

Temporal changes in the diet of two sympatric carnivorous mammals in a protected area of south-central Chile affected by a mixed-severity forest fire

A. H. Zúñiga, J. R. Rau, V. Fuenzalida,
A. Fuentes-Ramírez

Zúñiga, A. H., Rau, J. R., Fuenzalida, V., Fuentes-Ramírez, A., 2020. Temporal changes in the diet of two sympatric carnivorous mammals in a protected area of south-central Chile affected by a mixed-severity forest fire. *Animal Biodiversity and Conservation*, 43.2: 177–186, Doi: <https://doi.org/10.32800/abc.2020.43.0177>

Abstract

Temporal changes in the diet of two sympatric carnivorous mammals in a protected area of south-central Chile affected by a mixed-severity forest fire. Fire is a significant disruptive agent in various ecosystems around the world. It can affect the availability of resources in a given area, modulating the interaction between competing species. We studied the diet of the culpeo fox (*Lycalopex culpaeus*) and cougar (*Puma concolor*) for two consecutive years in a protected area of southern-central Chile which was affected by a wildfire. Significant differences were observed in the dietary pattern between the two species, showing their trophic segregation. In the two years of the study, the predominant prey for cougar was an exotic species, the European hare (*Lepus europaeus*), implying a simplification of its trophic spectrum with respect to that reported in other latitudes. The ecological consequences related to this scenario are discussed.

Key words: Dietary overlap, Predation, Post-fire dynamics, Microhabitat, Rodent cycles, Selectivity

Resumen

Cambios temporales en la dieta de dos mamíferos carnívoros simpátridas en una zona protegida del centro y el sur de Chile afectada por un incendio forestal de intensidad desigual. El fuego es un importante agente perturbador en varios ecosistemas de todo el mundo que puede afectar a la disponibilidad de recursos en una zona determinada, regulando la interacción entre especies competidoras. Estudiamos la dieta del zorro culpeo (*Lycalopex culpaeus*) y el puma (*Puma concolor*) por dos años consecutivos en un zona protegida del centro y el sur de Chile que se vio afectada por un incendio forestal. Se observaron diferencias significativas en el régimen alimentario de ambas especies, lo que pone de manifiesto su segregación trófica. En los dos años del estudio, la presa predominante del puma fue una especie exótica: la liebre europea (*Lepus europaeus*), lo que sugiere una simplificación de su espectro trófico respecto a lo reportado en otras latitudes. Se analizan las consecuencias ecológicas de este hecho.

Palabras clave: Superposición alimentaria, Depredación, Dinámicas posteriores a un incendio, Microhábitat, Ciclos de roedores, Selectividad

Received: 28 XI 19; Conditional acceptance: 04 II 20; Final acceptance: 26 III 20

Alfredo H. Zúñiga, Jaime R. Rau, Laboratorio de Ecología, Departamento de Ciencias Biológicas and Biodiversidad, Universidad de Los Lagos, Osorno, Chile.– Alfredo H. Zúñiga, Programa de Doctorado en ciencias mención conservación y manejo de Recursos Naturales, Universidad de Los Lagos, Puerto Montt, Chile.– Víctor Fuenzalida, Consultora Ambientes del Sur, Temuco, Chile.– Andrés Fuentes-Ramírez, Laboratorio de Biometría, Departamento de Ciencias Forestales, Universidad de La Frontera, Temuco, Chile and Instituto de Ecología y Biodiversidad, Santiago, Chile.

Corresponding author: Alfredo H. Zúñiga. E-mail: zundusicyon@gmail.com

ORCID ID: A. H. Zúñiga: 0000-0002-0504-7540; J. R. Rau: 0000-0003-0444-578X;
V. Fuenzalida: 0000-0003-3044-9610; A. Fuentes-Ramírez: 0000-0003-1258-7462



Introduction

Physical disturbances caused by fire are one of the main modifying agents in natural ecosystems. Largely due to the combustion of plant mass (Bond and Keeley, 2005), such disturbances can alter microhabitats, with constraints for the wild fauna (Pickett and White, 1985). The changes that forest fires cause in regard to the availability of resources can alter the dynamics of species' interactions by dividing the use of resources (Schoener, 1974). In such severe disturbances, species must find alternative mechanisms of co-use of the resources to make their coexistence possible in this new ecological context (Wiens, 1977).

Carnivores are a group of special relevance in the structuring of ecosystems due to the regulatory role they exert over the species at lower positions of the food web (Hairston et al., 1960). However, fires can cause significant changes in prey availability interactions, affecting the local species composition (Bouchert et al., 2014). Studies in the Northern Hemisphere (i.e., North America) concerning the response of predators to their prey in a context of disturbances caused by fire have found significant changes in predators' response in terms of the availability of prey (Bouchert, 2013; Cunningham et al., 2006). In contrast, in the Southern Hemisphere, and particularly in South America, the effect of forest fires on the diet of syntopic predators is largely unknown. This is of special importance for their conservation considering the low adaptability of the vegetation in this biogeographical area to high-severity fires (Montenegro et al., 2004). Consequent changes to the composition of local fauna (Johnston and Odum, 1956) as an outcome of the recovering process in the burned areas are probable.

The remaining native forest in southern Chile is characterized by its insularity compared to the rest of the Neotropic region, which is reflected in a high degree of endemism (Murúa, 1996). Among the predators present in the native forests of southern Chile, the most extended species are cougar (*Puma concolor* Linnaeus 1781) and culpeo fox (*Lycalopex culpaeus* Molina 1782) (Iriarte and Jaksic, 2012). The cougar is a big cat, with a wide distribution in the Neotropic region. It hunts a wide variety of prey, with sizes that vary between 1 and 60 kg (Iriarte et al., 1990; Iriarte and Jaksic, 2012). In some cases, the cougar preys on species linked to human settlement, like cattle and poultry, causing socio-ecological conflicts (Polisar et al., 2003). In the mountainous area of southern Chile, the cougar presents a context-dependent mixed pattern, in which it feeds on native fauna, as well as exotic and domestic animals, such as lagomorphs and cattle (Rau and Jiménez, 2002). On the other hand, the culpeo fox (*Lycalopex culpaeus*) is a medium-sized canid with a reported preference for small mammals (Zúñiga and Fuenzalida, 2016), but it could prey on larger herbivores (Novaro et al., 2009), possibly competing with the cougar for some prey. This could be particularly true in central-southern Chile, since according to national records the cougar is smaller here (Vidal, 2015), whereas the culpeo fox is larger at these higher latitudes in Chile (Fuentes and

Jaksic, 1979). Intense competitive dynamics can be expected where the differentiation of predator size is reduced (Gittleman, 1985). Additionally, forest fires not only affect the consumption of prey of both syntopic predators but also their dietary overlap (Pia, 2013). This can present relevant ecological consequences, as noted in reports of cougar attacks on canids of similar size to the culpeo fox, i.e., intraguild predation (Mazzolli, 2009), which would affect their persistence over time on a local scale.

The aim of this study was to determine the diet of two syntopic predators, the culpeo fox and the cougar, in a protected area of central-southern Chile that was affected by a high-severity forest fire (Fuentes-Ramírez et al., 2018). Knowledge of the predation patterns of these species will help to determine their responsiveness in the event of a fire, helping to improve the design and implementation of recovery actions for this ecosystem.

Materials and methods

Study area and description of the forest fire

The present study was conducted at the China Muerta National Reserve, in the foothills zone of the Region of La Araucanía, in central-southern Chile (38° 42' 00" S–71° 26' 00" W). The Reserve encompasses 1,1170 ha (CONAF, 2014), with an irregular and rugged topography and an altitude that ranges from 800 to 1,850 m a.s.l. The climate fluctuates between temperate to warm throughout the year, with fewer than 4 months of drought (in the summer season from December to March), and with ice and snow due to the effect of the altitude in winter and spring (Köppen, 1948). The mean temperature is 19°C in summer and 5°C in winter. The mean precipitation is 2,500 mm. The study area belongs to the Andean-Patagonian deciduous forest included in the mountain range sub-region of La Araucanía (Gajardo, 1995). The native trees of most note are *Araucaria araucana*, *Nothofagus pumilio* and *N. dombeyi*. In the bush stratum, *Chusquea culeou*, *Maytenus disticha* and *Gaultheria poeppigii* are of note (Luebert and Pliscoff, 2006).

The forest fire that affected the China Muerta National Reserve began on March 14, 2015 and was brought under control 23 days later, on April 6. The total surface affected by the fire, obtained through flyovers made during the monitoring operations and with field exams, was 3,765 ha, which excludes lands at high peaks with no vegetation and rocky terrains (CONAF, 2015). The levels of severity obtained were based on qualitative features, which varied between superficial damage of shrubs and canopy of trees, to carbonization of trees and disappearance of herbaceous and shrubby vegetation (CONAF, 2015).

Feces collection and dietary analyses

From December to May of 2017 and 2018 (summer-autumn in the Southern Hemisphere; second and third year post-fire, called hereafter the first and

second year), feces were collected from the culpeo fox and cougar along the route of the study area on the authorized trails. These trails included sites with no burning and sites affected by the fire. The sampling effort included an approximate surface of 1,000 ha, including burned and unburned sites. The feces of the species were recognized according to morphological criteria (Chame, 2003; Muñoz–Pedreros, 2010) and photographic records in the study area (Kays and Slauson, 2008). Later, feces were labeled and kept in paper bags for their analysis in the laboratory. There are no recordings of other carnivores in the area.

In the laboratory, the samples were dried at 60 °C and then separated manually to obtain the remains of the prey. The prey was identified by recognition of its cranial and dental morphological patterns in the case of rodents (Reise, 1973; Pearson, 1995), and of cuticular patterns of hairs and feathers for mammals and birds in general (Day, 1966). Reference collections were used for the rest of the taxa.

To quantify the diet of the culpeo fox and cougar, we determined the relative frequency (RF) of the prey items based on the total observed (Rau, 2000). To estimate the dietary breadth of each predator, we used a trophic diversity index (β ; Levins, 1968); establishes the use of the resources based on the total items observed. The standard deviation of this index was calculated using the jackknife method (Jaksic and Medel, 1987). To determine the interannual effect on diet, the standardized niche breadth index was used (Colwell and Futuyma, 1971) to compare the two years, due to differences in the availability of resources.

The trophic niche overlap was evaluated using Pianka's (1973) index, which considers the food items shared by the two species. Hutchenson's (1970) procedure was used to evaluate the diversity of the two predators, while pairwise comparisons were applied to assess the differences between species and the sampling periods. In order to evaluate the effect of the prey biomass on the dietary pattern of the two carnivores, we used the trophic isocline method (Kruuk and De Kock, 1980), using the total number of prey recorded in both years. This procedure is justified because it provides a more general picture of the importance of the prey biomass consumed by both predators. The estimation of prey biomass was based on the weight measurements reported by Amaya et al. (1979), Muñoz–Pedreros and Yáñez (2009) and Norambuena and Riquelme (2014). Due to their low contribution in terms of biomass, reptiles and arthropods were not included in this representation. We also calculated the geometrical mean of prey consumed for each species and study year (Jaksic and Braker, 1983).

Rodent selectivity by the culpeo fox

The frequency of rodent consumption by the culpeo fox was compared to the expected proportion of rodent species, which was obtained through live captures in Sherman traps (total sampling effort: 6,960 traps/night). These capture frequencies were seen as the availability of prey in the environment, and their respective comparisons were made by fit

testing (Sokal and Rohlf, 1995), which demonstrates the selectivity of this predator for a specific prey. We calculated Bonferroni confidence intervals when the comparison between the observed and expected frequencies was significant (Byers et al., 1984). This analysis was done using the HABUSE 4.0 program, which made it possible to determine this predator's type of selectivity (i.e., refusal, neutral, or positive). The capture frequencies considered were obtained in the autumn months of each of the two sampling years, which is when the largest number of records of rodents and carnivores were obtained.

Results

A total of 52 feces were collected, 36 of which corresponded to culpeo fox (22 in 2017 and 14 in 2018) and 16 to cougar (10 in 2017 and six in 2018; table 1). In the case of the culpeo fox, 23 feces (19 in 2017 and four in 2018) were found at unburned sites, and 13 (four in 2017 and nine in 2018) at burned sites. Of these, eight (five in 2017 and three in 2018) were in low severity and four were in high severity fire sites. In the case of the cougar, six feces (four in 2017 and two in 2018) were at unburned sites, and 10 (six in 2017 and four in 2018) were at burned sites. Of these, three (two in 2017 and one in 2018) were at sites of medium fire severity, whereas seven (four in 2017 and three in 2018) were observed at high-severity sites.

A total of eight trophic items were identified through feces, with five for culpeo fox and four for cougar, of which only one was shared by both species. The European hare, *Lepus europaeus*, was the only lagomorph seen and recorded by camera traps. From the relative consumption frequencies it can be seen that for the culpeo fox most of its dietary breadth in the first year consisted of rodents, followed by birds (order Passeriformes) (fig. 1). However, in the second year this pattern changed, with arthropods being the item of greatest frequency of consumption, reducing the proportion of rodents captured to almost half that of the previous year. Diversity of prey consumed showed significant differences between the years 1 and 2 (table 2). In the case of the cougar, lagomorph hares represented the core of its diet (fig. 1), with a proportion of consumption that increased in the second year. It is important to emphasize that in the second year the richness of prey decreased noticeably, with two types of prey consumed. Birds of the Order Anseriformes (*Chloephaga* sp.) had a similar representation in both years. No statistical differences in the diversity of prey were detected when both years were compared (table 2).

Regarding the dietary overlap between the two species, Pianka's index was $b = 0.069$ for the first sampling year and $b = 0.054$ for the second year. This low overlap was reinforced when the dietary breadth of the two species was compared between the sampling years and showed to be significantly different (table 2).

Regarding the effect of biomass on the consumption frequency of the two predators, in the

Table 1. Dietary composition, dietary breadth and overlap for *Lycalopex culpaeus* and *Puma concolor* in the China Muerta National Reserve, sampling years 1 and 2 (2 and 3 post-fire).

Tabla 1. Composición, amplitud y superposición de la dieta de *Lycalopex culpaeus* y *Puma concolor* en la Reserva Nacional China Muerta, en los años de muestreo 1 y 2 (2 y 3 después del incendio).

	Culpeo fox		Cougar	
	First year	Second year	First year	Second year
Mammals				
Rodents, Cricetidae				
<i>Abrothrix longipilis</i>	10 (23.25)	7 (12.72)	–	–
<i>Abrothrix olivaceus</i>	7 (16.27)	1 (1.81)	–	–
<i>Irenomys tarsalis</i>	3 (6.97)	1 (1.81)	–	–
<i>Oligoryzomys longicaudatus</i>	7 (16.27)	10 (18.18)	–	–
Rodents, Echymidae				
<i>Myocastor coypus</i>	–	–	1 (6.67)	–
Rodents, Lagomorpha				
<i>Lepus europaeus</i>	3 (6.97)	3 (5.45)	9 (60)	8 (66.67)
Artiodactyla				
<i>Sus scrofa</i>	–	–	1 (6.67)	–
Birds				
Indeterminate Passeriformes	6 (13.95)	8 (14.54)	–	–
Indeterminate Anseriformes	–	–	4 (26.66)	4 (33.33)
Reptiles				
<i>Liolaemus</i> sp.	3 (6.93)	–	–	–
Arthropods				
Indeterminate arthropods	4 (9.30)	5 (45.45)	–	–
Number of feces	22	16	10	6
Dietary breadth (β)	6.67 + 0.58	3.56 + 3.82	2.27 + 4.52	1.12 + 0.64
Standardized niche (Bsta)	0.70	0.36	0.31	0.06

case of the cougar the consumption of hares this was over the isocline of 50 % (fig. 2), whereas the recently introduced wild boar *Sus scrofa* (Skewes et al., 2012) and birds were positioned in the intermediate isoclines (between 5 and 20 %), with the representation of the aquatic rodent coypu, *Myocastor coypus*, below 1%. In contrast, the culpeo fox maintained the consumption of hares above the isocline of 20 %, the cricetid *Abrothrix longipilis* between 1 and 5 %, and the rest of the species was under the isocline of 1%. The geometrical mean of the weight of the culpeo fox's prey was 40.71 and 10.38 g for the first and second year respectively, and for the cougar it was 7,079.95 g and 5,361.64 g for the same periods.

A comparison of the frequencies of rodent trapping and rodent consumption by the culpeo fox revealed

differences in abundance terms between sampling year. In the first year, a non-significant relation was obtained between consumption and trapping frequencies of the three rodent species ($\chi^2 = 3.121$, $p = 0.20$), suggesting that prey consumption occurred at random according to prey availability (table 3). However, in the second year this trend changed significantly ($\chi^2 = 173.274$, $p < 0.0001$), resulting in a lower consumption than expected for *Abrothrix olivaceus*, but a higher consumption than expected for *Oligoryzomys longicaudatus*, a reservoir native rodent species and transmitter of the Hanta virus in Chile (Murúa, 1999). It should be noted that in the case of *Irenomys tarsalis*, this species of tree rodent was not detected in the Sherman traps, although it was in the feces, so it was not included in the analysis.

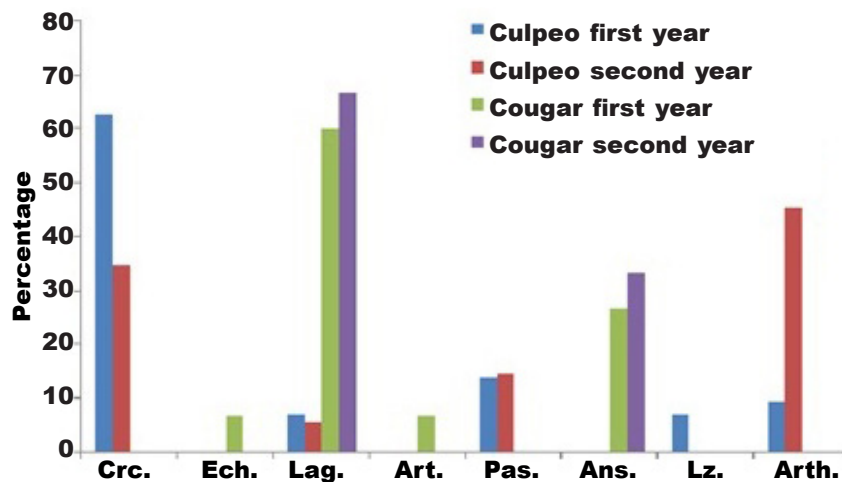


Fig. 1. Percentage representation of the dietary items consumed by the culpeo fox and cougar in the study area for the two consecutive sampling years (2017–2018): Crc., Cricetidae; Ech., Echimyidae; Lag., Lagomorpha; Art., Artiodactyla; Pas., Paseriformes; Ans., Anseriformes; Lz., Lizards; Arth., Arthropods.

Fig. 1. Porcentaje de la representación de los alimentos consumidos por el zorro culpeo y el puma en la zona de estudio durante los dos años de muestreo consecutivos (2017 y 2018): Crc., cricétidos; Ech., equimíidos; Lag., lagomorfos; Art., artiodáctilos; Pas., paseriformes; Ans., anseriformes; Lz., lacertilios; Arth., artrópodos.

Discussion

Reports from the same biogeographical area show differences in the dietary range of the culpeo fox and the cougar the (Rau and Jiménez, 2002; Zúñiga and Fuenzalida, 2016), revealing a simplification in the local food supply. These differences could be attributed in the first term to the structural change in the prey assemblage in the study area due to the fire, which would reduce abundance and the incorporation of exotic species. The great capacity of canivores to move large generally exceeds the capture areas of their prey (Carbone and Gittleman, 2002), and it is therefore not possible to infer the place of capture of the prey through the feces detection site. However, both species would present differences in the use of space, a situation that has been detected in the coastal mountain range (Zúñiga et al., 2017 allowing them to use the mosaic produced by fire in a differentiated way.

Disturbances by fire in native forest are regarded to promote the occurrence of exotic species, where the lagomorphs in particular benefit from the particularities of the microhabitats produced by the fire (Sokos et al., 2016), a situation that has been maintained systematically through different types of disturbances in the Chilean territory (Jaksic et al., 2002). The presence of lagomorphs in the study area would stimulate changes in the predators' feeding habits (Rubio et al., 2013), affecting the predation on native prey (Novaro et al., 2000), and therefore on the control the carnivores exert over this group. However, the effect of the fire on the hares could show variations in abundance over time (Sokos et al., 2016), which would vary the predation rate exerted on this group.

In the case of the cougar, the relative absence of medium to large native species in the study area has been compensated for by the consumption of hares, the largest species in the study area, with the exception of the introduced wild boar and sporadic groups of cattle wandering on the Reserve. Despite this, there are no records of cattle consumption by cougar. Consumption of coypu (*Myocastor coypus*),

Table 2. Comparison of the dietary diversity of the cougar and culpeo fox throughout the two sampling years.

Tabla 2. Comparación de la diversidad de la dieta del puma y el zorro culpeo durante los dos años de muestreo.

Comparisons	T-value	p-value
Culpeo fox first year vs. second year	2.63	0.0090
Cougar first year vs. second year	1.40	0.1849
Cougar vs. culpeo fox first year	9.58	< 0.0001
Cougar vs. culpeo fox second year	7.70	< 0.0001

Table 3. Consumption frequency of the culpeo fox *Lycalopex culpaeus* in relation to observations from Sherman traps, with the signs in the brackets (–), (+) or (=) establishes the type of selection by the corresponding prey (chance, positive or negative), according to Bonferroni intervals.

Tabla 3. Frecuencia de consumo del zorro culpeo, *Lycalopex culpaeus*, en relación con las observaciones de las trampas Sherman; los signos entre paréntesis (–), (+) e (=) establecen el tipo de selección para la presa correspondiente (neutra, positiva o negativa), de acuerdo con los intervalos de Bonferroni.

Cricetid species	Consumption frequency (observed/expected)	Bonferroni's confidence intervals
First year		
<i>Abrothrix longipilis</i>	(0.370/0.530)	(0.138–0.602) (=)
<i>Abrothrix olivaceus</i>	(0.259/0.269)	(0.049–0.470) (=)
<i>Oligoryzomys longicaudatus</i>	(0.259/0.158)	(0.049–0.470) (=)
<i>Irenomys tarsalis</i>	(0.111/0.040)	(0.000–0.272) (=)
Second year		
<i>Abrothrix longipilis</i>	(0.388/0.454)	(0.114–0.664) (=)
<i>Abrothrix olivaceus</i>	(0.055/0.515)	(0.000–0.185) (–)
<i>Oligoryzomys longicaudatus</i>	(0.555/0.030)	(0.275–0.836) (+)

which despite its size (10 kg; Muñoz–Pedreros and Gil, 2009) presents a lower occurrence, similar to that observed in the Central Valley (Zúñiga and Muñoz–Pedreros, 2014), showing casual consumption events. In the case of the birds of the Anatidae family, their systematic consumption in both study years suggests the importance of this prey in the study area. This observation is evidenced in trophic isoclines, where its frequency of consumption stands out. Also, its intermediate size (ca. 3 kg) could be a significant complement to the cougar's energy requirements. Reports of consumption of this type of birds have been found in areas with presence of wetlands (Rau and Jiménez, 2002). It is therefore of interest to determine whether in the study area the cougar would positively select these habitats, given its feeding behaviour. On the other hand, the record of wild boar captured by this feline, the other exotic species observed as prey in the study area, has only recently been recorded from reports of predation by cougars (Skewes et al., 2012), suggesting that its consumption at present would be of very low frequency. This is supported by observations in the study area that reveal that wild boars are concentrated in areas of lower altitude, presenting only occasional migrations of isolated individuals to areas of higher altitude (Gastón León, pers. comm.).

The dietary records obtained for the culpeo fox agree partially with observations made for this canid in this biogeographical area (Zúñiga and Fuenzalida, 2016), where rodents were the main trophic category of this species, which establishes a large differentiation with the cougar. The differences of capture between species would be explained by their use of the space,

which determines the likelihood of their capture (Simonetti, 1989; Vásquez, 1996). Thus, the greater representation of consumption by the two species of the genus *Abrothrix* seems to follow the generalist nature of both rodents in terms of microhabitat use, having been found at sites with low vegetation cover (Glantz, 1984), and to a lesser extent on *O. longicaudatus*, a scansorial species, since their preferential spatial habits are arboreal (Murúa et al., 1986). In the case of the tree mouse *Irenomys tarsalis*, its low consumption frequency could be a result of the smaller abundance due to the loss of trees and canopy as a result of the fire, which constitute its main microhabitat, given their predominantly arboreal habits (Kelt, 1993; Rau et al., 1995). Consequently, this rodent is one of the culpeo fox's trophic items most affected by the fire. The consumption of lagomorphs by the culpeo fox is less than reported in other locations (Rubio et al., 2013; Zúñiga and Fuenzalida, 2016), which assumes an effect of interference by the cougar, spatially restricting the culpeo fox (Zúñiga et al., 2017).

The dietary range of both species showed a divergence pattern based on the size of the captured prey. This trend is reinforced through the geometrical mean estimated for each predator. The trophic isoclines demonstrate that the cougar and the culpeo fox have a markedly different diet habit and the importance of their prey in a biomass/consumption frequency ratio. Thus, for the cougar, the hare was found above the 50% isocline, which reveals the relevance of this item compared to larger prey, but of lower frequency in the scats, and therefore a lower capture rate. In contrast, for the culpeo fox, the hare was between the 20% and 50% isocline, which implied an intermediate impor-

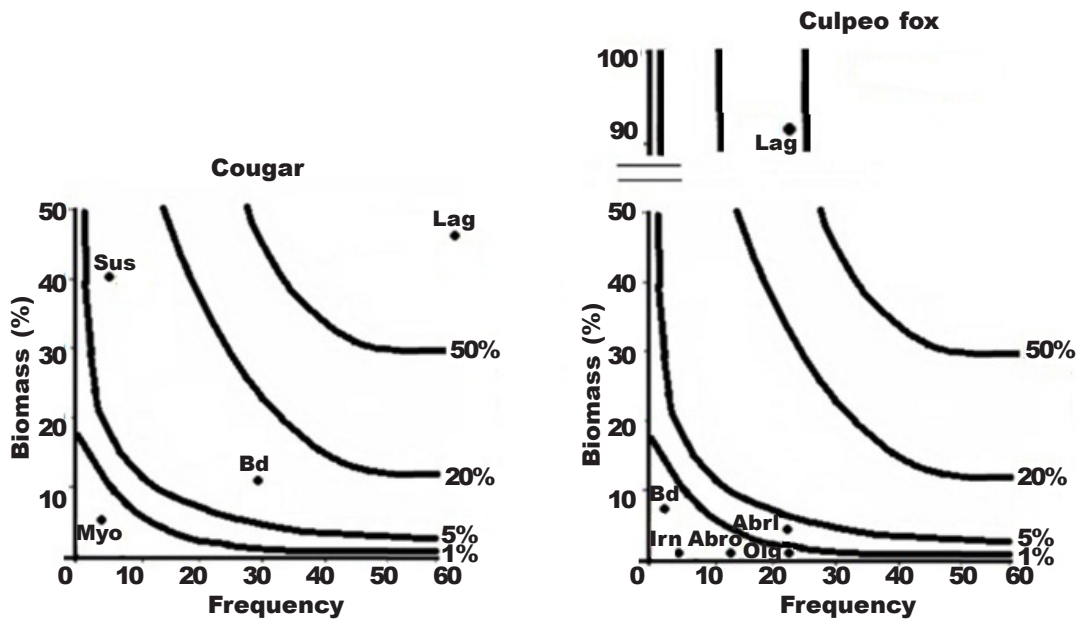


Fig. 2. Trophic isoclines for the cougar and the culpeo fox in the study area. The horizontal lines on the Y axis of the graph for culpeo fox indicate shortening for practical effects. Abri, *Abrothrix longipilis*; Abro, *Abrothrix olivaceus*; Bd, birds; Irn, *Irenomys tarsalis*; Lag, lagomorphs; Myo, *Myocastor coypus*; Olg, *Oligoryzomys longicaudatus*; Sus, *Sus scrofa*.

Fig. 2. Isoclinas tróficas del puma y el zorro culpeo en la zona de estudio. Las líneas horizontales del eje de las Y del gráfico correspondiente al zorro culpeo indican un acortamiento a efectos prácticos. Abri, *Abrothrix longipilis*; Abro, *Abrothrix olivaceus*; Bd, aves; Irn, *Irenomys tarsalis*; Lag, lagomorfos; Myo, *Myocastor coypus*; Olg, *Oligoryzomys longicaudatus*; Sus, *Sus scrofa*.

tance, due to its lower capture frequency, if compared to rodents as a whole. This group, despite its low position in the isoclines, together would place them above the 5% isocline, increasing their importance.

Interannual variation of the carnivores' diet

The interannual differences among carnivores are for each one of the two species studied due to changes in the availability of their prey. In the second year (2018), the steep drop in the Cricetidae rodent populations resulted in a lower capture frequency, which was a consistent decrease in the records of culpeo fox compared to the previous year. This suggests both a modification in the dietary range and a displacement of this canid. The sharp decrease in rodents is associated with interannual fluctuation processes in the availability of resources, as has been reported for rodents in the Northern Hemisphere (Hansson and Henttonen, 1988). Consequently, a reconfiguration of the culpeo fox's dietary pattern was observed, which is demonstrated in particular by the disproportionate appearance of arthropods in the dietary range compared to the previous year, greater even than that reported for the same biogeographical area (Zúñiga and Fuenzalida, 2016). The absence of reptile con-

sumption compared to the previous year could be the result of a disincentive of its search due to its low energy reward, which would force this canid to prioritize the search for larger prey, as well as a physiological constraint to favor this type of consumption (Silva et al., 2005). This pattern, added to the smaller number of fecal records compared to the previous year, supposes the migration of individuals to habitat patches with a greater supply of resources, a fact facilitated by the wide habitat area of this species (Salvatori et al., 1999). The absence of selectivity in the predation of Cricetidae rodents in the first year is explained by the great availability of this resource, which was observed by the capture success in live traps, which was around 20% (A. H. Zúñiga, unpublished data). In contrast, in the second sampling year, where there was a reduction in the number of captures compared to the previous year (1%), there was a change in the prey search pattern (as was the case for arthropods and to a lesser extent lagomorphs), with a lower representation of cricetid rodents.

In the case of the cougar, the absence of statistical significance observed when the diversity of prey was compared between the two years suggests a similar pattern in the use of resources during this period, partly by this felid being limited in the use of alternative

resources (Gelin et al., 2017). In a scenario of limited resources, however, the cougar could migrate to other places in search of prey of higher energy reward, which is part of a behavioral strategy in response to the seasonal decline of its prey (Pierce et al., 1999). This is supported by the large habitat area that the cougar can have (Grigione et al., 2002). Under this assumption, it is to be expected that the disturbance caused by fire was especially critical for the cougar due to the shortage of prey available and given its high energy requirements, which necessitate larger migrations in search of prey that complement their diet. This situation is in partial agreement with what was observed by Cunningham et al. (2006) in Mediterranean forests of the Northern Hemisphere, where the absence of fecal records of one of the predators made it possible to infer the limitation of the habitat in terms of dietary support.

One aspect to consider is the low sample size of the feces analyzed for both species, which were determined largely by the migratory action of the individuals in the study area as a result of the low supply of prey, mainly in the second year. This made its recordings in the study area difficult, suggesting caution when interpreting the results presented here.

In conclusion, culpeo fox and cougar showed trophic differentiation with regard to the diversity of their prey, as a consequence of their body size differences. Constraints of available resources as a consequence of an interannual variation would lead both species to modify their dietary pattern towards prey with lower energy reward. Long-term studies in the study area could explain the variations in dietary response based on the evolution of the ecosystem.

Acknowledgements

This research was partially funded by Fondo Nacional de Desarrollo Científico y Tecnológico FONDECYT 11150487 and CONICYT-PIA Basal FB 002-2014. We thank the Dirección de Investigación, Universidad de La Frontera, for their support and Fabián Jaksic for his valuable comments and suggestions that greatly improved the manuscript. Thanks too to Gastón and Jorge León, park rangers at the National Reserve China Muerta, for their contribution to fieldwork and information about the study area.

References

- Amaya, J. N. G., Alsina, M. G., Brandani, A. A., 1979. *Ecología de la liebre europea (Lepus europeus P.) II. Reproducción y peso corporal de una población del área de San Carlos de Bariloche*. Technical Report No. 9, Bariloche, Argentina.
- Bond, W. J., Keeley, J. E., 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends of Ecology and Evolution*, 20: 387–394.
- Bouchert, M. I., 2013. Mammalian carnivore use of a high-severity burn in conifer forests in the San Bernardino mountains of Southern California, USA. *Hystrix*, 23: 50–56.
- Bouchert, M. I., Farr, D. P., Rimbenieks-Negrete, M. A., Pawlowski, M. N., 2014. Responses of small mammals to wildfire in a Mixed Conifer Forest in the San Bernardino Mountains, California. *Bulletin of the South California Academy of Sciences*, 113: 81–95.
- Byers, C. R., Steinhorst, R. K., Krausman, P. R., 1984. Clarification of a technique of utilization-availability data. *Journal of Wildlife Management*, 48: 1050–1053.
- Carbone, C., Gittleman, J., 2002. A common rule for the scaling of carnivore density. *Science*, 295: 2273–2276.
- Chame, M., 2003. Terrestrial mammal feces: a morphometric summary and description. *Memorias do Instituto Oswaldo Cruz*, 98: 71–94.
- Colwell, R., Futuyma, J., 1971. On the measurement of the niche breadth and overlap. *Ecology*, 52: 567–572.
- CONAF, 2014. *Plan de manejo forestal Reserva Nacional China Muerta. Documento operativo*. Sistema Nacional de Áreas Silvestres protegidas del Estado. CONAF, Santiago de Chile.
- 2015. *Plan de restauración incendio Reserva Nacional China Muerta*. CONAF, Temuco.
- Cunningham, S. C., Kirkendall, L., Ballard, W., 2006. Gray fox and coyote abundance and diet responses after a wildfire in Central Arizona. *Western North American Naturalist*, 66: 169–180.
- Day, M. G., 1966. Identification of hair and feather remains in the gut and feces of stoats and weasels. *Journal of Zoology*, 18: 315–326.
- Fuentes, E., Jaksic, F., 1979. Latitudinal size variation of Chilean foxes: tests of alternative hypotheses. *Ecology*, 60: 43–47.
- Fuentes-Ramírez, A., Barrientos, M., Almonacid, L., Aarriagada-Escamilla, C., Salas-Eljatib, C., 2018. Short-term response of soil microorganisms, nutrients and plant recovery in fire-affected *Araucaria araucana* forests. *Applied Soil Ecology*, 131: 99–106.
- Gajardo, R., 1995. *La vegetación natural de Chile. Clasificación y distribución geográfica*. Editorial Universitaria, Santiago de Chile.
- Gelin, M. L., Branch, L. C., Thornton, D. H., Novaro, A. J., Gould, M. J., Caragiulo, A., 2017. Response of pumas (*Puma concolor*) to migration of their primary prey in Patagonia. *Plos One*, 12: e0188877, <https://doi.org/10.1371/journal.pone.0188877>
- Gittleman, J., 1985. Carnivore body size: ecological and taxonomical correlates. *Oecologia*, 67: 540–554.
- Glanz, W. E., 1984. Ecological relationships of two species of *Akodon* in Central Chile. *Journal of Mammalogy*, 65: 433–441.
- Grigione, M. M., Beier, P., Hopkins, R. A., Padley, W. D., Schonewald, C. M., Johnson, M. L., 2002. Ecological and allometric determinants of home-range size for mountain lions (*Puma concolor*). *Animal Conservation*, 5: 317–324.
- Hairton, N. G., Smith, F. E., Slobodkin, L. B., 1960. Community structure, population control, and competition. *American Naturalist*, 94: 421–425.

- Hansson, L., Henttonen, H., 1988. Rodent dynamics as community process. *Trends of Ecology and Evolution*, 3: 195–200.
- Hutchenson, K., 1970. A test for comparing diversities based on Shanon formula. *Journal of Theoretical Biology*, 29: 151–154.
- Iriarte, J. A., Franklin, W. L., Johnson, W. E., 1990. Biogeographic variation of food habits and body size of the American puma. *Oecologia*, 85: 185–190.
- Iriarte, A., Jaksic, F., 2012. *Los carnívoros de Chile*. Flora and Fauna/CASEB Ediciones, Santiago de Chile.
- Jaksic, F., Braker, E., 1983. Food–niche relationships and guild structure of birds of prey: competition vs. opportunism. *Canadian Journal of Zoology*, 61: 2230–2241.
- Jaksic, F., Iriarte, J. A., Jiménez, J. E., Martínez, D. R., 2002. Invaders without frontiers: Cross–border invasions of exotic mammals. *Biological Invasions*, 57: 157–173.
- Jaksic, F., Medel, R., 1987. El acuchillamiento de datos como método de obtención de intervalos de confianza y prueba de hipótesis para índices ecológicos. *Medio Ambiente*, 8: 95–103.
- Johnston, D. W., Odum, E. P., 1956. Breeding bird populations in relation to plant succession on the piedmont of Georgia. *Ecology*, 78: 50–62.
- Kays, R., Slauson, K. M., 2008. Remote cameras. In: *Non invasive survey methods for carnivores*: 110–140 (R. Long, P. Mackay, W. Zielinski, J. Ray, Eds.). Island Press, Washington.
- Kelt, D., 1993. *Irenomys tarsalis*. *Mammalian Species*, 447: 1–3.
- Köppen, W., 1948. *Climatología. Con un estudio de los climas de la tierra*. Fondo de Cultura Económica, México, D.F.
- Kruuk, H., De Kock, L., 1980. Food and habitat of badgers (*Meles meles* L.) of Monte Baldo, northern Italy. *Zietschrift fur Saugetierkunde*, 46: 295–301.
- Levins, R., 1968. *Evolution in changing environments*. Princeton University Press, New Jersey.
- Luebert, F., Plissock, P., 2006. *Sinopsis bioclimática y vegetacional de Chile*. Editorial Universitaria, Santiago de Chile.
- Mazzolli, M., 2009. Mountain lion *Puma concolor* attacks on a maned wolf *Chrysocyon brachyurus* and a domestic dog in a forestry system. *Mastozoología Neotropical*, 16: 465–470.
- Montenegro, G., Ginocchio, R., Segura, A., Keely, J. E., Gómez, M., 2004. Regímenes de incendios y respuestas de la vegetación en dos regiones de clima mediterráneo. *Revista Chilena de Historia Natural*, 77: 455–464.
- Muñoz–Pedreros, A., 2010. *Huellas y signos de mamíferos de Chile*. CEA Ediciones, Valdivia, Chile.
- Muñoz–Pedreros, A., Gil, C., 2009. Orden Rodentia. In: *Mamíferos de Chile*: 93–157 (A. Muñoz–Pedreros, J. Yáñez, Eds.). CEA Ediciones, Valdivia, Chile.
- Muñoz–Pedreros, A., Yáñez, J., 2009. *Mamíferos de Chile*. CEA Ediciones, Valdivia, Chile.
- Murúa, R., 1996. Comunidades de mamíferos del bosque nativo en Chile. In: *Ecología de los bosques templados del sur de Chile*: 113–133 (J. Armesto, C. Villagrán, M. K. Arroyo, Eds.). Editorial Universitaria, Santiago de Chile.
- 1999. Hantavirus en Chile: los mastozoólogos como un grupo ocupacional de riesgo epidemiológico. *Revista Chilena de Historia Natural*, 72: 7–12.
- Murúa, R., González, L. A., Meserve, P., 1986. Population ecology of *Oryzomys longicaudatus philippii* (Rodentia: Cricetidae) in Southern Chile. *Journal of Animal Ecology*, 55: 281–293.
- Norambuena, H., Riquelme, J., 2014. *Profesor Dr. Francisco Behn Kuhn (1910–1976) biografía y catálogo de su colección de aves chilenas*. CEA Ediciones, Valdivia, Chile.
- Novaro, A., Funes, M. C., Walker, R. S., 2000. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. *Biological Conservation*, 92: 25–33.
- Novaro, A., Moraga, C. A., Briceño, C., Funes, M. C., Marino, A., 2009. First records of culpeo (*Lycalopex culpaeus*) and cooperative defense by guanacos (*Lama guanicoe*). *Mammalia*, 73: 143–150.
- Pearson, O., 1995. Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanín National Park, southern Argentina. *Mastozoología Neotropical*, 2: 99–148.
- Pia, M. V., 2013. Trophic interactions between puma and endemic culpeo fox after livestock removal in the high mountains of central Argentina. *Mammalia*, 77: 273–283.
- Pianka, E., 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4: 53–74.
- Pickett, S. T. A., White, P. S., 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando.
- Pierce, B. M., Bleich, V. C., Vehausen, J., Bowyer, R. T., 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. *Journal of Mammalogy*, 80: 986–992.
- Polisar, J., Maxit, I., Scognamillo, D., Farrell, L., Sunquist, M. E., Eisenberg, J. F., 2003. Jaguars, pumas, their prey base, and cattle ranching: ecological interpretations of a management problem. *Biological Conservation*, 109: 297–310.
- Rau, J., 2000. Métodos de ecología trófica. In: *Mamíferos de Chile*: 397–406 (A. Muñoz–Pedreros, J. Yáñez, Eds.). CEA Ediciones, Valdivia, Chile.
- Rau, J., Jiménez J., 2002. Diet of puma (*Puma concolor*, Carnivora: Felidae) in coastal and Andean ranges of southern Chile. *Studies on Neotropical Fauna and Environment*, 37: 201–205.
- Rau, J., Martínez, D. R., Low, J. R., Tillería, M. S., 1995. Depredación por zorros chilla (*Pseudalopex griseus*) sobre micromamíferos cursoriales, escansoriales y arborícolas en un área silvestre protegida del sur de Chile. *Revista Chilena de Historia Natural*, 68: 333–340.
- Reise, D., 1973. Clave para la determinación de los cráneos de marsupiales y roedores chilenos. *Gayana*, 27: 1–20.
- Rubio, A., Alvarado, R., Bonacic, C., 2013. Introduced European rabbit as a main prey of the native carni-

- vore culpeo fox (*Lycalopex culpaeus*) in disturbed ecosystems of central Chile. *Studies on Neotropical Fauna and Environment*, 83: 89–94.
- Salvatori, V. G., Vaglio-Laurin, P., Meserve, P. L., Boitani, L., Campanella, A., 1999. Spatial organization, activity and social interactions of culpeo foxes (*Pseudalopex culpaeus*) in North–central Chile. *Journal of Mammalogy*, 31: 757–764.
- Schoener, T. W., 1974. Resource partitioning in ecological communities. *Science*, 185: 27–39.
- Silva, S. I., Jaksic, F. M., Bozinovic, F., 2005. Nutritional ecology and digestive response to dietary shift in the large South American fox, *Pseudalopex culpaeus*. *Revista Chilena de Historia Natural*, 78: 239–246.
- Simonetti, J., 1989. Microhabitat use by small mammals in Central Chile. *Oikos*, 56: 309–318.
- Skewes, O., Moraga, C., Arriagada, A., Rau, J. R., 2012. El jabalí europeo (*Sus scrofa*): un invasor biológico como presa reciente del puma (*Puma concolor*) en el sur de Chile. *Revista Chilena de Historia Natural*, 85: 227–232.
- Sokal, R. R., Rohlf, F. J., 1995. *Biometry*. W. H. Freeman and Company, New York.
- Sokos, C., Birstas, P., Papaspyropoulos, K. G., Tsachalidis, E., Giannakopoulos, A., Milis, C., Spyrou, V., Manolakou, K., Valiakos, G., Iakovakis, C., Athanasiou, L. V., Sfougaris, A., Billinis, C., 2016. Mammals and habitat disturbance: the case of brown hare and wildfire. *Current Zoology*, 62: 421–430.
- Vásquez, R. A., 1996. Patch utilization by three species of Chilean rodents differing in body size and mode of locomotion. *Ecology*, 77: 2343–2351.
- Vidal, F., 2015. *El puma en la Araucanía*. Ediciones Universidad Santo Tomás, Santiago de Chile.
- Wiens, J. A., 1977. On competition on variable environments. *American Scientist*, 65: 590–597.
- Zúñiga, A. H., Muñoz–Pedreros, A., 2014. Hábitos alimentarios de *Puma concolor* (Carnivora, Felidae) en bosques fragmentados del sur de Chile. *Mastozoología Neotropical*, 21: 157–161.
- Zúñiga, A. H., Fuenzalida, V., 2016. Dieta del zorro culpeo (*Lycalopex culpaeus* Molina 1782) en un área protegida del sur de Chile. *Mastozoología Neotropical*, 23: 201–205.
- Zúñiga, A. H., Jiménez, J. E., Ramírez De Arellano, P., 2017. Activity patterns in sympatric carnivores in the Nahuelbuta Mountain Range, southern–central Chile. *Mammalia*, 81: 445–453.