Title

Priority Habitats for Carnivores Surrounding Protected Areas in Andean Temperate Forests of Chile

Running head: Priority for carnivores outside protected areas

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Abstract

The establishment of protected areas as a conservation strategy is common practice. However, it is recognized that the long-term persistence of many species, particularly carnivores, depends on habitats in buffer zones. I explored which habitats and species should be a priority in surrounding lands of Andean protected areas in the temperate forest eco-region of South-Central Chile; recently awarded the status of Biosphere Reserve. I used Occupancy modeling to determine the proportion of sites used by each species, explicitly accounting for detection. I tested for differences between forests adjacent to protected areas versus forest fragments in the agricultural matrix, and alternatively if the degree of fragmentation affected occupancy. Differences in activity patterns between species were analyzed to describe temporal segregation. On average, species used a similar proportion of sites in the study area, although differences in habitat were observed. Five native carnivores and domestic dogs were detected. Puma (*Puma concolor*) and Chilla fox (*Lycalopex griseus*) in large forest fragments and highland areas; Molina´s Hog nosed skunk (*Conepatus chinga*) and Kod-kod or Güiña (*Leopardus guigna*) were affected by the degree of forest cover rather than proximity to protected lands; and finally Culpeo fox (*Lycalopex culpaeus*) and Domestic dog (*Canis familiaris*) mostly associated to the agricultural matrix. Avoidance of competing species was observed. Priority for conservation should be the protection of existing fragments and prevention of further fragmentation, and the Puma, Molina's Hog nosed skunk and Güiña should be priority species for conservation planning. Further research is needed on cost-effective incentives to protect remnant fragments and comparisons of occupancy with protected habitats.

Introduction

One of the reasons why conservation biology is considered a crisis discipline (Soule 1985) is because extinction rates are 100 to 1000 times the "natural" background rate (Begon et al. 1996). Since resources for conservation are limited, strategies need to be efficient (Primack 1998). A strategy that flourished during the 1970's was the establishment of protected areas (Borgerhoff-Mulder & Coppolillo 2005). Efficiency of protected areas (hereafter PAs) and the conservation of many species depends on activities in surrounding habitats or buffer areas (Primack 1998).

This is particularly the case for carnivores, where the survival and long-term viability of many species is highly dependent on the dynamics of surrounding buffer zones. In general, carnivore conservation must set aside protected areas sufficiently large for entire carnivore guilds, promote connectivity of PAs, management of buffer areas, conflict resolution (Creel et al. 2001; Woodroffe 2001) and understanding inter-specific interactions (Linnell & Strand 2000). Biological traits such as body size and large home range make carnivores especially prone to extinction (Purvis et al. 2001). Wide-ranging behavior forces carnivores to interact in human dominated landscapes outside protected lands, making them highly susceptible to human-induced mortality surrounding and within PAs because of conflict, leading to local extinctions (Woodroffe & Ginsberg 1998). Protected areas are usually established in less productive lands and restricted in size (Borgerhoff-Mulder & Coppolillo 2005), which does not ensure habitat suitability for entire carnivore guilds, nor long-term viability of populations (Carroll et al. 2003; Woodroffe 2001). However, establishing new PAs or expanding existing networks is not a realistic option in many areas.

In Chile, nearly 20% of lands are under national protection, but not equally distributed. In the temperate forest region (35ºS to 55ºS), the park system is extensive, but heavily biased towards high elevations in the Andes, deemed insufficient for securing long-term conservation of biodiversity (Armesto et al. 1998). Furthermore, the size of many PAs is inadequate to support viable populations of large mammals, even if assuming that the entire PA is suitable habitat, which is highly unlikely (Simonetti & Mella 1997). Carnivore guild studies in Chile have been conducted on canids and felids (Lucherini et al. 2009; Napolitano et al. 2008; Acosta & Simonetti 2004; Jiménez 1996; Johnson & Franklin 1994) but no such studies exist in Andean ecosystems of the temperate forest of Southern Chile, where most PAs in this eco-region are situated (Armesto et al. 1998). In addition, the temperate rainforest eco-region is a conservation priority for Neo-tropical carnivores mainly because of the vulnerability and rarity of species (Loyola et al. 2008). Consequently, understanding dynamics of guilds in temperate forest environments adjacent to PAs in Chile is important for management.

The focus of this paper is on a carnivore guild interacting within buffer areas of high elevation PAs in Andean temperate forest environments in South-Central Chile. The carnivore guild studied is composed of six species. In order of body size: Puma (*Puma concolor*), Domestic dog (*Canis familiaris*), Culpeo fox (*Lycalopex culpaeus*), Chilla fox (*Lycalopex griseus*), Kod-kod or Güiña (*Leopardus guigna*) and Molina´s Hog nosed skunk (*Conepatus chinga*; hereafter Skunk). All native species (i.e. excluding domestic dogs) are solitary carnivores protected by law.

The aims of this research are (1) to determine factors affecting landscape patterns of habitat use for each species in surrounding lands of PAs, (2) compare activity patterns between species to describe potential interactions; and (3) suggest priority habitats and species where conservation action should focus efforts. The limits of PA buffers are usually set up arbitrarily from the border (e.g. 10 km) or based on information relating to more conspicuous species (e.g. birds, plants). Thus, I analyzed habitat use in forests adjacent to highland PAs versus forest fragments in the agricultural matrix, and alternatively tested whether the degree of fragmentation explains species use. Furthermore, I analyzed if species differ in their temporal patterns and expect that subordinate competitors occupy different habitats and or alter activity patterns (Ritchie & Johnson 2009; Creel et al. 2001). Finally, I suggest recommendations for conflict mitigation and further research.

Methods

Study Area and Site Selection

The study was conducted in the Villarrica Catchment in the foothills of the Andes in the Araucanía district of South-Central Chile (39º15´S, 71º48´O). Mean temperature varies from 15.1ºC (January) to 1.9ºC (July). Mean annual precipitation is 1,945 mm, falling as snow over 750 meters above sea level (m.a.s.l.) (Di Castri & Hajek 1976). Vegetation comprises deciduous forest dominated by the *Nothofagus* genus at lower altitudes and mixed deciduous and conifer forests at higher altitudes (Gajardo 1993). The elevation gradient of the catchment varies from 230 m.a.s.l. in the agricultural valley to >1200 m.a.s.l.; with PAs situated >800 m.a.s.l. The area has been recently awarded the status of Biosphere Reserve (UNESCO 2010) and the main PAs are two National Parks - Huerquehue and Villarrica - and the Villarrica National Reserve (Fig. 1).

To reduce confounding factors, I selected south facing forests at sites adjacent to PAs and large forest fragments (>200 ha) based also on elevation; restricted to 400-800m.a.s.l. Criteria for small fragments was patch area 20-40 ha and distance >2 km. Arc View GIS 3.2 (ESRI 1999) and ENVI 4.2 (ITT 2010) software were used to measure distance and area of sites. A total of 4 areas adjacent to PAs, 2 large fragments (>200 ha) and 9 small fragments (<40 ha) were selected within 1,739km^2 (Fig. 1). All areas were surveyed and effort and sample units (i.e. cameras) varied according to the survey period.

Surveys

Camera trap surveys were conducted during spring/summer 2006, winter 2007, continuously during 2008, and autumn/winter 2009; accumulating over 10,000 camera trap/days. During 2006-2007 a total 27 cameras stations (>500m) were deployed in adjacent areas to PAs and large forest tracks (>200 ha) for 2468 camera/days. During Autumn/Winter 2009, 18 sites (>3 km) were systematically deployed for 1,258 camera/days in several higher elevation valleys adjacent to PAs. Elevation of sites during both survey periods varied between 500-1200 m.a.s.l.

During 2008, 27 cameras stations were deployed (>2 km) between January 2008 and March 2009 for a total of 6400 camera/days. A total of 12 sites were in areas adjacent to PAs and 15 in the agricultural matrix; 6 in large fragments and 9 in small fragments (Fig. 1). Three camera stations were placed systematically in each area adjacent to PAs and large fragments, ensuring that the whole forest site was covered without apparent gaps. One camera station was placed in small fragments. Two fragments were < 2km but I considered a major river as a barrier (Fig. 1). For each camera site, elevation, percentage of forest cover, distance to nearest water course and inhabited human household were obtained from a geographic information system of the Villarrica catchment (LPT-UCT, unpublished data).

In total, 25 active and 2 passive Trailmaster analog (i.e. film) camera traps (Trailmaster 2006) were deployed. Cameras were programmed to operate during 24 hours a day and checked every 20-25 days. Cameras were placed along trails within the forest, and placed >150-200 m from the forest edge. Scent lures were used to increase detection in the immediate area of the camera.

Occupancy and Model Selection

From the 2008 data, I constructed presence-absence detection histories for each species. Each observation of the detection history was a sampling occasion of 10 days collapsed into one. I applied single-species single-season models (MacKenzie et al. 2006) during summer/autumn, autumn/winter and spring /summer; considered as representative of environmental variation. I considered a season to be 120 days or 12 sampling occasions.

I estimated the probability of a site being occupied (ψ), and detection probability (*p)* for each species and season. Maximum likelihood was used to estimate parameters (MacKenzie et al. 2006) with the software PRESENCE (Hines 2006). The effect of site specific covariates on ψ or p was explored by means of a logit-link function (i.e. logistic regression), assessed with 95% CI of the β_1 parameter (MacKenzie et al. 2006). Significance of the covariate effect on the parameter was accepted if 0 was not included in the confidence interval (MacKenzie et al. 2006). Two-sided confidence interval was used for all species, however, for Güiña I expected a positive association with forest cover (Acosta & Simonetti 2004; Dunstone et al. 2002) and therefore I used one-sided CI following MacKenzie et al. (2006).

Only one covariate per ψ model was included. I compared occupancy in sample units adjacent to PAs versus fragments in the agricultural matrix using categorical variables - 0 or 1 respectively - and degree of fragmentation as the proportion of forest cover within a 3 km radius from the camera. An additional model was applied to domestic dog data, testing whether the distance to the nearest inhabited human household explained ψ. Covariates for p included PA, forest cover, distance to the nearest water course, elevation and activity of domestic dog. Elevation was only included for autumn/winter models as a proxy to environmental conditions (e.g. temperature, snow fall). Dog activity was applied only to Culpeo fox models to explore effects on detection. The frequency of dog capture was calculated for each season as the number of independent photos (>24hr)/camera days; as a proxy to activity level (Hilty & Merelender 2003). Models with no effect of covariates (i.e. constant model) were also included. Global models were trimmed to determine the most parsimonious model for the empirical data (Burnham & Anderson 1998).

Due to the wide-ranging characteristics of carnivores, the closure assumption of occupancy models are not being met (Long & Zielinski, 2008). If movement in or out of the sites is random during a survey season the closure assumption may be relaxed and the interpretation of the occupancy parameter is proportion/probability of a site used (Long & Zielinski, 2008; MacKenzie et al. 2006). I compared estimates of p between early and late season (i.e. first and last 6 sampling occasions) to assess if movement occurred at random (i.e. no difference).

Akaike Information Criterion (AIC) values were used to select the model that best fitted the observed data. AIC values and model weights were corrected for small sample size (AICc) (Burnham & Anderson 1998). I only consider models with $\Delta AIC_c < 2$ for the analysis because they have substantially more support (Burnham & Anderson 1998). Akaike weights were calculated for all models, providing an indication of evidence in favor of a given model within the set (Burnham & Anderson 1998). Evidence in favor of a particular variable was obtained from the sum of model weights where the variable was included (MacKenzie et al. 2006; Burnham & Anderson 1998). I used the weights of models with a $\Delta AIC_c < 2$ to determine average estimates of ψ and p (Burnham & Anderson 1998). Models with convergence problems due parameters near allowable values (i.e. 0 and 1) were eliminated (e.g. MacKenzie et al. 2004). Model fit and over-dispersion of the global model were assessed with 1000 parametric bootstraps. Goodness of fit was interpreted following MacKenzie and Bailey (2004).

Activity Patterns

Data were pooled from all survey periods. An independent event at a camera site was determined as a photograph taken at a period of >1 hr between records (e.g. Di Bitetti et al. 2006). Domestic dog photos associated with human activity were excluded. I used Kuiper´s test of non-randomness against a uniform distribution because it is able to detect unimodal and bimodal patterns (Batschelet 1981). Since distribution is unknown, I used the Mardia-Watson-Wheeler non-parametric test (Batschelet 1981) for multi-sample and pair-wise comparisons. Analyses were carried out in the software Oriana (KCS 2009).

Results

A total of 463 photographic events (>1 hr) from all survey periods were registered: 6% Puma, 40% Culpeo fox, 23% domestic dog, 5% Chilla fox, and both Güiña and Skunk with 13% (Fig. 2). Considering all survey periods, Culpeo fox, Güiña, Skunk and domestic dog were detected in areas adjacent to PAs, as well as in large and small forest fragments. Pumas were also detected in areas adjacent to PAs and large forest fragments, but not in small fragments. In turn, Chilla foxes were only detected in areas adjacent to PAs, but at higher elevations (i.e. >900 m.a.s.l. during 2006-2007 and 2009 surveys), as well as inside PAs from opportunistic observations (N. Galvez pers. obs). Hence, Chilla fox was not included in the occupancy estimates because it was not detected during the 2008-2009 surveys, restricting sample units to <800 m.a.s.l.

Occupancy and detection

The proportion of sites at which a species was detected, naïve ψ estimate (i.e. not accounting for detection probability), was constant across seasons (Table 1). The mean (SD) naïve estimate for each species was: Skunk 0.24 (0.05), Güiña 0.35 (0.03), Culpeo fox 0.34 (0.03), Puma 0.10 (0.05) and Domestic dog 0.26 (0.02). Model average estimates of ψ show that species used a similar proportion of sites in the area, although some seasonal variations within species were observed (Table 1). Puma models and Autumn/Winter models for Güiña were not analyzed due to unreliable estimates caused by few repeated detection (i.e. only one detection during the season). Differences between early and late occasions were not supported by the data since it was not included in selected models (Table 1), therefore proportion/probability of sites used is the interpretation of ψ. Global models showed appropriate fit during all seasons ($p>0.10$; Table 1), and there was no evidence of over-dispersion.

Molina's Hog-nosed Skunk

Seasonal changes in average ψ showed a decrease during Autumn/Winter (Table 1). Forest cover consistently showed more support for explaining higher ψ of the species over all seasons (Table 1). During Summer/Autumn, the summed model weights for forest cover versus areas adjacent to PAs were 79% and 21% respectively, hence 3.67 times more evidence in favor of forest cover. Similarly, during Autumn/Winter, forest cover (88% summed model weight) had 7.67 more support than the constant model (12%). In Spring/Summer the constant model was the highest ranked; however forest cover still presented some support within selected models (63%). Relationship of forest cover with ψ was positive in all seasons, however the effect was only significant – nearly categorical - during Autumn/Winter (Table 2). Detection was significantly higher at sites with lower forest cover and near households (Table 2). During Autumn/Winter, detection was significantly higher in areas adjacent to PAs, however within these forests detection was negatively related to elevation (Table 2).

Kodkod or Güiña

Estimated ψ by Güiña was similar for both seasons (Table 1). Although it could not be estimated for Autumn/Winter due to low detection, the naïve estimate was high and similar to other seasons (0.37). Forest cover showed mixed support for explaining ψ. In Summer/Autumn, the evidence provided for forest cover was 2.5 times the evidence in support of the constant model (Table 1). However during Spring/Summer evidence in favor of the constant model was almost twice that of forest cover with summed model weights of 0.66 and 0.34 respectively. Furthermore, only a weak positive association between ψ and forest cover was found. Forest cover appears to have an effect, but the magnitude is poorly supported (Table 2). Overall detection of Güiña was low (Table 1) and positively associated with forest cover (Table 2).

Culpeo fox

Average occupancy estimates of Culpeo fox did not vary greatly during the year, and no factor had significant support (Table 1). In Summer/Autumn, there was no particular factor with more evidence of support from summed model weights between forest cover (32%), areas adjacent to PAs (40%) and the constant model (28%). During Autumn/Winter, neither forest cover nor areas adjacent to PAs were considered important factors of ψ from the data collected (Table 1). Likewise, in Spring/Summer the factor of areas adjacent to PAs did not show much support compared to the constant model. Sites use by the species was negatively related to forest cover but the effect was not significant. Also, sites used by the species in areas adjacent to PAs showed mixed results. During Summer/Autumn ψ was lower in areas adjacent to PAs, however, in Spring/Summer estimated ψ was higher (Table 1). In turn, effects of covariates on p from top ranked models were fairly consistent across seasons (Table 2). Detection significantly increased at sites with lower forest cover. Also it was significantly higher at sites where domestic dog activity was observed. Finally, detection of Culpeo fox was significantly higher in sites not adjacent to PAs during Spring/Summer (Table 2).

Domestic dog

Average ψ of domestic dogs remained constant between Summer/Autumn and Autumn/Winter, with a slight decrease in Spring/Summer (Table 1). Support for a particular variable on ψ of domestic dogs was only observed during Summer/Autumn. Whether areas were adjacent or not to PAs had twice the support compared to the constant model (Table 1), and ψ of dogs was significantly higher in fragments of the agricultural matrix (Table 2). The same pattern was observed during all seasons (Table 1), but effects during Autumn/Winter and Spring/Summer were not significant. Average detection probability was similar across seasons (Table 1). Detection was significantly higher in areas not adjacent to protected lands (Table 2). During Summer/Autumn detection was higher as forest cover increased, however it was higher near households (Table 2).

Activity Patterns

The activity of native species was mainly nocturnal and during twilight periods, but domestic dog activity was significantly diurnal (Fig. 2). Differences in activity patterns between species were highly significant (W_{10}= 103.6, $p<0.01$). Main differences in species comparisons were observed in the patterns of Skunk and domestic dog. The Skunk differed significantly from Puma, Güiña and Culpeo, but not from the Chilla fox (Fig. 2). The latter four species did not differ significantly from each other. However, the difference of both foxes to Puma were nearly significant (Chilla fox W_2=5.26; p=0.072; Culpeo fox W_2=4.87, p=0.088). In turn, Domestic dog differed significantly from all native species (Fig. 2).

Discussion

Habitat use patterns

Evidence suggests that the Skunk and Güiña are affected by the amount of cover rather than if forests are adjacent to PAs, favoring the hypothesis that forest cover is important for the conservation of both species in the buffer area. In turn, Culpeo fox and domestic dog are highly associated with the agricultural matrix. Culpeo fox uses all habitats, although favors activity in the agricultural matrix. On the contrary, domestic dog presence and activity are consistently higher in the agricultural matrix. Evidence from the entire survey period (i.e. 2006-2009) suggests that Puma and Chilla fox are confined to large forest tracks and areas adjacent to PAs.

The Skunk is a generalist species known to use forests (Quintana et al. 2000). In Patagonian steppes, Donadio et al. (2001) found that activity was higher in open habitats compared to shrub forests, using the latter for resting rather than foraging. Proportion of sites used by the species had a positive association with forest cover, possibly due to the presence of refuge or resting dens. Furthermore, detection or activity was higher at sites with less cover, potentially as a result of foraging behavior in habitats with higher edges or proximity to open habitats. Also, detection was higher next to human households, possibly indicative of access to food resources associated with livestock production in edge habitats (Donadio et al. 2004). During Autumn/Winter the Skunk was the only species where detection was negatively affected by elevation. However, detection was higher in areas adjacent to PAs, suggesting that within these forests, activity is restricted at higher sites due to environmental conditions.

The small felid Güiña - the most threatened species of the guild (Acosta & Lucherini 2008) - is documented to prefer native forest (Acosta & Simonetti 2004; Dunstone et al. 2002). Similarly, both proportion of sites used and detection were positively affected by forest cover.

However, the strength of the relationship is stronger for detection. This calls attention to previous work inferring habitat preference based solely on detection (Acosta & Simonetti 2004), highlighting the need for further research. The highly elusive nature of this species (i.e. low detection) is possibly a result of low density and ranging behavior. Finally, presence of this cat in small fragments of the agricultural matrix supports documented ability to cross heterogeneous landscapes (Sanderson et al. 2002) and highlights the importance of these remnant forests for the conservation of this endangered felid.

The Culpeo fox is a generalist and resilient species, not particularly under threat (Jiménez & Novaro 2004), which explains some of the patterns observed. Between Summer/Autumn and Spring/Summer there could be shifts in the use of the landscape, possibly by the increase of resources in forests adjacent to PAs during the latter season. During winter, the species is widespread in the area because only constant models explained the data. This suggests that a general reduction in resources forces the species to increase its foraging area. Nevertheless, detection was consistently higher in areas with less cover suggesting, that activity of the species is favored in sites with higher edge or proximity to open habitats.

Domestic dogs use a large proportion of sites associated with the human landscape. In a study within the temperate forest eco-region, Silva et al. (In press) found that dogs belonged to households rather than feral. I suggest a similar situation for Andean areas where there is substantially higher use in the agricultural matrix, higher detection closer to human households and diurnal activity patterns. However, distance to human households did not explain ψ by dogs and detection was higher with increasing forest cover, suggesting that dogs travel significant distances from households potentially causing negative effects on native wildlife in remnant forest patches.

Detrimental effects of dogs on native fauna have been documented inside PAs of the coastal range (Silva et al. 2010). However marginal presence and activity in areas adjacent to Andean PAs suggests partial segregation of dogs from these areas that are potential entry points to PAs. Some plausible explanations are higher energy expenditure required to explore high elevation areas and/or the presence of Puma is causing exclusion by predation or fear (Donadio & Buskirk 2005). If the latter is correct, presence of Puma could be reducing predation pressure of Andean populations of the endangered deer Pudu (*Pudu puda*), by regulating abundance and activity of dogs. Domestic dogs are a threat to the Pudu (Silva et al. 2010) and the species was only detected in adjacent forests to PAs and large fragments during the entire study period (N. Galvez et al. unpublished data).

The Chilla fox seems to avoid the larger canids – Culpeo and dogs - by restricting use only to highland areas. Culpeo fox excludes the Chilla fox by competitive interference (Johnson & Frankling 1994); however, there is evidence that exclusion is not complete (Jiménez 1996), so there could be an overlap in adjacent areas to PAs. Also, spatial segregation from competition with dogs, since recent research shows that domestic dogs kill and harass Chilla foxes (Silva et al. In press).

Mountainous terrain and forested areas are preferred by the Puma in temperate forest environments of Chile (Quintana et al. 2000), possibly explaining their presence only in large fragments and areas adjacent to PAs. The non-detection of the species in small fragments of the agricultural matrix during the entire 2008 survey suggests that the matrix could be limiting dispersal. Conflict with small farmers in the area (Murphy & Macdonald 2010) and the availability of forest cover for refuge could be limiting Puma presence in fragmented areas.

Activity and interactions

In general, there is evidence for temporal segregation that suggests co-existence in the buffer area. The Skunk is interacting spatially with all carnivores of the guild; however temporal pattern significantly differs from all species (Fig. 2). Although the species is at high risk of predation, defense mechanism of anal secretions deters potential predators (Hunter & Caro 2008), suggesting avoidance by other guild members. However, Puma has been documented to predate on a congener species *Conepatus humboltii* (Johnson & Franklin 1994 cited in Donadio & Buskirk 2005), therefore avoidance by the skunk could explain co-existence. Activity of Güiña did not differ from larger native predators and since it is potentially at risk, behavior mechanisms might be operating. This small feline frequently uses the vertical portion of habitat by climbing trees (Sanderson et al. 2002), which perhaps is the mechanism used in case of encounter.

Canids are under the greatest competition pressure of all American carnivores (Hunter & Caro 2008). The largest carnivore of the guild – Puma – has been documented to kill Culpeo and Chilla fox (Donadio & Buskirk 2005); possibly explaining why differences in activity patterns of the two canids and Puma were nearly significant. However, this would need further assessment comparing only data of areas where Puma was detected. Evidence suggests that both foxes avoid domestic dogs by differences in activity patterns.

Guild conservation priorities

Perhaps the greatest long-term threat to carnivores is land conversion (Ginsberg 2001), therefore protection of existing fragments and prevention of further fragmentation is a priority. Especially species with higher sensitivity to forest fragmentation like the Skunk and the endangered Güiña. Also, adjacent areas to PAs and large fragments are important for the top predator Puma which could be playing a key role in guild dynamics. Carnivores can be used as focal species for conservation planning due to variation of sensitivity to landscape changes (Carroll et al. 2001). Consequently, I suggest that the Güiña, Skunk and Puma are priority species for conservation planning in the buffer area, which would be effective for the entire guild.

All forests surrounding PAs are privately owned; therefore strategies must involve working with landowners. However, there must be cost-effective economic incentives to support protection of these remnant forests. The Araucanía district is an increasing nature tourism destination, thus revenue from tourism activities could be an option. However, understanding perception and attitudes of landowners regarding carnivores, remnant forests on their lands and how they perceive future land use is urgently needed.

Furthermore, human-carnivore conflict must be addressed, especially for Puma, Güiña (Inskip & Zimmermann 2009) and Culpeo fox (Jiménez & Novaro 2004). It is documented that livestock husbandry practices can effectively reduce predation and conflict with carnivores (Ogada et al. 2003). Conflict mitigation should follow preventive measures such as appropriate night closures for small ruminant livestock and poultry, since activity of species is nocturnal or crepuscular. Domestic dogs are also responsible for livestock predation in the area (Murphy & Macdonald 2010), hence strategies should involve awareness campaigns for appropriate tenancy.

Local action plans that include guild-level studies are considered a priority for carnivore conservation (Ginsberg 2001). The results of this study provide quantitative information that can inform PA managers and decision makers on priority areas in surrounding lands where to target efforts. Further research should compare surrounding lands to habitats inside high elevation PAs to better understand boundary dynamics and importance of protected habitats for the carnivore guild. Finally, the guild-landscape dynamic studied confirms the complexities of carnivore communities and that management can benefit from guild-level studies.

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Table 1. Estimated proportion of sites used (ψ) and detection probability (*p*) of best fitting models of the carnivore guild during Summer/Autumn, Autumn/Winter, and Spring/Summer in buffer areas of protected lands in Andean temperate forest of South-Central Chile[a]

Species/season	Model	ΔAIC_c	*wi*	K	Est.ψ (SE)	Est. *p* (SE)	Model fit[b]
Molina´s Hog-nosed Skunk							
Summer/Autumn	ψ (cover),p(cover+water)	0	0.50	5	0.63 (0.12)	0.15 (0.04)	0.12
naïve ψ = 0.26	ψ (cover),p(water+human)	1.13	0.28	5	0.50 (0.10)	0.20 (0.04)	
	ψ (PA),p(water+human)[c]	1.7	0.21	5	0.72 (0.21); 0.26 (0.14)	0.20 (0.04)	
			Model average		0.56 (0.12)	0.17 (0.04)	
Autumn/Winter	ψ (cover),p(cover+PA+elevation)	0	0.22	6	0.51 (0.08)	0.11 (0.04)	0.41
naïve ψ = 0.18	ψ (cover),p(cover+PA)	0.28	0.19	5	0.36 (0.09)	0.24 (0.04)	
	ψ (cover),p(.)	1.01	0.13	3	0.23 (0.09)	0.26 (0.08)	
	ψ (cover),p(PA+human)	1.15	0.13	5	0.29 (0.09)	0.22 (0.07)	
	ψ (.),p(.)	1.31	0.12	2	0.22 (0.09	0.27 (0.09)	
	ψ (cover),p(cover+PA+water)	1.45	0.11	6	0.36 (0.08)	0.34 (0.05)	
	ψ (cover),p(cover+human)	1.62	0.10	5	0.27 (0.08)	0.30 (0.08)	
			Model average		0.34 (0.10)	0.23 (0.06)	
Spring/Summer	ψ (.),p(.)	0	0.37	2	0.67 (0.39)	0.05 (0.04)	0.94
naïve ψ = 0.28	ψ (cover),p(.)	0.7	0.26	3	0.77 (0.15)	0.05 (0.02)	
	ψ (cover),p(human)	1.03	0.22	4	0.74 (0.17)	0.04 (0.02)	
	ψ (cover),p(human+cover)	1.73	0.15	5	0.78 (0.13)	0.05 (0.01)	
			Model average		0.73 (0.23)	0.05 (0.02)	
Kodkod or Güiña							
Summer/Autumn	ψ (cover),p(human)	0	0.43	4	0.65 (0.15)	0.09 (0.03)	0.51
naïve ψ = 0.37	ψ (cover),p(.)	0.83	0.29	3	0.65 (0.17)	0.09 (0.03)	
	ψ (.),p(.)	0.85	0.28	2	0.63 (0.22)	0.09 (0.04)	
			Model average		0.64 (0.18)	0.09 (0.03)	

Spring/Summer	ψ (.),p(cover)	0	0.33	3	0.80 (0.33)	0.07 (0.03)	0.53
naïve ψ = 0.32	ψ (cover),p(.)	1.03	0.20	3	0.62 (0.19)	0.08 (0.03)	
	ψ (.),p(.)	1.3	0.17	2	0.61 (0.28)	0.08 (0.03)	
	ψ (.),p(cover+PA)	1.57	0.15	4	0.71 (0.23)	0.08 (0.04)	
	ψ (cover),p(cover+PA)	1.69	0.14	5	0.62 (0.10)	0.10 (0.03)	
			Model average		0.69 (0.24)	0.08 (0.03)	
Culpeo fox							
Summer/Autumn	ψ (cover),p(cover+dog)	0	0.32	5	0.53 (0.15)	0.14 (0.04)	0.50
naïve ψ = 0.37	ψ (.),p(cover+dog)	0.22	0.28	4	0.84 (0.29)	0.12 (0.03)	
	ψ (PA),p(cover+dog) ^{c}	0.29	0.27	5	0.21 (0.22); 0.84 (0.22)	0.14 (0.04)	
	ψ (PA),p(cover+PA+dog) ^{c}	1.77	0.13	6	0.14 (0.14); 0.99 (0.33)	0.12 (0.04)	
			Model average		0.64 (0.22)	0.13 (0.04)	
Autumn/Winter	ψ (.),p(cover)	0	0.44	3	0.58 (0.17)	0.15 (0.04)	0.64
naïve ψ = 0.33	ψ (.),p(cover+Dog)	0.28	0.38	4	0.58 (0.16)	0.17 (0.04)	
	ψ (.),p(cover+dog+elevation)	1.73	0.18	5	0.52 (0.13)	0.06 (0.02)	
			Model average		0.57 (0.16)	0.14 (0.04)	
Spring/Summer	ψ (PA),p(PA+dog)^{c}	0	0.61	5	0.91 (0.63); 0.34 (0.12)	0.35 (0.04)	0.59
naïve ψ = 0.32	ψ (.),p(cover+PA+dog)	0.91	0.39	5	0.40 (0.12)	0.25 (0.06)	
			Model average		0.52 (0.22)	0.31 (0.05)	
Domestic Dog							
Summer/Autumn	ψ (PA),p(.)^{c}	0	0.66	3	0.00 (0.00) 0.61 (0.20)	0.15 (0.05)	0.69
naïve ψ = 0.26	ψ (.),p(cover+PA+water+human)	1.38	0.33	6	0.81 (0.16)	0.07 (0.03)	
			Model average		0.68 (0.20)	0.12 (0.05)	
Autumn/Winter	ψ (PA),p(.)^{c}	0	0.44	3	0.14 (0.14); 0.79 (0.33)	0.12 (0.06)	0.69
naïve ψ = 0.25	ψ (.),p(cover+PA)	0.69	0.31	4	0.73 (0.28)	0.08 (0.04)	
	ψ (.),p(PA+elevation)	1.11	0.25	4	0.68 (0.27)	0.09 (0.04)	

			Model average		0.62 (0.26)	0.10 (0.05)	
Spring/Summer	ψ (.),p(water)	0	0.59	3	0.49 (0.2)	0.12 (0.04)	0.54
naïve ψ = 0.28	ψ (PA),p(water)[c]	0.71	0.41	4	0.18 (0.18); 0.60 (0.2)	0.13 (0.04)	
			Model average		0.46 (0.18)	0.12 (0.04)	

(a) Naïve ψ is the pproportion of sites used not accounting for detection probability; AIC_c is Akaike Information Criteria corrected for small sample size; ΔAIC_c is the difference of values from the top ranked model; *wi* is the AIC_c model weight; K is the number of parameters; Est. ψ is the estimated proportion of sites used; Est. p is the estimated detection probability. Covariates of models are protected area (PA); forest cover (cover), distance to human households (human), distance to nearest water course (water) and activity of domestic dog (dog).

(b) Probability of test statistic >= than observed from 1000 parametric bootstraps of the Global model. Non significance means observed test statistic did not differ from bootstrap distribution.

(c) For protected area (PA) two values are presented; estimated ψ(SE) of sites adjacent to protected areas followed by estimates of sites in forest fragments of the agricultural matrix.

Table 2. Covariates with significant effects on proportion of sites used (ψ) and detection probability (p) of top ranked models during Summer/Autumn, Autumn/Winter, and Spring/Summer[a]

Species/season	Parameter	Covariate[b]	β_1	SE	95%CI[c]	
Molina's Hog-nosed Skunk						
Summer/Autumn	p	cover	-7.3	2.2	-11.6	-3.0
	p	water	0.25	0.09	0.07	0.43
	p	human	-0.57	0.21	-0.98	-0.16
Autumn/Winter	ψ	cover	45.8	14.0	18.4	73.1
	p	PA	-4.1	1.6	-7.2	-1.0
	p	elevation	-1.15	0.36	-1.9	-0.44
	p	Cover	-12.1	4.3	-20.5	-3.7
	p	human	-0.23	0.11	-0.45	-0.01
Spring/Summer	p	human	-0.35	-0.18	0.003	-0.70
Kod-kod or Güiña[d]						
Spring/Summer	ψ	cover	16.8	10.2	-0.04	∞
	p	cover	4.2	2.1	0.70	∞
Culpeo fox						
Summer/Autumn	p	cover	-4.9	1.7	-8.2	-1.6
	p	dog	16.5	5.0	6.6	26.3
Autumn/Winter	p	cover	-5.3	2.2	-9.6	-0.90
Spring/Summer	p	dog	119.1	41.4	37.9	200.3
	p	PA	3.4	1.4	0.63	6.1
Domestic Dog						
Summer/Autumn	ψ	PA	36.8	3.1	30.8	42.9
	p	PA	27.6	3.24	21.2	34.0
	p	cover	6.0	2.7	0.72	11.18
	p	human	-0.57	0.23	-1.02	-0.12
Autumn/Winter	p	PA	2.8	1.2	0.38	5.1
Spring/Summer	p	water	0.27	0.09	0.09	0.45

(a) $\beta 1$ is the regression parameter. Covariates of models are protected area (PA); forest cover (cover), distance to human households (human), distance to nearest water course (water) and activity of domestic dog (dog).

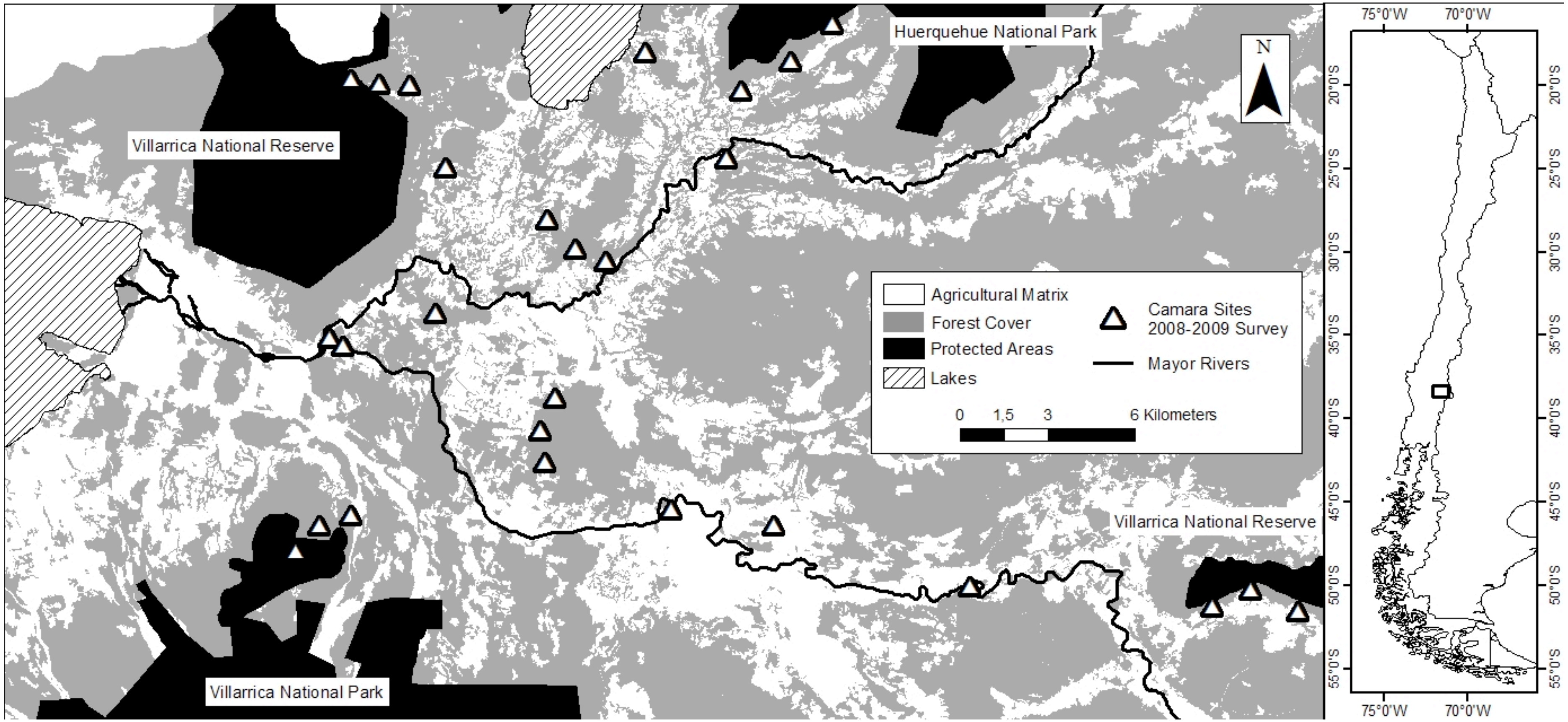
(b) Positive values for β_1 parameter of PA indicate higher ψ or p in sites not adjacent to PAs.

(c) Significance is accepted if 0 is not included in 95%CI of β_1 parameter ($\beta_1 \pm 1.96*S.E$).

(d) One sided CI (90% lower limit $\beta_1 - 1.65*S.E$).

Figure 1. Study area and survey design during 2008-2009 in the Araucanía Region of the temperate forest of South-Central Chile

Figure 2. Activity patterns of the Carnivore guild in Andean Temperate Rainforest of Southern Chile. Circumscribed circles and bars show number of observations. Graphs are clockwise with y axis showing mid-night (top) and mid-day (bottom); x axis show 0600 hours (right) and 1800 hours (left). Significance of non-randomness in the activity pattern is given at $\alpha < 0.05$ (*) and <0.01(**) (Kuiper´s one sample uniform test). Different letters represent significant differences between species at $\alpha < 0.05$ (Mardia-Watson-Wheeler pairwise comparison)


Huerquehue National Park
N
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Agricultural Matrix
Forest Cover
Protected Areas
Lakes
Camara Sites
2008-2009 Survey
Mayor Rivers
0
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3
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Villarrica National Reserve
Villarrica National Park
75°0'W
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55°0'S

Figure 1

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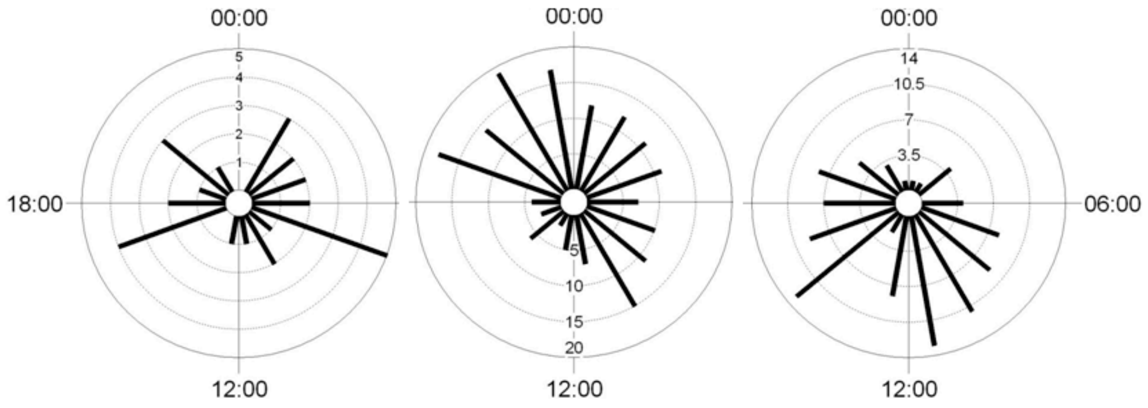
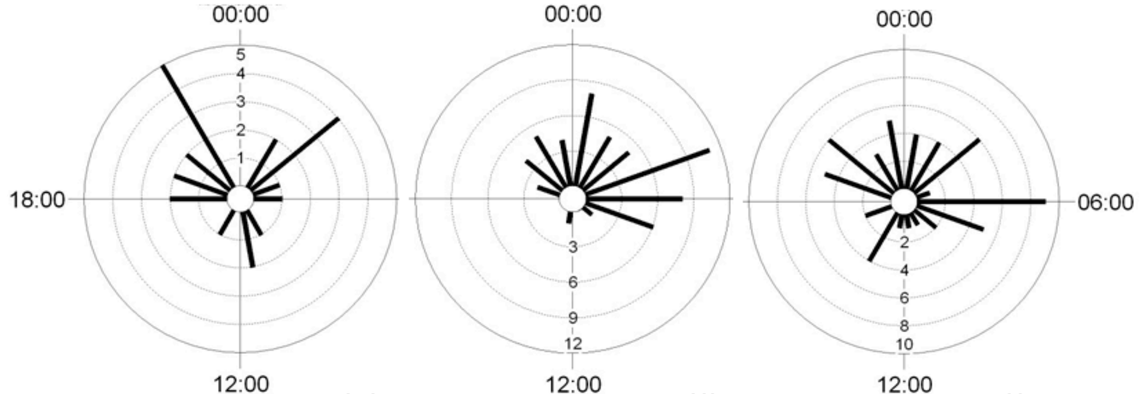


Puma (n=30)^{a} Culpeo fox (n=184) ^{**a} Domestic dog (n=107) ^{**c}



Chilla fox (n=23)^{*ab} Skunk (n=60)^{**b} Güiña (n=59)^{**a}

Figure 2