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Activity patterns in sympatric carnivores in the Nahuelbuta Mountain Range, southern-central Chile

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Abstract: Species interactions determine the structure of biological communities. In particular, interference behavior is critical as dominant species can displace subordinate species depending on local ecological conditions. In carnivores, the outcome of interference may have important consequences from the point of view of conservation, especially when vulnerable species are the ones suffering displacement. Using 24 baited camera traps and a sampling effort of 2821 trap nights, we examined the activity patterns and spatial overlap of an assemblage of five sympatric carnivores in the Nahuelbuta Mountain Range, in southern-central Chile. In this forested landscape we found predominantly nocturnal activity in all species, but not for the puma (*Puma concolor*) and to a lesser extent, for the guigna (*Leopardus guigna*). In terms of spatial overlap, there was a non-significant negative relationship between the puma and the culpeo (*Lycalopex culpaeus*), and a positive relationship among the three smaller species of the assemblage, the guigna, the hog-nosed skunk (*Conepatus chinga*), and the Darwin's fox (*Lycalopex fulvipes*). Culpeo displayed a negative spatial relationship with the three later species appearing to be a product of interference behavior. Species-specific ecological differences, including prey types and spatio-temporal partitioning among the carnivores appear to allow their coexistence.

Keywords: assemblage; camera traps; circadian cycle; coexistence; interference.

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Introduction

Species interactions are one of the most studied topics in community ecology, as interspecific behavior can largely determine the composition and structure of community assemblages (Case and Gilpin 1974). For carnivores, interspecific interactions are particularly relevant because of their role in top-down control in terrestrial ecosystems (Terborgh and Winter 1980). Nevertheless, given the key role of consumers and through trophic cascades, changes in the environment could promote an increase of medium-sized carnivores or mesopredators, due to top predator removal (Prange and Gehrt 2007) which can cause substantial changes in the dynamics of interaction among sympatric species (Kamler et al. 2013), with adverse effects on subordinate species. Thus, to minimize risks, subordinate species tend to avoid encounters with dominant species (Berger and Gese 2007).

Coexistence among competitors can occur by minimizing resource use overlap through niche segregation and complementarity (Jiménez et al. 1996). To avoid interference, subordinate species could modify their activity patterns according to that of the dominant species (Carothers and Jaksic 1984). Therefore, subordinate species should avoid direct encounters among potential competitors and prevent interspecific competition (Kronfeld-Schor and Dayan 2003). Shifting activity patterns, however, would require flexibility to cope with other environmental requirements and ecological contexts (Di Bitetti et al. 2009, Hayward and Slotow 2009). Further, species' ecological and morphological characteristics and resource use can increase the complexity of interference and the dynamics of the interactions. Donadio and Buskirk (2006) proposed that taxonomic and spatial similarities among species, as well as their size and respective prey, will determine the interaction outcome.

Although studies describing activity patterns in carnivores have recently increased in the Neotropics, they mainly focus on pair-wise species interactions (Jácomo et al. 2004, Lucherini et al. 2009), which limits the knowledge about relationships in ecological communities. In this sense, in most assemblages, the spatio-temporal

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dynamics of interactions among syntopic (sensu Rivas 1964) carnivore species is largely unknown. In the Nahuelbuta Mountain Range of southern Chile, mammals, especially carnivores, form an assemblage of interest given the biogeographical isolation of this region (Armesto et al. 1996a) and because this is the only known location where a diversity of carnivores that otherwise do not co-exist, are syntopic (Murúa 1996). Thus, although only one species in this area has been studied (Jiménez 2000), time partitioning has not been addressed. Here, we hypothesize that the small scale co-occurrence of carnivores in Nahuelbuta can be explained by species' spatial and temporal segregation as a mechanism to avoid interspecific interference through direct encounters.

Materials and methods

Study area

Caramávida is a private 10,097-ha area located on the western slope of the Nahuelbuta Mountain Range (37°41′S, 73°14′W) in south-central Chile (Figure 1). The climate is Mediterranean-humid (Di Castri and Hajek 1976), with main precipitation falling during the austral winter months. The terrain is relatively rugged and elevations range from 700 to 1000 m above sea level. The landscape presents a combination of pristine and disturbed southern beech (*Nothofagus* spp.) and monkey-puzzle (*Araucaria araucana*) forests (Luebert and Pliscoff 2004). Lower elevation areas generally lack native forests and are heavily impacted and eroded with extensive plantations of *Pinus radiata* and *Eucalyptus globulus*. Few open areas with herbaceous vegetation and shrubs in various stages of recovery remain due to past agricultural practices and current livestock grazing. Caramávida contains a high number of endemic fauna (32 species; Armesto et al. 1996b) and has high risks related to human activities, such as logging. Due to this, the area has been considered a priority site in need of urgent conservation (Muñoz et al. 1996).

Assessment of activity patterns in carnivores

To detect carnivores, we operated 24 Bushnell Trophy Cam camera traps (Bushnell Corporation, Overland Park, KS, USA) between September 2010 and February 2011. We obtained images that allowed unequivocal species identification (Kays and Slauson 2008), with recorded date and time on each image. Four transects of six cameras each were arranged throughout the study area so that they covered all the vegetation formations of the area (Luebert and Pliscoff 2004). Cameras were spaced 500 m apart one from one another (Rovero and Marshall 2009), and installed 1 m above the ground, fixed to tree trunks and baited with canned mackerel (*Trachurus murphy*, Zielinski and Kucera 1995). Lines of cameras were arranged, on average, 2 km in distance one from the other (Figure 1). Cameras were active 24 h per day along the whole survey period.

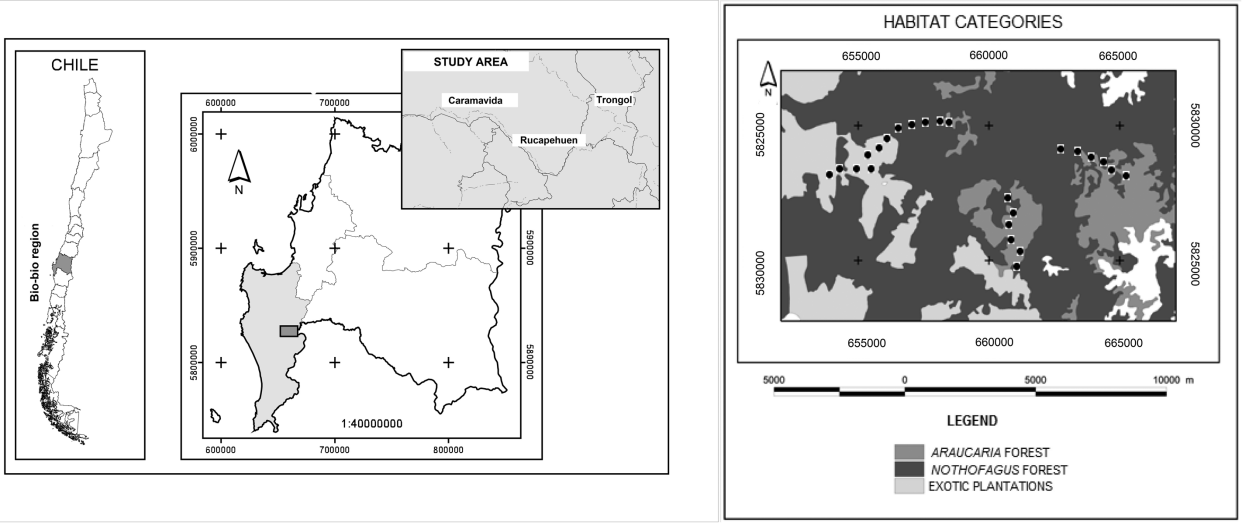

Figure 1: Study area and habitat types present. Dots indicate the locations of cameras.

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Activity patterns for each species were estimated as the average number of images obtained per hour across all the daily records. To ensure temporal independence, species captured in each camera were counted once during a single-hour interval. Daytime was grouped into four discrete periods (Fedriani 1997): dawn (06:01–08:00 h, 8.3% of the daily cycle), day (08:01–18:00 h, 41.7%), dusk (18:01–20:00 h, 8.3%), and night (20:01–06:00 h, 41.7%). Co-use of activity time was assessed through Pianka's overlap index (Pianka 1973). To determine whether species pair-wise differences were statistically significant, values should fall outside confidence intervals of an expected random pattern. We obtained these intervals through stochastic reallocations with 10,000 iterations, using the statistical package Spaa (Zhang et al. 2010) in R statistical software version 0.2.0. The alpha level was set at 5%.

Spatial overlap among species

We log-transformed the frequency of recordings of species to meet normality assumptions (Zar 1984), applied Bonferroni's correction to each series of analyses (Holm 1979) and used Pearson's correlation to determine if avoidance behavior among carnivores existed. We compared recorded images at each camera station (n = 24) during the entire monitoring period. We interpreted spatial avoidance between a pair of species when their spatial correlations were negative (Neale and Sacks 2001).

Results

By using an overall sampling effort of 2821 trap nights, we detected five carnivore species: puma (*Puma concolor*, n = 32 independent recordings), culpeo (*Lycalopex culpaeus*, n = 75), Darwin's fox (*Lycalopex fulvipes*, n = 75), Molina's hog-nosed skunk (*Conepatus chinga*, n = 80), and guigna (*Leopardus guigna*, n = 40). All carnivores, but puma, concentrated their activity patterns mainly at night (Figure 2), especially the culpeo and the Darwin's fox (86.6% and 94.4% of their total records, respectively), and to a lesser extent, the hog-nosed skunk and the guigna (73.6% and 70.5% of their total records, respectively). Only the puma showed a higher proportion of activity during daytime (51.5% of their total recordings). All species were minimally active during dusk and dawn. Thus, all five species differed in their activity behavior from a homogeneous pattern (all $\chi^2_3 > 20$, $p \leq 0.001$).

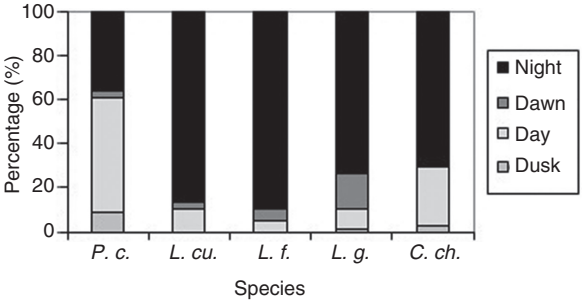

Figure 2: Percent activity patterns of carnivores in Caramávida according to light availability periods.
P. c., *Puma concolor*; L. cu., *Lycalopex culpaeus;* L. f., *Lycalopex fulvipes;* C. ch., *Conepatus chinga;* L. g., *Leopardus guigna.* Periods: night (20:01–06:00 h), dawn (06:01–08:00 h), day (08:01–18:00 h), and dusk (18:01–20:00 h).

Carnivores' daily activity patterns differed in their variability (Coefficient of variation, puma: 73.7, culpeo: 105.1, Darwin's fox: 120.2, hog-nosed skunk: 104.8, and guigna: 104.7; Figure 3). However, differences in peaks among species were not statistically significant (Kruskal-Wallis test, H = 6.529; df = 4; p = 0.163). Pianka's overlap index was different among species pairs (Table 1), varying between intermediate (puma vs. all other species) and high overlaps (among culpeo, hog-nosed skunk, guigna, and Darwin's fox). However, high overlaps were only statistically significant for Darwin's fox with culpeo, and hog-nosed skunk (Table 1).

The co-use of space in the sympatric carnivores was highest among the small species. There was a non-significant spatial avoidance behavior between the puma and culpeo, and among the culpeo and the other three smaller species, with different degrees of significance (Table 2), which includes negative relationships with Darwin's fox. The puma used the environment in a similar way as the skunk, guigna, and Darwin's fox, where all these correlations were statistically significant. Darwin's fox showed a significative and positive correlation with skunk.

Discussion

Activity patterns in carnivores

Activity patterns of carnivores in Nahuelbuta partially differed from those reported for carnivores in other latitudes, indicating a level of flexibility in the species' responses to varying environmental conditions (Tattersal 1979). Most species in Caramávida were nocturnal, which

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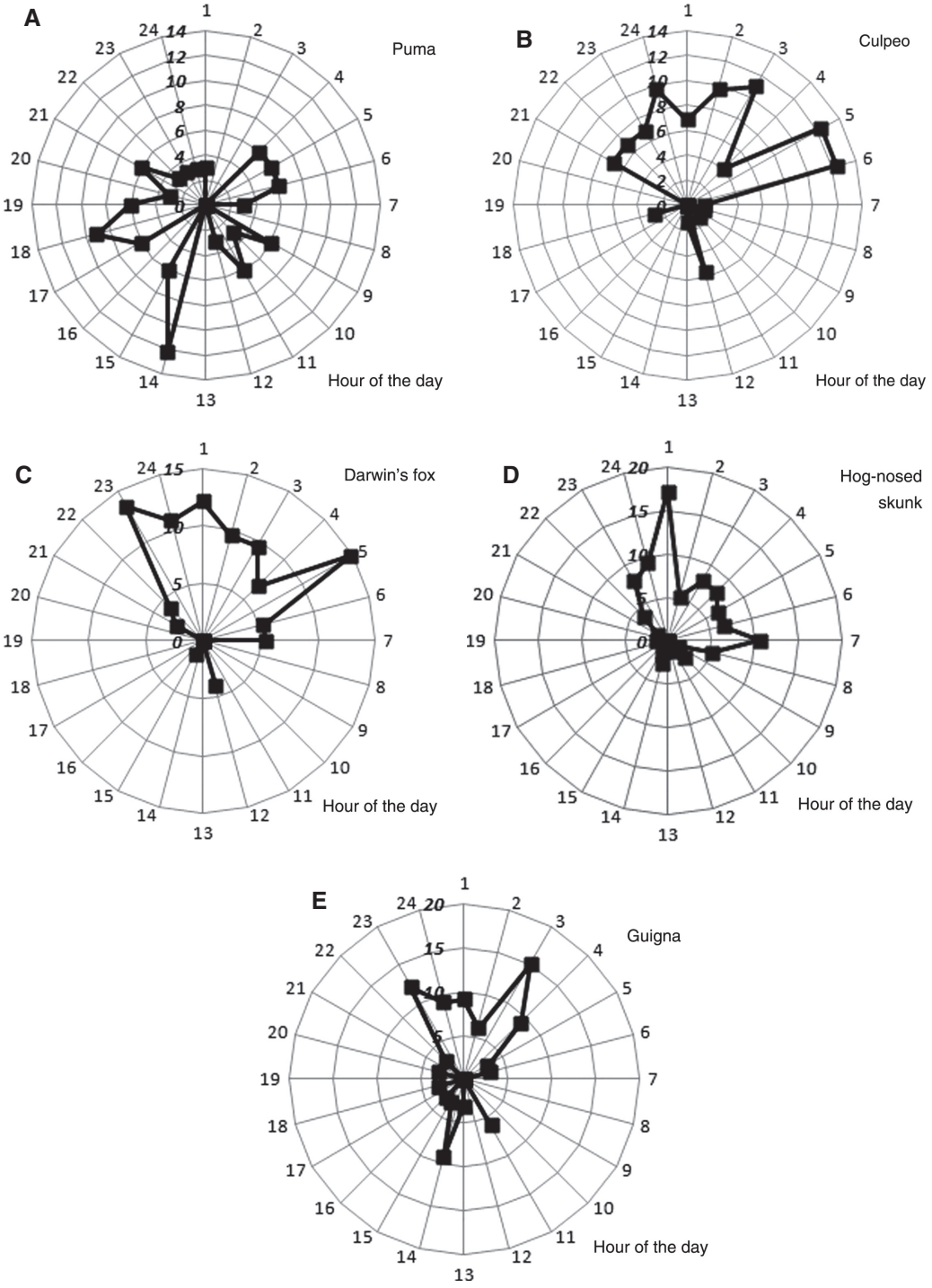

Figure 3: Activity time of carnivores in Caramávida, Nahuelbuta Mountain Range. Squares indicate the percent frequency distribution for each species.

coincided with the activity pattern of their main prey, small mammals (Greer 1965, Muñoz-Pedreros et al. 1990, Murúa 1996). This indicates a maximization of the effectiveness in prey capture by the carnivores (Zielinski 1988).

The puma showed a relatively homogeneous activity pattern throughout the day. However, McCain (2008) indicated that the puma was flexible in its activity patterns, adjusting its activity to that of its most frequent prey. For Caramávida, we would expect the puma to follow the activity pattern of its main prey in southern Chile, the pudu deer (*Pudu puda*) (Rau and Jiménez 2002), whose presence was also recorded by camera traps

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Table 1: Overlaps in activity time among carnivores in Caramávida according to Pianka's Index.

Species	P. c.	L. cu.	L. f.	C. ch.	L. g.
P. c.		0.48	0.42	0.47	0.53
L. cu.	0.25–0.86		0.89	0.77	0.70
L. f.	0.20–0.79	0.10–0.77[a]		0.87	0.77
C. ch.	0.26–0.82	0.16–0.78	0.11–0.77[a]		0.74
L. g.	0.26–0.82	0.14–0.79	0.11–0.77	0.17–0.79	

Under the diagonal, the expected 95% confidence intervals obtained through bootstrapping are shown.
[a]Statistically significant. P. c., *Puma concolor*; L. cu., *Lycalopex culpaeus*; L. f., *Lycalopex fulvipes*; C. ch., *Conepatus chinga*; L. g., *Leopardus guigna*.

Table 2: Spatial overlap among carnivores in Caramavida using Pearson's correlation analyses (r).

Species	Weight (kg)	P. c.	L. cu.	L. f.	C. ch.	L. g.
P. c.	64		−0.141	0.553	0.782	0.616
L. cu.	7	0.461		−0.363	0.215	0.301
L. f.	3	0.005[a]	0.089		0.653	0.522
C. ch.	3	0.001[a]	0.014	0.001[a]		0.504
L. g.	2.5	0.002[a]	0.163	0.011	0.014	

Below the diagonal, the significance values (p) are shown.
[a]Statistically significant according to Bonferroni's correction.
P. c., *Puma concolor*; L. cu., *Lycalopex culpaeus*; L. f., *Lycalopex fulvipes*; C. ch., *Conepatus chinga*; L. g., *Leopardus guigna*.
Weights for all species according to Iriarte and Jaksic (2012) and Wilson and Reeder (2005) are also shown.

in Caramávida in the present study (unpublished data), mainly in *Nothofagus* forests. The activity pattern of the pudu deer is mainly diurnal (Eldridge et al. 1987). Additionally, the temporal behavioral pattern of the puma in Caramávida differed from that in other latitudes, where this felid interacted with other similar-sized or larger carnivores. In the plains of west-central Venezuela, the puma was mostly nocturnal, unlike the sympatric jaguar (*Panthera onca*) (Scognamillo et al. 2003). In contrast, Lucherini et al. (2009), working in the Andes Mountain Range where the puma is the largest mammalian predator, found that this felid was less active during the night, yet it overlapped with sympatric felids of smaller size. In northern Argentina, Paviolo et al. (2009) found a positive relationship between the degree of puma safety (i.e. the likelihood of it being hunted by humans) and the amount of diurnal activity. At Caramávida, we do not have records of puma poached during the last 15 years, which may explain the relaxation of its activity patterns, although other factors cannot be excluded.

Time pattern of culpeo activity in Caramávida partially contrasts with observations in northern Chile (Jiménez 1993, Jiménez et al. 2000), in Argentina (Lucherini et al. 2009), and in Patagonia (Johnson and Franklin 1994, Monteverde and Piudo 2011), where culpeos exhibited a relatively even activity level throughout the day. In our study area, the culpeo was exclusively nocturnal, which would be associated primarily with the activity level of their prey (Corley et al. 1995).

The temporal pattern observed in the Darwin's fox supports its behavior reported for Nahuelbuta National Park, where it was described as being mainly nocturnal (Jiménez 2000). However, it diverges somewhat from the population on Chiloé Island where it was somewhat more diurnal (Jiménez 2007). This may have occurred because unlike in Caramávida it is the largest carnivore in Chiloé, and there were no potential interactions with larger, sympatric carnivores.

The mainly nocturnal activity of the hog-nosed skunk in Caramávida is similar to that reported for Argentinian Patagonia (Donadio et al. 2001). In contrast to other species of the local assemblage, the hog-nosed skunk feeds mainly on invertebrates (Kasper et al. 2009), whose activity pattern differ from small mammals (Erikstad et al. 1989, Kočárek 2002). Therefore, the skunk segregates from the other carnivores as a result of their feeding behavior.

The activity pattern of the guigna differed from that observed in other localities in southern Chile, where it is mainly nocturnal (Hernández 2010, Delibes-Mateos et al. 2014). Yet, our results are partially consistent with observations from San Rafael National Park (Dunstone et al. 2002) and from Chiloé Island (Sanderson et al. 2002), where the guigna was partially diurnal. Perhaps in Caramávida, the preferences for diurnal prey or the presence of three other nocturnal, syntopic carnivores would affect the guigna's behavior. With respect to a cougar, this activity pattern could help to avoid encounters, due the fact that puma can kill smaller felids (Koehler and Hornocker 1991).

Spatial overlap between carnivores

Our data revealed relatively high spatial overlaps in some of the comparisons of the sympatric species, which demonstrates a lack of spatial avoidance behavior. We suggest that spatial segregation complements that of the activity patterns as a mechanism to avoid interference. Additionally, with the exception of the puma, members of the carnivore assemblage in Caramávida had similar body sizes (Table 2), but still, different feeding habits and diet

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may allow ecological differentiation (Zapata et al. 2007, Moreira-Arce et al. 2016), resulting in a lower likelihood of interference interactions. Alternatively, resources may be abundant for species to exploit at the shared sites. Thus, they may converge in their use, rendering few strong interactions among species (Paquet 1992). Likewise, because the study area is relatively undisturbed, it may allow for greater niche breadth and overlap among syntopic carnivores. However, we lack the data to test this hypothesis.

There are at least two caveats in our analyses. One is that the data were lumped over several months; therefore, the interactions were assumed to be static over time and may have changed along time, where seasonality would be a key factor in the distribution and abundance of prey available (Koehler and Hornocker 1991), affecting the dynamics of interaction among carnivores. The other is that the Bonferroni correction may be overly conservative (Rice 1989), and thus, no significant pattern was detected, although there were differences in the data distribution that may have had biological significance.

As prey size varies, a low dietary overlap may exist between the puma and other sympatric carnivores (Rau and Jiménez 2002, Garneau et al. 2007); therefore, if this is the case, the puma appears to trophically overlap little with the other carnivores (Kortello et al. 2007). Only the culpeo may depredate similar-sized prey as the puma (Rau and Jiménez 2002, Novaro et al. 2009); therefore, we would expect a higher likelihood of interactions and thus, higher niche segregation between these species. Indeed, pumas killed culpeos in sympatric habitats (Novaro 2005). Also, despite the taxonomic similarity of the puma and the guigna, the size difference between the puma and guigna's prey (Dunstone et al. 2002), would result in a low probability of interference.

The absence of statistical significance in the relationship between puma and culpeo suggests a lack of avoidance by this canid, however, this pattern must to be seen with caution, due to the differences in size (Iriarte and Jaksic 2012), as well as its eventual trophic overlap (Pia 2013). However, the inverse spatial correlation between the culpeo and the other small carnivores suggests the existence of segregation and niche partitioning. However, this could be partially driven by the top-down effect that the puma would exert on the culpeo, as similarly reported in other complex carnivore communities in Brazil (De Oliveira and Pereira 2014). Our spatial data of culpeo and Darwin's fox suggests a certain avoidance behavior likely by the latter species, which is smaller. In this case, given the large body and prey size differences, a predator-prey relationship is more likely to occur between these species (see Jaksic et al. 1980, Jiménez et al. 1990). In this sense, the significance obtained in the relationship with Darwin's fox ($p = 0.089$) could be less important than the biological relevance. In the Northern hemisphere, the coyote (*Canis latrans*) exert an important degree of interference in smaller carnivores, affecting their spatial ecology (Wooding 1984), and a pattern that is applicable in the study area. In fact, Darwin's foxes in Chiloé, in the absence of larger, sympatric carnivores expanded their spatiotemporal niches (Jiménez 2007). This is an important consideration for demographic management of this critically endangered canid (Jiménez 2000).

Aside from having different prey preferences, the skunks have a specialized defensive mechanism of spraying irritable secretions and have aposematic coloration (Hunter 2009), which could deter predators. Given this, the skunks would not develop an avoidance behavior towards the other members of the assemblage. This fact is consistent with the high and positive correlations of recordings among skunk and smaller carnivores, which suggests a lack of interference expectable according to size similarities. For the interaction between the culpeo and guigna, it is important to note that the latter is also partially arboreal, and so differs from the strictly terrestrial culpeo (Sanderson et al. 2002).

In the forests of Caramávida, it is possible to observe a spatio-temporal dynamic of interactions among sympatric carnivores that appear to segregate along different niche axes: carnivores vary in body size, differ in feeding habits, but have similar patterns of habitat use and activity periods. In spatial terms, we could distinguish a small group composed of the puma and culpeo and another group of culpeo and the three other smaller carnivores. In the first group, potential direct encounters appeared to be avoided by the smaller culpeo, as its activity was mainly nocturnal. In the second group, the species were mainly nocturnal and smaller in size. Here, coexistence seems possible by the insectivorous behavior of the hog-nosed skunk, and the carnivorous diet and the three-dimensional use of the forest by the guigna. Being a diet-generalist would allow the Darwin's fox to not compete with the skunk and the guigna, and it could escape predation and interference from the puma via temporal avoidance and culpeo via spatial avoidance.

Due to its association with humans, it is likely that the influence of domestic dogs in the carnivores of the study area would be less important because of the low numbers of recorded individuals (two independent records). Dogs were always found associated close to people on horseback. However, due to the strong interference effect that these dogs can impose on wild canids (Silva-Rodríguez et al. 2010), added to the proximity of human settlements

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to the study area (<14 km), their impacts may be important. For this reason, and to maintain the native carnivore assemblage, periodical monitoring of domestic dogs in Caramávida is needed.

Noteworthy, the chilla fox (*Pseudalopex griseus*) was absent from the studied carnivore assemblage in Caramávida. This occurred despite its generalist habitat use behavior and their wide distribution in forested areas at this latitude (Murúa 1996), and even when it is relatively common in nearby Nahuelbuta National Park (Jiménez 2000). This may be explained by agonistic interactions with the culpeo fox. Negative interactions between these two foxes that have been reported in different latitudes (Jiménez 1993, Johnson and Franklin 1994), and in Caramávida may have resulted in the exclusion of chilla from the assemblage.

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