, mediated by scent marks, may produce avoidance behaviors (Ripple and Beschta 2004, Apfelbach et al. 2005). We found evidence of habitat- and human-mediated influences on species interactions, including several instances of potential avoidance behaviors between carnivores, despite low densities of some species.

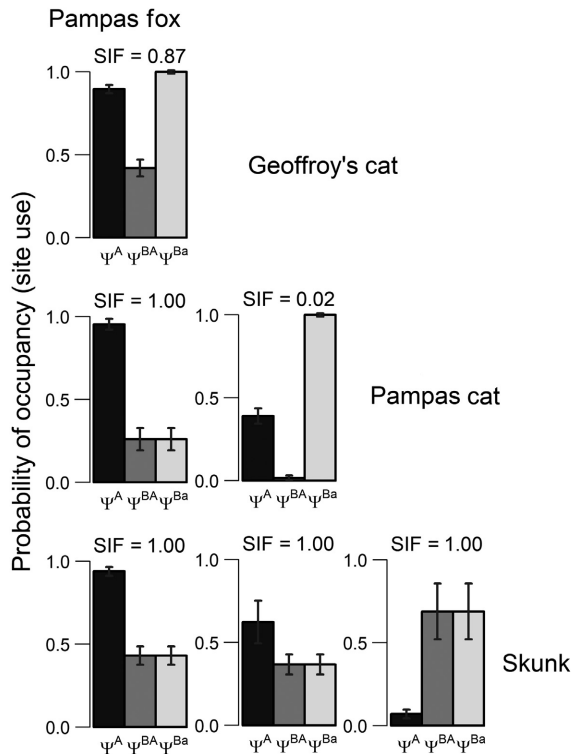
a) Overall puma occupancy



b) High puma occupancy



c) Medium puma occupancy



d) Low puma occupancy

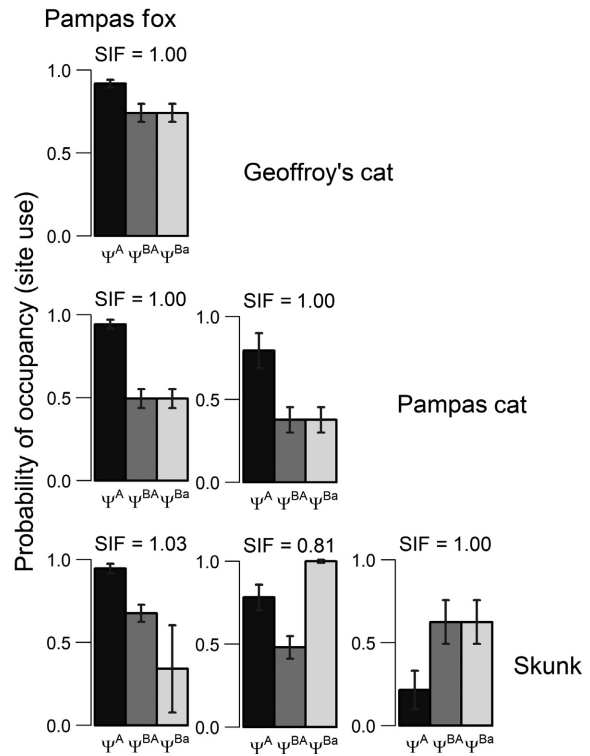


Fig. 5. Co-occurrence between pairs of mesopredators in Caldén forest region, Argentina, from 2010 to 2013, (a) over all 706 camera stations and at stations with (b) high ( $n = 177$ ), (c) medium ( $n = 176$ ), and (d) low ( $n = 177$ ) probabilities of puma occupancy from single species models. The parameter  $\psi^A$  (black columns) is the probability that the area is occupied by dominant species A;  $\psi^{BA}$  (medium gray columns) is the probability that the area is occupied by subordinate species B given that dominant species A is present;  $\psi^{B\bar{A}}$  (light gray columns) is the probability that the area is occupied by subordinate species B given that dominant species A is not present. SIF is the species interaction factor with SIF = 1.0 indicating independent occurrence, SIF < 1.0 indicating lack of co-occurrence, SIF > 1.0 indicating co-occurrence between mesocarnivores. Species are ordered from top to bottom according to their presumed hierarchy of dominance.

Our research contributes important information about ecological processes outside protected areas to improve the management and conservation of wildlife populations. The puma is currently the apex predator in many South America systems. We found that pumas do influence subordinate predators in complex way and that protected areas and high-quality habitats (i.e., high abundances of large and medium prey) are important factors determining spatial distribution of carnivores, especially pumas. These protected areas might have a

different effect on the species, as our results indicated, depending on the main habitat protected and species preferences. Thus, to conserve top predators and mesopredators, it is necessary to create new protected areas in the region, because currently <1% of the entire area of La Pampa province is protected. New protected areas linked by small forest patches would likely lead to increased predator and prey abundances. It is essential that we continue to improve our understanding of human impacts on the entire predator assemblage to

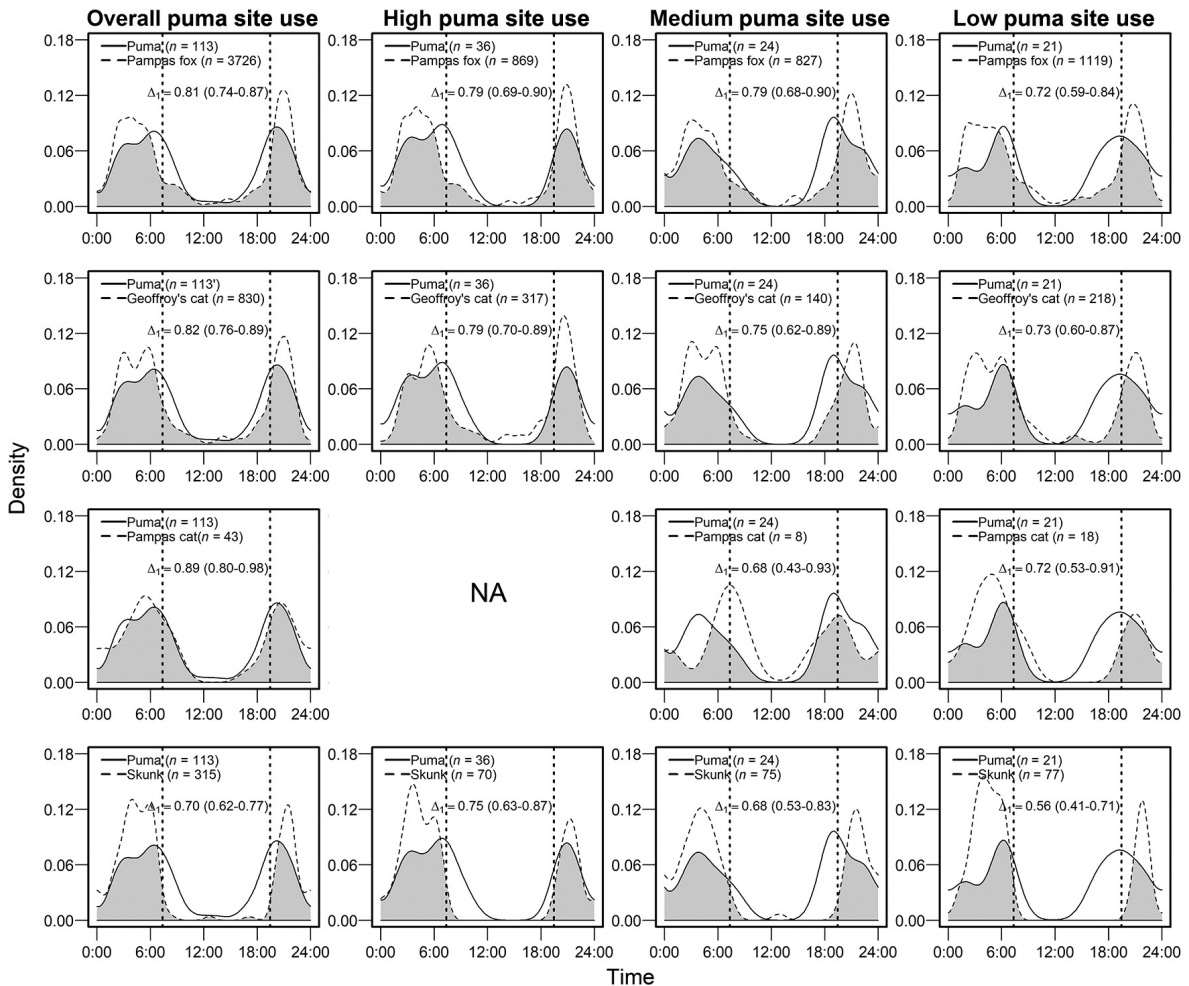


Fig. 6. Kernel density estimation on circular data from camera-trapping records of activity patterns of pumas vs. three mesopredator species in areas of high ( $n = 177$ ), medium ( $n = 176$ ), low ( $n = 177$ ), and overall ( $n = 706$ ) puma occupancy (from top single puma model and the probability of puma habitat use) in Caldén forest region, Argentina, from 2010 to 2013. The coefficient of overlap ( $\Delta_1$ ) equals the area below both curves, shaded gray. The x-axis is time with the vertical black dashed lines representing the sunrise the sunset and 12:00 representing noon. NA indicates  $\Delta_1$  was not calculated because the number of records was too few.

inform decisions that enhance ecosystem functions and services, trophic structure, and the interactions among carnivores inside and outside of protected areas.

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## SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2482/full>

## OPEN RESEARCH

Data (Zanón Martínez et al. 2021) are available on the Dryad digital repository: <https://doi.org/10.5061/dryad.5qfttdz42>