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Ravines as conservation strongholds for small wildcats under pressure from free-ranging dogs and cats in Mediterranean landscapes of Chile

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ABSTRACT

The Chilean Mediterranean ecosystem is threatened by anthropogenic pressures, such as habitat loss by intensive agriculture and urban sprawl. Abandoned dogs (*Canis lupus familiaris*) and cats (*Felis silvestris catus*) pose conservation challenges for Chilean wildlife including the pampas cat (*Leopardus colocolo*) and the güiña (*Leopardus guigna*). We used camera trap data to investigate influences of natural and anthropogenic landscape features on spatiotemporal trends of these species. We also used co-occurrence modeling and kernel density estimation to investigate spatial and temporal patterns overlap of wildcats, free-ranging (FR) dogs, and FR-cats. FR-dogs showed the highest detection and site use probabilities, while güiñas had the lowest across 80 camera trap sites. Top models showed no spatial avoidance between species and co-occurrence of wildcats was positively influenced by forest habitat. However, FR-dogs negatively affected detection of wildcats. Ravines surrounded by forest positively influenced güiña and pampas cat detection probabilities when dominant species were not present. FR-dogs and wildcats had significantly different temporal activity patterns and low overlap coefficients, while wildcats and FR-cats showed high overlap in activity patterns. We suggest changing current policies to control domestic animals and strategic planning in agricultural areas of central Chile to better conserve native wildcat species.

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Introduction

Wildlife species are under multiple pressures that impact their survival and their community level interactions in human-modified landscapes across the world (Crooks 2002; Bateman & Fleming 2012; Lewis et al. 2015; Di Minin et al. 2016). Landscape change not only reduces available native habitat but also leads to an increase in human-facilitated populations of free-ranging (hereafter, FR) dogs (*Canis lupus familiaris*) and cats (*Felis silvestris catus*), which have become major concerns given their detrimental effects on wildlife (Vanak & Gompper 2010; Hughes & Macdonald 2013; Gompper 2014; Bonacic et al. 2019). Both FR-carnivore species have been listed among the most widespread and destructive invasive species worldwide, even in remote areas (Cassano et al. 2014; Zapata-Ríos & Branch 2016; Farris et al. 2016; Treves & Bonacic 2016).

Small wildcats are a group of species that can be severely affected by the presence of FR-dogs and FR-cats through predation (Silva-Rodríguez & Sieving 2011; Hughes & Macdonald 2013; Schüttler et al. 2018), competition (Vanak & Gompper 2010; Young et al. 2011; Cruz et al. 2018) and disease transmission (Acosta-Jamett et al. 2011; Mora et al. 2015; Sieg et al. 2020). Wildcats provide valuable ecosystem services such as controlling populations of small mammals (e.g. rodents and rabbits) that usually cause significant damage to agricultural crops (Roemer et al. 2009; Williams et al. 2018). In anthropized areas, wildcats are usually forced to survive in small remnant habitat patches. Habitat encroachment may increase the potential for competition and the chances of direct or indirect encounters with FR-dogs and FR-cats (Crooks 2002; Lewis et al. 2017; Cruz et al. 2018). Dominant (commonly larger) species, like FR-dogs and FR-cats, may exclude smaller subordinate species, such as wildcats, from territories (Linnell & Strand 2000; St-Pierre et al. 2006; Farris et al. 2016; Cruz et al. 2018). In turn, subordinate species

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may avoid locations with higher dominant species activity or density (Farris et al. 2016), modify their circadian activity patterns (Zapata-Ríos & Branch 2016), and/or adopt defensive behaviors to reduce the risk of encounters with dominant species (Vanak et al. 2013). A better knowledge of spatiotemporal patterns and interactions among species is needed to understand how wildcats, FR-dogs and FR-cats coexist, which is essential for designing strategic plans for wildcat conservation and domestic animal management in human-modified environments.

Mediterranean ecosystems worldwide are suffering severe land-use changes as a result of agricultural and urban sprawl (Underwood et al. 2009; Cox & Underwood 2011). These Mediterranean regions harbor protected, but also unprotected, natural and semi-natural areas (e.g. private lands), some of which support numerous native species and their associated habitats (e.g. Soto & Palomares 2015). For instance, the Iberian lynx (*Lynx pardinus*) and the European wildcat (*Felis silvestris*) are two wild felids that inhabit Mediterranean areas and have long been threatened by habitat loss, fragmentation and degradation, as well as by hybridization with domestic cats (i.e. *F. silvestris*). Central Chile is the Mediterranean area with the greatest proportion of its land in the unprotected category (75%), but with high conservation potential (Cox & Underwood 2011; Márquez-García et al. 2019). This area is a biodiversity hotspot that is inhabited by more than half of the country's human population and has a long history of land use changes (Armesto et al. 2007). Furthermore, Chile has the highest percentages of FR-dogs in South America, due to the high levels of dog abandonment and lack of responsible ownership (Acosta-Jamett 2015; Schüttler et al. 2018).

Mediterranean central Chile still offers habitat for wild carnivores including two small wildcats, the pampas cat (*Leopardus colocolo*; 3–4 kg) and the güiña (*Leopardus guigna*; ≤ 2 kg). Both species are listed among small Neotropical wildcats that urgently require *in situ* research (Brodie 2009). The pampas cat is considered Near Threatened and the güiña is Vulnerable to extinction according to IUCN Red List (Napolitano et al. 2015; Lucherini et al. 2016). Both species are declining due to extensive habitat loss and degradation, predation by dogs, hunting, and road kills. To date, studies regarding the natural history or ecology of small wildcats in Mediterranean central Chile are scarce (but see García et al. 2020; Napolitano et al. 2020). The few studies on pampas cats that have been conducted on diet, habitat use, and activity patterns are mainly in the northern Andean deserts of Chile (Napolitano et al. 2008; Lucherini et al. 2009). Güiñas have been studied in the temperate rainforests of Southern Chile where they tolerate a high degree of habitat loss (Gálvez et al. 2013, 2018; Delibes-Mateos et al. 2014; Hernández et al. 2015; Fleschutz et al. 2016).

Little is known about the presence of small wildcats in the Mediterranean eco-region of central Chile and there are no studies on the patterns of spatiotemporal co-occurrence with FR-dogs and FR-cats. In this study we focus on the ensemble of wildcats, FR-dogs and FR-cats, and we assessed the (i) spatiotemporal patterns (i.e. species capture rates, spatial distribution (occupancy), and temporal activity patterns); (ii) inter-specific co-occurrence and co-detection probabilities; and (iii) how likely two species could spatially co-occur based on the species interaction factor (i.e. odds ratio for either positive, neutral, or negative associations; Farris et al. 2016; Osorio et al. 2020). We explored the extent to which natural habitat and human modification of the landscape influenced species co-occurrence/co-detection within a conditional two-species occupancy modeling framework (Richmond et al. 2010). We examined whether site use and detection probabilities of the subordinate wildcats were influenced by the presence and detectability of dominant FR-dogs and FR-cats across the landscape. We expected an increase in negative associations between wildcats and FR-dogs and FR-cats as human influence increases. Based on results, we discussed recommendations for conservation and management of wildcats, FR-dogs, and FR-cats, and provide insights regarding habitat and land management and conservation in Mediterranean landscapes where multiple land uses occur.

Material and methods

Study area

The study was conducted in a Biosphere Reserve (BR) known as 'La Campana-Peñuelas BR' (CPBR) (estimated total area: 241,787 ha) in the Mediterranean region of central Chile (Figure 1). The area is characterized by a temperate climate with austral hot-dry summers (December to March) and cold-rainy winters (June to September) (Schulz et al. 2010). Similar to many BRs in Mediterranean ecosystems, the CPBR is highly fragile due to agricultural practices, deforestation, fires, and urban sprawl and is divided into three main land uses: (a) transition zones (77%); (b) buffer zones (16%); and (c) three core protected areas (7%) (Moreira-Muñoz & Salazar 2014; Salazar et al. 2015). The vegetation mosaic includes native habitats (sclerophyll forests and scrub), exotic plantations (e.g. *Eucalyptus globulus* and *Pinus radiata*), and various crops (e.g. vineyards), which are differentially distributed across the area. Between 1985 and 2011, CPBR has shown an increase in urban (~2670 ha) and agricultural areas (~6000 ha) (Salazar et al. 2015). Consequently, native habitats are surrounded by agricultural fields, rural households associated with farms, roads, and main human settlements (Schulz et al. 2010). Abandoned dogs and cats, or those lacking human control, are regularly

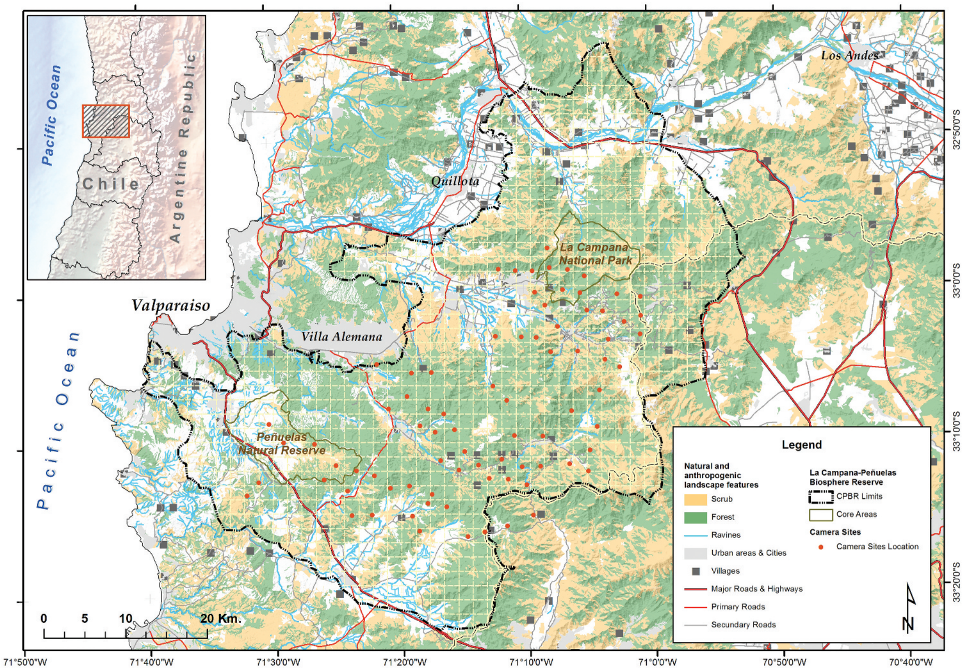


Figure 1. Camera sites (n = 80) established for wildcats and free-ranging dogs and cats in La Campana-Peñuelas Biosphere Reserve, Chile in 2012 and 2013.

seen free-roaming in rural areas. Many farmers and winegrowers have maintained hills and ravines with patches of native forest and scrub on their lands within the CPBR.

Sampling design

A total of 80 sampling units were surveyed using stratified random sampling by type of habitat (Figure 1). Each sampling unit consisted of a grid cell of 300 ha, classified by type of vegetation using ArcGIS 10.1 (ESRI 2011) as follows: (a) native habitats (sclerophyll forest or scrub); (b) agricultural crops (e.g. vineyards); (c) exotic plantations (e.g. Eucalyptus) and mixed vegetation (native vegetation ≥ 50%). We removed all sampling units with non-native vegetation, inaccessible sites and those without entry consent. A total of 48 forest and 32 scrub sampling units from available cells and according to habitat availability were chosen. At each sampling unit a single camera (Bushnell Trophy Cam HD #119,537 model, Overland Park, Kansas, United States) was installed (hereafter, sites). We had three survey deployments. Our first initial deployments had a total of 10 sites from January to September 2012 followed by another deployment of 10 sites, different from the first deployment, from January to May 2013. Both of these initial survey deployments, together with the third, served as a dataset for capture rates and activity patterns (see below). The third deployment included all 80 sites with two rotation periods of 40 cameras each between July and December 2013 to evaluate occupancy and co-occurrence of target species (see below).

Cameras were placed ≥2 km apart at neighboring sites in natural trails outside human-used trails. Lure (WildCat Hawbaker's Lure®, Fort Loudon, Pennsylvania, United States) and catnip spray were used at all sites to increase detection probability of carnivores. To validate the minimum distance between camera sites, we applied L-function (Besag's transformation of Ripley's K-function) using the R-package 'spatstat' (Baddeley et al. 2020) in R software v.3.2.3 (R Development Core Team 2015; see Appendix S1 in the online supplemental material for details). This analysis showed that the mean distance between neighboring camera sites was 2503.37 m (minimum 2 km and maximum 3 km).

Measurement of covariates

We measured predictor covariates that represented the extent of natural habitat and human influence, which have been shown to be relevant for carnivores overall and for our target species in other areas (Long et al. 2011; Gálvez et al. 2013; Sepúlveda et al. 2015; Fleschutz et al. 2016; García et al. 2020; Osorio et al. 2020). From each camera site, we determined the sclerophyll forest and scrub cover proportion using the Native Forest Inventory of the National Forestry Corporation of Chile (CONAF 2011) and estimated the Euclidian distances to the nearest ravine, primary road, secondary road, and human settlement by ArcGIS. Habitats and distance to the nearest ravine were considered natural covariates, while distances to human settlements, primary roads, and secondary roads were anthropogenic ones. Sclerophyll forests (e.g. *Cryptocarya alba* and *Peumus boldus* species) are secondary native forests growing after anthropogenic disturbances (e.g. fire or clearcutting) and remnants are restricted to steep hills of the coastal mountain range and ravines. Ravines include native hygrophilous forest species with either surface or underground water. Scrub includes succulent and tall scrub vegetation (e.g. *Acacia caven*) concentrated on plains and slopes (Schulz et al. 2010).

We expected the probability of occupancy of both wildcats to be positively influenced by natural habitats, in particular, sclerophyll forest, which has been regarded as an influential variable to güiña spatial distribution (e.g. Fleschutz et al. 2016; Schüttler et al. 2017). We also expected that the probability of detection would increase for both wildcats closer to ravines because they are water sources and potential refuges that could facilitate their movements between habitat patches (e.g. Hilty & Merenlender 2004). Since human influence increases near human settlements and roads, we expected site use and detection probabilities of wildcats to increase farther away from these landscape features. For FR-dogs and FR-cats we expected the opposite: a higher probability of site use and detection in scrub habitats situated in areas near human settlements and roads, such as has been reported elsewhere (Kays & DeWan 2004; Silva-Rodríguez et al. 2010; Ferreira et al. 2011).

We used the Z-score method to normalize all covariate values for our occupancy models and verified collinearity between continuous variables by Pearson's product-moment ($p < 0.05$) or Spearman's rho tests (cutoff value $| r | > 0.70$) using R software. We did not include correlated variables in the same model. To control for spatial autocorrelation, covariates were previously corrected to incorporate the variation explained by a Map of Spatial Eigenvectors, i.e. the variation explained by spatial autocorrelation. Covariate corrections were performed using the R-package 'spdep' (Bivand et al. 2009).

Daily capture rates, probability of occupancy and detection of carnivores

We considered the active sampling period, expressed as camera-days (e.g. Osorio et al. 2020), as calculated by the total days elapsed between the camera setting date and camera recovery date or the last effective photographic record if a camera was not functioning upon retrieval. With the data of all of our deployments, we calculated two independent capture events. First, we calculated capture events at 60-min intervals to estimate species daily activity patterns. Photographs of the same species within a 60-min interval were considered as a single and independent capture event (CE_{60min}), unless animals were clearly different individuals (i.e. records of different individuals included within the 60-min interval). In our case, individual differentiation was only possible for some domestic dogs and cats by collar, coat patterns and breed.

We also used capture events at 24-h intervals to estimate the general activity level for species in our study area as a capture rate. This Daily Capture Rate (DCR) considered all photographs of the same species within a 24-h time-frame (as a single independent capture event), divided by total camera-days at each site and multiplied by 100 camera-days (O'Brien et al. 2003). DCR is considered a low biased estimator of trap rates when several species are compared across sites and has been used as a proxy of activity level in other studies (e.g. Hilty & Merenlender 2004; Farris et al. 2016; Osorio et al. 2020). We applied a Mann–Whitney U test to assess significant differences between species' DCR ($\alpha = 0.05$) using the R-package 'stats'. We used the Moran's *I* index with a matrix of Euclidean distances to estimate spatial autocorrelation of the DCRs by species (see Appendix S2 for method details).

With our third survey deployment (July–December 2013) we used an occupancy modeling approach (Mackenzie et al. 2006) to determine the probabilities of occupancy (*psi*) and detection (*p*) of wildcats, and FR-dogs and FR-cats. We surveyed the 80 sites for 105 days and we assumed that changes in species' migration or dispersion were unlikely to occur, thus, the occupancy status remained static within this time (i.e. closure assumption; Mackenzie et al. 2006; Linkie et al. 2007; Shannon et al. 2014). Because we used relatively close camera spacing compared to the home ranges of wildcats, our interpretation of *psi* represents the probability of site use rather than true occupancy (e.g. Farris et al. 2016).

We evaluated the influence of predictor covariates for *psi* and *p* of natural habitat cover and human impacts in the landscape for our study species using maximum likelihood estimation within single-species, single-season models in the program PRESENCE, version 12.7 (Hines 2006). Binary capture histories were built for each species using independent DCRs to determine the presence or absence of target species at each camera site and we further collapsed data into 5-day blocks (sampling occasions) to improve model convergence. Thus, sampling occasions at sites totaled either 12 or 9 five-day blocks (e.g. Linkie et al. 2007). Camera malfunctions between maintenance checks were considered missing observations in the capture histories of our sampling occasions.

Model selection was conducted in two stages. We first modeled *p* using predictor covariates, while holding *psi* constant, to find the model that best explained detection (Mackenzie et al. 2006; Schuette et al. 2013). Then, we modeled *psi* while fixing *p* constant. Finally, the best models for *p* and *psi* were combined, to find the overall best model that explained both parameters simultaneously (e.g. Long et al. 2011; Silva-Rodríguez & Sieving 2012; Osorio et al. 2020). We ranked models using Akaike's Information Criterion (AIC) and considered models with a ΔAIC of ≤ 2 as competing (Burnham & Anderson 1998). We conducted a goodness of fit test on our general model to ensure the data fit the underlying model structure. We reported model averaged parameter estimates (*psi* and *p*) from competing models (ΔAIC ≤ 2) and the predictor covariates from the top-ranked models (ΔAIC = 0).

Spatial co-occurrence analysis

We assessed co-occurrence, co-detection, and interactions between species via two-species occupancy modeling, including the influential predictor covariates from our single-species models (Mackenzie et al. 2006; e.g. Osorio et al. 2020). We used the conditional parameterization (*psi*Ba/*r*Ba) for single-season co-occurrence proposed by Richmond et al. (2010), modeled in PRESENCE. The goal of this modeling approach is to determine whether a site is occupied (used in our case) by two different species, and to assess if the 'dominant' species affects the 'subordinate' species' occupancy and detection probabilities. For that, we must assume a 'subordinate' species (denoted as B) and a 'dominant' species (denoted as A). We assumed that the dominant species would have a similar or larger body size and potential for superior defense mechanisms, so they could interfere and exclude smaller subordinate species from our sampled sites. We considered domestic dogs as a dominant species to all others due to growing evidence that they harass, kill, and compete with wild carnivores and other threatened fauna (Silva-Rodríguez & Sieving 2011; Sepúlveda et al. 2015; Schüttler et al. 2018). The domestic cat also was assumed a dominant species to wildcats, that could alter wildcats' behavior. However, due to similarities in body size with wildcats, we also modeled domestic cats as a subordinate species that could be less proficient in wild environments than wildcats (e.g. pampas cat), and because of information gaps on FR-cat behaviors in natural areas of Chile. Additionally, the pampas cat was assumed dominant to the güiña given its larger body size (Iriarte & Jaksic 2012; Hunter 2019).

We estimated eight parameters (Richmond et al. 2010). The first three parameters represent the probabilities of occupancy of either the dominant (species A) or subordinate (species B): (1) *psi*A – probability of occupancy for species A; (2) *psi*BA – probability of occupancy for species B given species A is present (denoted with uppercase A); and (3) *psi*Ba – probability of occupancy for species B given species A is absence (denoted with lowercase a). We determined if occupancy of the subordinate species depends on the presence of the dominant species by comparing model performance of *psi*BA versus *psi*Ba (i.e. *psi*BA < psiBa; *psi*BA = *psi*Ba; *psi*BA > *psi*Ba).

The remaining parameters represent probabilities of detection for species A and B that are conditional on the occupancy status of both species: (4) *p*A – probability of detection for species A, given species B is absent; (5) *p*B – probability of detection for species B, given species A is absent; (6) *r*A – probability of detection for species A, given both species are present; (7) *r*BA – probability of detection for species B, given both species are present and species A is detected; (8) *r*Ba – probability of detection for species B, given both species are present and species A is not detected. From these detection parameters, we can determine, for instance, whether or not the detection of the subordinate species depends on the presence of the dominant by comparing model performance of *p*B related to *r*BA and *r*Ba. We can also determine if the probability of detection of subordinate species changes or not according to detection (rather than presence) or not of the dominant species comparing model performance of *r*BA and *r*Ba.

We tested four models for each species pair following Farris et al. (2016) that result from the combination of co-occurrence and co-detection models, each representing different hypotheses regarding the dependence/independence of the occupancy and detection parameters between species (see Table 1 for descriptions). We compared each co-occurrence/co-detection model without (.) and with predictor covariates (Cov.). To add covariates to each model, we first modeled detection parameters and subsequently the best detection model was used to include covariates to occupancy parameters. The covariate effects on occupancy and detection were considered supported if the 95% CI of the β regression parameters did not overlap zero. We ranked models according to AIC considering competing models as those with ΔAIC < 2.0. We also compared these models to models with only habitat covariates to determine whether habitat alone, species interactions alone, or a combination of habitat and species interactions, better explained co-occurrence of the target species.

We estimated the species interaction factor (SIF), a derived parameter that measures the spatial interaction between two species, to determine if they use habitat independently (SIF equal to 1.0 or 95% CIs overlaps 1.0), if they co-occur more than expected by chance (SIF > 1.0; 95% CIs do not overlap 1.0) or co-occur less than expected by chance (SIF < 1.0; 95% CIs do not overlap 1.0; Farris et al. 2016; Osorio et al. 2020). A SIF > 1 indicates a positive relationship between the species pair (e.g. potential attraction), while A SIF < 1 indicates spatial avoidance or exclusion. We used 'deltamethod' function of the R-package 'msm' (Jackson 2011) to calculate the SIF (see Richmond et al. 2010 for formulation) and its 95% CI, based on the occupancy estimates (*psi*A, *psi*BA and *psi*Ba), and the variance–covariance matrix from PRESENCE output.

Table 1. Descriptions of co-occurrence/co-detection models used in the conditional two-species occupancy modeling of wildcats and free-ranging dogs and cats across 80 camera trapping sites in 2013 in La Campana-Peñuelas Biosphere Reserve, Chile, modified from Richmond et al. (2010).

Co-occurrence models		Co-detection models	
*psi*BA = *psi*Ba (Cov.) or (.)	Site use of species B is not affected by presence of species A. Site use can be explained by covariate (Cov.) or not (.).	*r*BA = *r*Ba (Cov.) or (.)	Detection probability of species B is not affected by detection of species A when both species are present. Detectability can be explained by covariate (Cov.) or not (.).
*psi*BA ≠ *psi*Ba (Cov.) or (.)	Site use of species B is affected by presence of species A. Differences in site use can be explained by covariate (Cov.) or not (.).	*r*BA ≠ *r*Ba (Cov.) or (.)	Detection probability of species B is conditional (affected) on detection of species A when both species are present. Differences in detectability can be explained by covariate (Cov.) or not.

For conditional two-species occupancy modeling we assumed a 'subordinate' (i.e. B) and 'dominant' species (i.e. A). Parameters that represent the probabilities of occupancy and detection were *psi*A, *psi*BA, *psi*Ba and *p*A, *p*B, *r*A, *r*BA, *r*Ba, respectively. Two co-occurrence models arise when comparing *psi*BA and *psi*Ba (*psi*BA = *psi*Ba or *psi*BA ≠ *psi*Ba) and two co-detection models when comparing *r*BA and *r*Ba (*r*BA = *r*Ba and *r*BA ≠ *r*Ba). Combination of co-occurrence and co-detection models resulted in four models: **Model 1** (*psi*A, *psi*BA = *psi*Ba, *p*A, *p*B, *r*A, *r*BA = *r*Ba); **Model 2** (*psi*A, *psi*BA = *psi*Ba, *p*A, *p*B, *r*A, *r*BA ≠ *r*Ba); **Model 3** (*psi*A, *psi*BA ≠ *psi*Ba, *p*A, *p*B, *r*A, *r*BA ≠ *r*Ba); **Model 4** (*psi*A, *psi*BA ≠ *psi*Ba, *p*A, *p*B, *r*A, *r*BA = *r*Ba).

Activity pattern and temporal overlap analysis

Activity patterns were estimated non-parametrically using a kernel density estimation approach (Ridout & Linkie 2009), only when ≥ 10 independent CE$_{60\text{min}}$ were obtained (Linkie & Ridout 2011). Each species' CE$_{60\text{m}}$ was considered a random sample of the underlying continuous distribution describing the detection probability of that species in a given interval of the day (Ridout & Linkie 2009). The overlap in activity patterns between species was estimated using the coefficient of overlap (Δ). Δ ranges from 0 (no overlap) to 1 (complete overlap). We used a 10,000 replicates smooth bootstrap to validate the overlap models yielding 95% CI limits for Δ. Activity pattern analysis and estimation of coefficients of overlap were performed using the R-package 'overlap' (Meredith & Ridout 2014). Overlap coefficients were classified as 'low', 'moderate', or 'high' relative to the overall pairwise comparisons performed. Given the descriptive character of the coefficients of overlap, we conducted a Mardia–Watson Wheeler (MWW) test to assess significant differences between daily activity patterns of species pairs (e.g. Monterroso et al. 2014). A Bonferroni correction was performed to control Type I error rate (α), adjusting by the number of pairwise comparisons (k) performed. Thus, $\alpha' = \alpha/k$. These tests were performed using the R-package 'circular' (Agostinelli & Lund 2013). We also evaluated the species' preference/strength of selection for a determined diel period (dawn, day, dusk, and night), using a modified Ivlev's selectivity index (see Appendix S3; e.g. Lucherini et al. 2009; Monterroso et al. 2014; Osorio et al. 2020).

Results

Daily capture rates, probability of occupancy and detection of carnivores

From a total effort of 5763 camera-days we obtained a total of 2185 photographs of all our target species: 141 independent capture events (CE$_{60\text{min}}$) for wildcats and 386 independent CE$_{60\text{min}}$ for FR-dogs and FR-cats (Appendix Table S4.1). FR-dogs were captured at 44 of the 80 sampled sites, pampas cats at 15, güiñas at 12 and FR-cats at 10 sites. DCRs showed that FR-dogs and pampas cats were the most frequently captured species, but FR-dogs were spatially more homogeneously distributed compared to the other species (Appendix Fig. S4.1). Mann–Whitney U test showed significant differences in DCRs between FR-dog and wildcats and also with FR-cat ($p < 0.05$), while no significant differences between wildcats and FR-cats were observed (Appendix Table S4.2). The Moran's I index analysis showed a high spatial clustering for FR-dogs, but not for the wildcats or FR-cats (Appendix Table S4.3).

Single-species occupancy analysis showed higher detection probability (from model averaged parameter estimates) for FR-dogs ($p = 0.30 \pm$ SE 0.03) and FR-cats ($p = 0.27 \pm$ SE 0.04) compared to wildcats ($p = 0.14 \pm$ SE 0.03 for pampas cat, and $p = 0.10 \pm$ SE 0.05 for güiña) (Figure 2; see competing models details in Appendix Table S5.1). Predictor covariates for detection probabilities from top ranked models were: ravines for FR-dog (p increases further away from ravines), distance to secondary roads for FR-cat (p decreases further away from secondary roads), distance to human settlements for pampas cat (p increases further away from human settlements), and distance to primary roads for güiña (p increases further away from primary roads) although the effect was weak for güiñas (Appendix Table S5.2).

FR-dogs showed the highest probability of site use (*psi* = 0.49 ± SE 0.06), followed by the pampas cats (*psi* = 0.31 ± SE 0.09), FR-cats (*psi* = 0.16 ± SE 0.05) and finally the güiña (*psi* = 0.15 ± SE 0.07). Habitat type showed more support than any other covariate in explaining site use of güiña and FR-cat. Güiña had higher probability of site use in forest habitat while FR-cat was higher in scrub habitat, although with only weak support (Appendix Table S5.2). In the top model, site use of FR-dogs and pampas cats was not explained by any covariate. However, a second competing model showed habitat type as a predictor for site use of both species but not strongly so. FR-dog had higher probability of site use in scrub habitat while pampas cat was higher in forest habitat.

Spatial co-occurrence analysis

For each pair of species, we tested a total of 40 different models including habitat predictor covariates from the best singles season models above. In top-ranked models, all species pairs showed an independent spatial relationship (i.e. species used habitats independent of one another; SIF equal to 1 and CIs overlapped 1.0), and site use was best predicted by the habitat type (*psi*BA = *psi*Ba (Habitat), with the exception of the FR-dog/pampas cat pair (Table 2). However, some competing models indicated a significant lack of co-occurrence (i.e. SIF < 1.0 and CIs do not overlap 1.0) for some species pairs (Table 2).

In the top-ranked models, dominant FR-dogs influenced detection probabilities of both subordinate wildcats (*r*BA ≠ *r*Ba (Cov.); Table 2 and Figure 3). Individual detectability of FR-dogs (*p*A) consistently increased with distance away from ravines, contrary to pampas cats and güiñas, which showed higher detectability near ravines and away from primary roads, in the absence of FR-dog (Figure 3). In the presence of FR-dogs, pampas cat detection probability was higher when FR-dogs were detected at the camera sites (*r*BA > *r*Ba) and increased at greater distances from human settlements (Table 2 and Figure 3). In contrast, detection probability of güiñas was higher when FR-dogs were not detected (*r*BA < *r*Ba) and increased with distance away from primary roads (Table 2 and Figure 3).

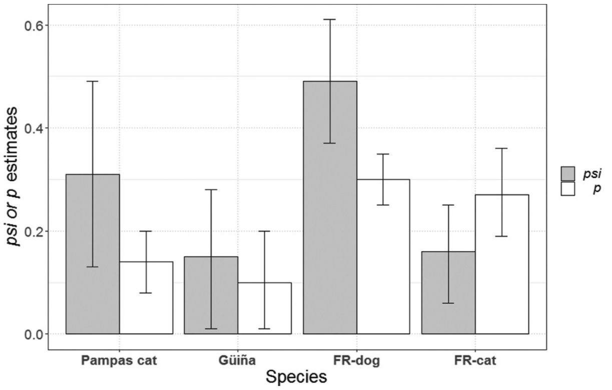


Figure 2. Estimated probability of site use (*psi*) and detection (*p*) for both wildcats (pampas cat and güiña) and for free-ranging dogs and cats across 80 camera trapping sites in La Campana-Peñuelas Biosphere Reserve, Chile in 2013. The bars show model averaged parameter estimates (of *psi* and *p*) from competing models (ΔAIC ≤ 2) and error bars display 95% confident intervals.

In contrast to detection, top-ranked models showed that FR-dogs did not affect site use probabilities of pampas cat and güiña (i.e. wildcats used sites regardless to the FR-dog presence (*psi*BA = *psi*Ba). In the FR-dog and pampas cat top-ranked model, FR-dog site use probability (*psi*A) was not explained by habitat covariates, and pampas cat site use was equal whether FR dogs were present or absent (Table 2). However, the third competing model showed support for lack of co-occurrence between FR-dogs and pampas cats, and pampas cat site use probability decreased when dogs were present (*psi*BA < *psi*Ba (.)). The FR-dog and güiña model showed that site use probabilities were habitat-mediated (*psiA* (Habitat), *psi*BA = psiBa (Habitat)). FR-dog showed slightly higher site use probability in scrub habitat ($psiA_{scrub}$ = 0.54, $psiA_{forest}$ = 0.49, β_{Hab} (95% CI) = −0.18, (−0.66; 0.99)) while the güiña site use probability was higher in forest habitat ($psiBA_{forest}$ = 0.72, β_{Hab} (95% CI) = 51.70, (46.50; 56.90)).

Top-ranked models for the FR-cat and pampas cat pair (or vice versa) showed no influence of the dominant on detection (*r*BA = *r*Ba (Cov.)) or site use probabilities of the subordinate species (*psi*BA = *psi*Ba (Cov.)) (Table 2). When FR-cat was modeled as the dominant species, individual detectability of FR-cat consistently increased further away from ravines, while pampas cats showed higher detectability further away from human settlements (*p*B and *r*BA = *r*Ba) (Table 2 and Figure 3). The site use probabilities were habitat-mediated, with FR-cat site use being higher in scrub ($psiA_{scrub}$ = 0.46, $psiA_{forest}$ = 0.15, β_{Hab} (95% CI) = −1.60, (−3.29; 0.08)) and for pampas cat, higher in forest habitat (*psi*BA = $psiBa_{forest}$ = 0.37, *psi*BA = $psiBa_{scrub}$ = 0.18, β_{Hab} (95% CI) = −1.60, (−0.39; 2.40)), but these effects were weak. When pampas cats were the dominant species, detection probabilities showed a similar pattern to the aforesaid for pampas cat (i.e. pA was greater further away from human settlements) and for FR-cat (i.e. pB was greater further away from ravines). Likewise, site use probability for pampas cats tended to increase in forest ($psiA_{forest}$ = 0.37, $psiA_{scrub}$ = 0.18, β_{Hab} (95% CI) = 0.99, (−0.41; 2.39)), and for FR-cat increase in scrub habitat (*psi*BA = $psiBa_{scrub}$ = 0.47, *psi*BA = $psiBa_{forest}$ = 0.17, β_{Hab} (95% CI) = −1.60, (−3.20; 0.27)). Interestingly, three competing models indicated significant lack of co-occurrence between FR-cat and pampas cat (Table 2). In these models, the site use probability of FR-cat diminished when pampas cat, as the dominant species, was present and pampas cat site use probability decreased when FR-cat as the dominant was present (psiBA < *psi*Ba (Habitat)). This could reflect mutual avoidance. The FR-cat and güiña pair was excluded from the analysis since they only co-occurred at one site during this survey and models failed to converge.

Table 2. Two-species occupancy modeling for wildcats (pampas cat and güiña), and for free-ranging dogs and cats in La Campana-Peñuelas Biosphere Reserve across 80 camera trapping sites in 2013. Mean (±SE) of occupancy and detection parameters, and confidence intervals (95% CI) on SIF are shown.

Species A	Species B	M	Species co-occurrence				Species co-detection				Species interaction factor		AIC	ΔAIC	AIC*w*	*k*
			*psi*BA (SE)	Cov.	*psi*Ba (SE)	Cov.	*r*BA (SE)	Cov	*r*Ba (SE)	Cov	SIF	95% CI				
Pampas cat	Güiña	1	0.11 (0.05)	Habitat*	0.11 (0.05)	Habitat*	0.04 (0.05)	Hs	0.04 (0.05)	Hs	1	0.96; 1.04	324.1	0	0.25	11
		1	0.13 (0.05)	(.)	0.13 (0.05)	(.)	0.03 (0.02)	Hs	0.03 (0.02)	Hs	1	-	325.2	1.1	0.14	9
		4	0.08 (0.06)	Habitat*	0.15 (0.07)	Habitat*	0.04 (0.05)	Hs	0.04 (0.05)	Hs	0.63	0.60; 0.66*	325.6	1.5	0.12	12
Dog	Pampas cat	2	0.48 (0.12)	(.)	0.48 (0.12)	(.)	0.25 (0.04)	Hs*	0.07 (0.02)	Hs*	1	-	683.5	0	0.29	10
		3	0.45 (0.11)	Habitat*	1.00 (0.00)	Habitat*	0.25 (0.04)	Hs*	0.07 (0.02)	Hs*	0.61	0.17; 1.06	683.6	0.1	0.28	13
		3	0.42 (0.13)	(.)	1.00 (0.00)	(.)	0.25 (0.04)	Hs*	0.07 (0.02)	Hs*	0.59	0.33; 0.84*	684.2	0.7	0.20	11
		2	0.50 (0.11)	Habitat*	0.50 (0.11)	Habitat*	0.25 (0.04)	Hs*	0.07 (0.02)	Hs*	1	0.70; 1.30	684.6	1.1	0.17	12
Dog	Güiña	2	0.43 (0.08)	Habitat*	0.43 (0.08)	Habitat*	0.00 (0.00)	Rd1	0.10 (0.04)	Rd1	1	0.40; 1.60	559.2	0	0.80	12
Pampas cat	Cat	1	0.29 (0.09)	Habitat	0.29 (0.09)	Habitat	0.48 (0.06)	Hs*	0.48 (0.06)	Hs*	1	0.83; 1.17	366.1	0	0.22	11
		4	0.19 (0.10)	(.)	0.50 (0.35)	(.)	0.49 (0.06)	Hs*	0.49 (0.06)	Hs*	0.47	−0.21; 1.15	366.9	0.8	0.14	10
		2	0.30 (0.10)	Habitat	0.30 (0.10)	Habitat	0.59 (0.11)	Hs*	0.45 (0.07)	Hs*	1	0.83; 1.17	367.0	0.9	0.14	12
		2	0.28 (0.10)	(.)	0.28 (0.10)	(.)	0.58 (0.11)	Hs*	0.45 (0.07)	Hs*	1	-	367.2	1.1	0.12	10
		4	0.22 (0.11)	Habitat	0.43 (0.23)	Habitat	0.49 (0.06)	Hs*	0.49 (0.06)	Hs*	0.61	0.45; 0.76*	367.3	1.2	0.12	12
Cat	Pampas cat	1	0.29 (0.07)	Habitat	0.29 (0.07)	Habitat	0.25 (0.06)	Hs	0.25 (0.06)	Hs	1	0.89; 1.11	371.4	0	0.25	11
		4	0.16 (0.11)	Habitat	0.40 (0.16)	Habitat	0.25 (0.06)	Hs	0.25 (0.06)	Hs	0.50	0.45; 0.55*	372.1	0.7	0.18	12
		2	0.29 (0.07)	Habitat	0.29 (0.07)	Habitat	0.34 (0.09)	Hs	0.22 (0.07)	Hs	1	0.89; 1.11	372.2	0.8	0.17	12
		3	0.16 (0.11)	Habitat	0.40 (0.16)	Habitat	0.34 (0.09)	Hs	0.22 (0.07)	Hs	0.50	0.45; 0.55*	372.9	1.5	0.12	13

The larger ‘species A’ was assumed to be dominant and the smaller ‘species B’ subordinate. ‘M’ is the combination of co-occurrence/co-detection models. We report all models ΔAIC ≤ 2 and show: the probability of site use (*psi*) of the subordinate species with (*psi*BA) and without (*psi*Ba) the presence of the dominant species, and the probability of detection (*r*) of the subordinate species (given both species were present) when dominant species was detected (*r*BA) and not (*r*Ba). For each model influential covariates are shown: habitat, distance to nearest human settlement (Hs) and distance to primary road (Rd1). Species interaction factor (SIF) indicates: and when 95% CIs do not overlap 1,0, respectively. independence when SIF is equal to 1, lack of co-occurrence when SIF < 1.0, and co-occurrence when SIF > 1.0. Supported effects of covariates and SIF are highlighted with asterisks when 95% CIs do not overlap 0 or 1.0, respectively.

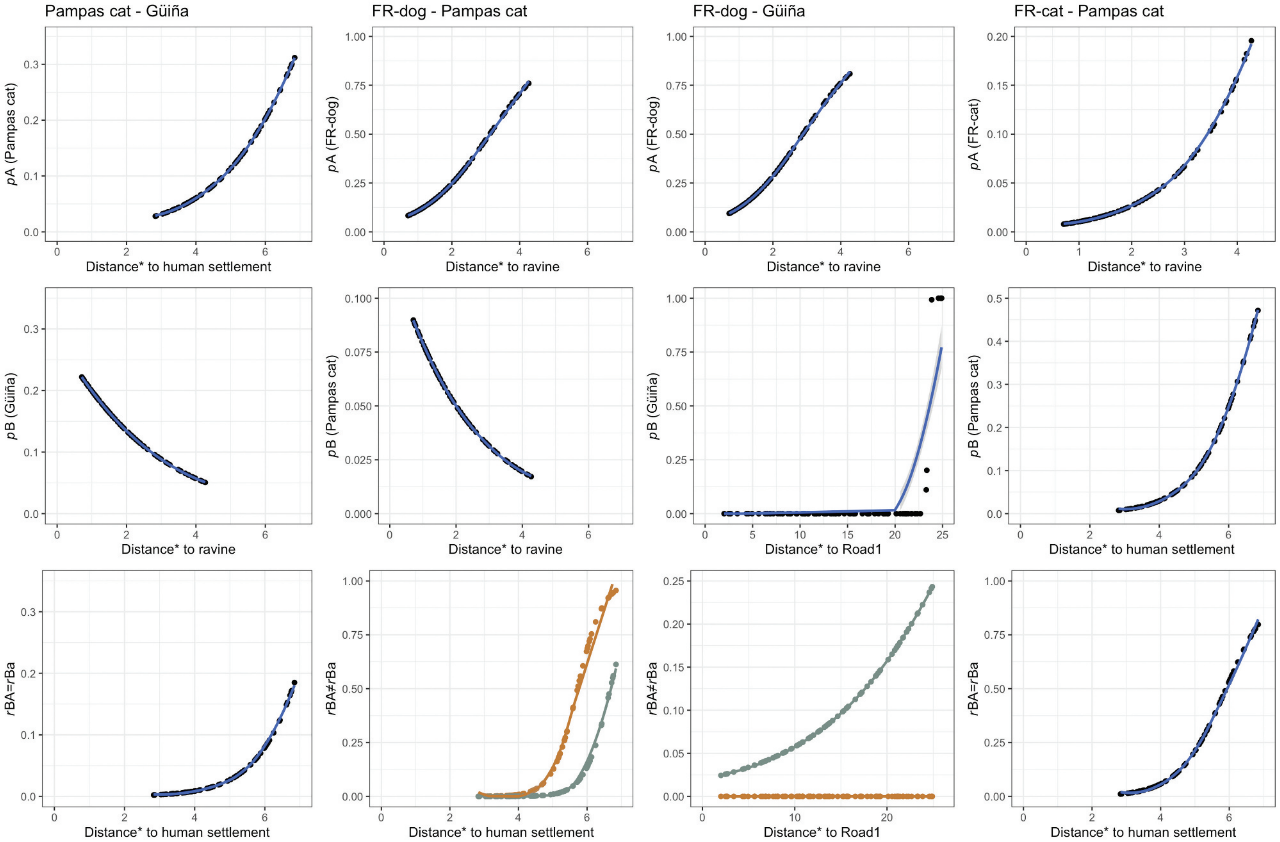


Figure 3. Detection probabilities from the top-ranked two-species occupancy models for wildcats (pampas cats and güiñas) and free-ranging dogs and cats from 80 camera trapping sites in La Campana-Peñuelas Biosphere Reserve in 2013. The influential predictor covariates, distances* to landscape features in km, along the x-axis are shown. Each column corresponds to a species pair. The first row shows the detection probability for the dominant species, given the subordinate species is absent (*p*A); the second row, the detection probability for subordinate species, given the dominant is absent (*p*B); and the third row, the detection probability for subordinate species, given both species are present and the dominant was detected (*r*BA) and not detected (*r*Ba). Brown and green lines highlight *r*BA and *r*Ba, respectively, when *r*BA ≠ *r*Ba.

For wildcats, the top-ranked model showed that detection probability of güiñas increased near ravines (*p*B), and for pampas cats, increased the further away from human settlements (*p*A) (Figure 3). At sites where both species were present, detection probability of güiñas was not affected by pampas cat detection (rBA = rBa (Cov.)) but increased further away from human settlements (Figure 3). The probability of site use by güiñas was independent of the dominant pampas cat presence and was explained by habitat (*psi*BA = *psi*Ba (Habitat)) (Table 2). Pampas cat site use probability was slightly higher in forests (*psi*A$_{forest}$ = 0.31, *psi*A$_{scrub}$ = 0.22, β_{Hab} (95% CI) = 0.42, (−1.00; 1.84)) while site use of güiña strongly increased in forest habitat (*psi*BA = psiBa$_{forest}$ = 0.20, *psi*BA = psiBa$_{scrub}$ = 0, β_{Hab} (95% CI) = 100.84, (98.69; 103.00)). The third competing model showed strong support for lack of co-occurrence between these wildcats, and site use probability of güiña declines when pampas cats were present (*psi*BA < *psi*Ba).

Activity patterns and temporal overlap

FR-dogs showed mainly diurnal/twilight activity while FR-cats and wildcats exhibited more nocturnal patterns. The Jacob's Selectivity Index indicated that FR-dogs consistently selected dawn, day, and dusk hours (Table 3). Pampas cat significantly selected for night and dusk, and güiña selected near exclusively night hours. FR-cats showed some selection for night, significantly avoiding daylight hours (Table 3).

FR-dogs and wildcats had significant differences in activity patterns and low overlap coefficients (Δ; Figure 4 and see Appendix Table S6.1 for details). The pampas cat and güiña showed similar activity patterns yielding a high Δ, with a higher density of activity before midnight for pampas cats and before dawn for güiñas. FR-cats exhibited similar activity patterns to the wildcats but with a peak after midnight, showing a moderate Δ with pampas cats and high Δ with güiñas (Figure 4).

Discussion

The presence of wildcats suggests that CPBR still holds available native habitats for carnivores despite increasing human pressure on the study area, with some sites appearing to be more suitable for wildcats, such as ravines, where native vegetation remains and human perturbation is lower (Schulz et al. 2010; García et al. 2020). FR-dogs were widely distributed and active across the study area (i.e. DCR results) and showed the highest probability of detection (i.e. single species results). Pampas cat was the second most frequently captured species, contrary to a recent report by García et al. (2020) who recorded pampas cats only once in Mediterranean areas of Chile. Güiña was the third and FR-cat the fourth most registered species (i.e. DCR results), however, the probability of detection of FR-cat was higher than güiña across the sampled sites, which highlights the importance of considering detection probabilities for more accurate inferences on species' spatial patterns. Our single-species occupancy results revealed that the probabilities of detection of both wildcats were higher further away from anthropogenic predictor covariates, contrary to FR-dogs and FR-cats, which were more frequently detected closer to human landscape features. This is supported by García et al. (2020) who reported that human population density negatively affected detection frequency of güiña. In our research, güiñas were only registered in native forest, so, habitat covariate (forest) fully explained their probability of site use, and pampas cats showed probabilities of site use in both native habitats (forest and scrub) in a competing model,

Table 3. Diel period strength of selection for pampas cats, güiña, free-ranging dogs and cats from data collected across 80 camera trapping sites in La Campana-Peñuelas Biosphere Reserve in 2012–2013. Values of modified Ivlev's selectivity index (JSI) and 95% confidence intervals (95% CI) are shown. Significant selection or avoidance for diel periods are highlighted with asterisks *.

	Night		Dusk		Day		Dawn	
Species	JSI	95% CI	JSI	95% CI	JSI	95% CI	JSI	95% CI
Pampas cat	0.28	(0.11; 0.49) *	0.39	(0.23; 0.70) *	−0.58	(−0.77; −0.39) *	0.05	(−0.22; 0.50)
Güiña	0.59	(0.3; 0.83) *	−0.05	(−0.37; 1.05)	−0.82	(−1.04; −0.64) *	0.09	(−0.18; 0.86)
FR-dog	−0.61	(−0.71; −0.52) *	0.21	(0.08; 0.39) *	0.31	(0.22; 0.41) *	0.34	(0.24; 0.49) *
FR-cat	0.22	(−0.05; 0.54)	−0.03	(−0.35; 0.73)	−0.32	(−0.61; −0.01) *	0.11	(−0.20; 0.86)

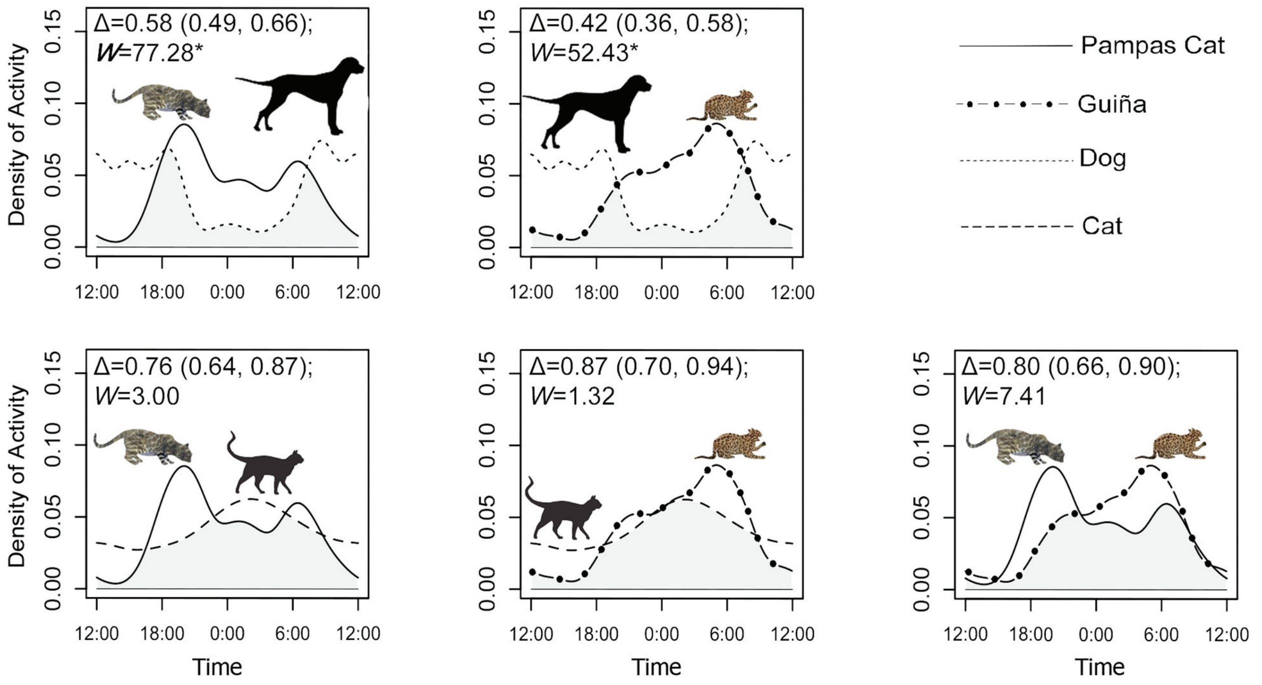


Figure 4. Activity patterns overlap from data collected across 80 camera trapping sites in La Campana-Peñuelas Biosphere Reserve in 2012–2013. Upper panels show activity patterns of free-ranging (FR) dogs and wildcats (pampas cats and güiñas). Lower panels show the activity patterns of FR-cats and wildcats (left and middle panels), and between pampas cats and güiñas (far right panel). Overlap coefficient (Δ) and 95% CI (in parenthesis) are shown. W is the value of Mardia Watson Wheeler test and shows statistically significant differences between activity patterns highlighted with an asterisk * ($\alpha' = 0.008$).

being slightly superior in forest. This suggest that wildcats certainly used native habitats (mainly forest or both forest/scrub) but far away as possible from human influence. Instead, FR-dogs and FR-cats, although registered in both habitats, used mostly scrub habitat closer to human landscape features.

Spatial co-occurrence analysis showed that FR-dog detectability affected the detection probabilities of both wildcats, with detection of güiña being lower when FR-dogs were detected. Although the presence of FR-dogs did not affect güiña site use probability, our results were uncertain with respect to whether they affected the probability of site use by pampas cats or not. Likewise, pampas cats and FR-cats used habitats regardless of the presence of one another in the top ranked models, but other competing models showed mutual avoidance. We found temporal segregation between FR-dogs and wildcats, but not between wildcats and FR-cats, which showed moderate to high overlap in activity patterns.

The independent spatial relationships (i.e. SIF equal to 1) between FR-dog and wildcats could be explained by the opposite pattern observed in the use of space and time. Free-ranging dogs were mostly associated with human sites, further away from the ravines, and exhibited a diurnal activity pattern as reported elsewhere (Srbek-Araujo & Chiarello 2008; Silva-Rodríguez & Sieving 2012; Sepúlveda et al. 2015; Schüttler et al. 2018). It has been reported that even though dogs used habitat according to availability, native forest is used less than expected, possibly due to higher distance from houses (Sepúlveda et al. 2015). Although most dogs were photographed unaccompanied by people in our study, many dogs were recorded in scrub sites near to crops and rural dwellings, suggesting they are FR-dogs associated with humans. Free-ranging dogs are commonly owned but not confined to a dwelling or outdoor area and often roam during daylight (diurnal activity pattern), probably following humans during their work or recreational activities (Srbek-Araujo & Chiarello 2008; Sepúlveda et al. 2015; Moreira-Arce et al. 2015a). In contrast, wildcats mainly used forest habitats farther from anthropogenic landscape features (e.g. García et al. 2020) and showed nocturnal activity. Opportunities for direct encounters with FR-dogs could be ameliorated by these spatial and temporal segregations, consistent with what has been observed elsewhere (Srbek-Araujo & Chiarello 2008; Frigeri et al. 2014; Sepúlveda et al. 2015; Moreira-Arce et al. 2015a). However, FR-dogs were also detected in forest sites where both wildcats occurred; thus, FR-dogs wandered beyond sites in close proximity to households, entering into natural areas (e.g. Srbek-Araujo & Chiarello 2008; Figure 5). Perhaps low-quality food and poor care encourage FR-dogs to search for food inside forest patches, similar to reports in other areas (Silva-Rodríguez & Sieving 2011; Sepúlveda et al. 2015; Schüttler et al. 2018).

Interestingly, the pampas cat and güiña responded inversely to domestic dog presence and detectability. The pampas cat had higher detection probability when FR-dogs were detected, while güiña showed lower detectability. The last result also concurs with the study of García et al. (2020), where detection frequency of domestic dogs negatively affected detection of güiñas in vineyard landscapes. Differences in behavior of the wildcats may explain our results. For example, güiñas are good tree climbers (Altamirano et al. 2013), which could be considered a fine scale defense mechanism (flight response), as they could easily climb tall trees to avoid dogs. Little is known about the behavior of pampas cats; however, food habits in the high Andes suggest they are mainly terrestrial (e.g. Napolitano et al. 2008).

FR-cats were detected only at ten sites, but their detection probability was higher than güiña. The FR-cat detection pattern agrees with the notion that they do not venture far from farms or households, but rather spend most of their time outside in yards and gardens of their immediate neighbors (Kays & DeWan 2004; Ferreira et al. 2011). We found strong overlap in nocturnal activity between FR-cats and both wildcats, as well as some evidence of mutual avoidance between the pampas cat and FR-cats in competing models. Daily activity of FR-cats varies largely depending on landscape, housing conditions, and human care (e.g. feeding frequency by owners) (Piccione et al. 2013; Schüttler et al. 2018). In fact, Schüttler et al. (2018) found evidence that rural household cats with an inadequate food supply brought more prey home than village cats. Therefore, if lack of care and control by cat owners worsens in areas where wildcats exist, the likelihood of cats entering natural habitats to feed may increase, generating higher risk of interactions and disease transmission for native species (Silva-Rodríguez & Sieving 2011; O'Brien et al. 2012; Mora et al. 2015; Sieg et al. 2020). This is important since domestic cats have contributed to mortality and extinction of wildlife species worldwide (Medina et al. 2011).

Site use probability of güiña was irrespective of the pampas cat presence, and instead influenced by habitat. The exclusive use of forest sites by güiñas is consistent with previous studies showing that they are strongly associated with native forest fragments (Dunstone et al. 2002; Sanderson et al. 2002; Acosta-Jamett & Simonetti 2004; Gálvez et al. 2013). Fleschutz et al. (2016) reported that güiñas actually are a forest-dependent species but with a broader habitat niche than previously assumed (e.g. Acosta-Jamett & Simonetti 2004) given their ability to tolerate habitat loss and fragmentation and occupy small forest fragments in the south of Chile (Dunstone et al. 2002; Gálvez et al. 2013, 2018; Schüttler et al. 2017).

Figure 5. Photographic records of the small wildcats (pampas cat and güiña) and free-ranging dogs in a camera trap co-occurrence site at La Campana-Peñuelas Biosphere Reserve in 2013. (**a**) Pampas cat (*Leopardus colocolo*); (**b**) güiña (*Leopardus guigna*); (**c**) pointer FR-dog and (**d**) foxhound FR-dog.

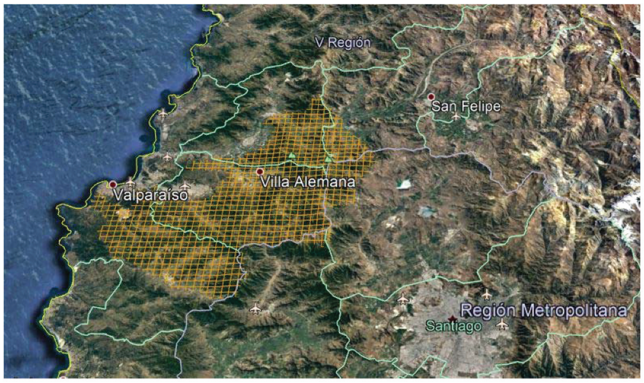
Thus, we encourage continued research in CPBR and other areas from the northernmost distribution of güiña (such as García et al. 2020; Napolitano et al. 2020) with a broader scope in habitats to elucidate how flexible güiñas could be in the use of different environments. Instead, pampas cats used both forest and scrub habitats and, thus, they appear potentially to be a generalist species as reported elsewhere (Bagno et al. 2004; Lucherini et al. 2016).

Since a competing model showed a significant lack of spatial co-occurrence between wildcats (i.e. SIF < 1; güiña showed lower site use probabilities when pampas cat was present), suggesting spatial avoidance of pampas cat by güiñas, we cannot rule out some level of mutual interference. Also, we found no temporal segregation between both wildcats (both species show high nocturnal activity overlap) which could drive an inter-specific competition. However, coexistence between pampas cats and güiñas might be mediated by fine-scale spatio-temporal segregation or diet partitioning, rather than competition, which should be studied further (e.g. Soto & Palomares 2015; Moreira-Arce et al. 2016; Osorio et al. 2020). The main nocturnal activity pattern for güiñas in our study area is consistent with that reported in temperate rainforests of southern Chile (Delibes-Mateos et al. 2014; Hernández et al. 2015). The güiña synchronizes its diel activity with small rodents as primary prey (e.g. *Oligoryzomys longicaudatus*) and climbs trees to prey upon arboreal small mammals (e.g. *Irenomys tarsalis* and *Dromiciops gliroides*) (Altamirano et al. 2013; Moreira-Arce et al. 2015b). Likewise, the nocturnal activity pattern of the pampas cat was similar to the behavior reported in the northern high Andean plateau, where the species preys upon small rodents (e.g. *Cavia tschudii*) and ground birds (e.g. flamingo species, *Phoenicopteridae*) (Napolitano et al. 2008; Lucherini et al. 2009; Fajardo et al. 2014).

Ravines were a key natural element that influenced detection probability of all species when the corresponding dominant or subordinate species was not present. Ravines are surrounded by native forests and showed the lowest probability of detection of FR-dogs and FR-cats, and the highest for wildcats. This concurs with García et al. (2020), who found that a higher 'naturalness' at a small landscape scale positively influenced detection of güiñas in vineyards of Mediterranean Chile. Ravines could play roles as corridors, suitable refuges, or as escape routes for wildcats when confronted with anthropogenic perturbations. Since the largest areas of suitable forest habitat are private, it would be a desirable task for conservation agencies to expand on their partnerships with private land owners (Zorondo-Rodríguez et al. 2014). Within the wine industry of this area, many land managers keep forest fragments and have stated their commitment to local sustainable development policy through a Wine, Climate Change and Biodiversity Program (WCB) of Chile (Márquez-García et al. 2019). Program winegrowers have adopted management practices that maintain biodiversity, but also recognize that some practices are complex or inefficient and disconnected with wine quality and production. Further research and education on ecosystem services of forested environments surrounding vineyards, and mesocarnivores as biological pest regulators, may encourage new vineyards to participate in the WCB program and invest in conservation (Márquez-García et al. 2019; García et al. 2020).

Our study highlights that understanding patterns of spatiotemporal co-occurrence is useful in predicting plausible responses to anthropogenic pressures and thus inform management and conservation of endangered species in human-dominated landscapes. Due to the growing spread of dogs and cats in Mediterranean ecosystems of central Chile, we strongly urge management actions to control their potential consequences, such as: (i) encourage owners to establish outdoor enclosures or tether their animals at night; (ii) advise cat owners on techniques to maintain cats indoors or to acquire tracker accessories for FR-cats (e.g. electronic alarms or colorful bell collars); (iii) remove unowned dogs from native habitats; and (iii) design clear protocols for abandoned animals (e.g. adoption of collected individuals). Our spatial and temporal findings provide a baseline for future studies aimed at understanding the dynamics of wildcats, evaluating landscape policy, and the identifying important areas for conservation and connectivity for wildcats in conservation planning programs.

Geolocation information



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Author contributions

E.B, C.B and N.G, conceived and designed this study; E.B conducted fieldwork and collected data; E.B, N.G, C.O and D. M, performed the statistical analyses. E.B, N.G, C.O, M.J.K, D. M and C.B assisted in interpretation and wrote the article.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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