

Landscape use and food habits of the chilla fox (*Lycalopex griseus*, Gray) and domestic dog (*Canis lupus familiaris*) in a peri-urban environment of south-central Chile

Alfredo H. Zúñiga^{1,2}, Jaime R. Rau^{2*}, Rodolfo Sandoval³, Víctor Fuenzalida⁴

¹Department of Agricultural Sciences and Natural Resources, Universidad de La Frontera, Temuco, Chile

²Laboratory of Ecology, Department of Biological Sciences & Biodiversity, Universidad de Los Lagos, Campus Osorno, Casilla 933, Osorno, Chile

³Nahuelbuta Biodiversity Conservation Network, Contulmo, Chile

⁴Ambientes del Sur Consultants, Temuco, Chile

Abstract

ZÚÑIGA, A.H., RAU, J.R., SANDOVAL, R., FUENZALIDA, V., 2022. Landscape use and food habits of the chilla fox (*Lycalopex griseus*, Gray) and domestic dog (*Canis lupus familiaris*) in a peri-urban environment of south-central Chile. *Folia Oecologica*, 49 (2): 159–167.

Cities intensely modify natural environments and impose pressures on biodiversity. In this sense, carnivorous mammals are one of the groups most affected due to their food and space requirements. The feeding and spatial behavior of the chilla fox (*Lycalopex griseus*, G., 1837) and dogs were studied in the vicinity of a peri-urban protected area in south-central Chile. The diet of both canids was compared seasonally, for which feces were collected along trails in three habitats: native forest, exotic plantations and scrublands. Dog feces were collected at the same site to establish whether they were avoided by foxes. Chilla fox has been highlighted for consuming a high proportion of hares followed by rodents of the Muridae family, both being exotic mammals in Chile, whereas dogs showed a predominant consumption of anthropogenic food. Significant differences were observed for chilla fox in dietary diversity, mainly in summer and fall. No spatial segregation was observed with the domestic dog, which was evidenced in a high overlap in the use of all habitats. This scenario, together with continuous human presence, are elements that must be considered in the medium-term to evaluate the effects of anthropogenic pressures on native carnivores in the study area.

Keywords

biomass, canids, exotic prey, habitat, spatial overlap

Introduction

Carnivorous mammals are a group of relevance in ecosystem processes, which is evidenced mainly in the control of herbivorous species and the dispersal of plant species (HAIRSTON et al., 1960; ROSALINO et al., 2010). However, their populations are in continuous decline due to anthropogenic pressure on their natural habitats (LUCK 2007), which affects their spatial requirements (CROOKS, 2002). The process of habitat loss has intensified with urbanization in recent years (ZHAO et al., 2006), with negative consequences for local biodiversity. Furthermore, the association of urbanized environments are

associated with an increase of the probability of conflicts with local fauna (SCHELL et al., 2021), which limits their occurrence on their sites (SCHUETTE et al., 2013). In addition, the presence of domestic dogs (*Canis lupus familiaris*) around these settlements may restrict the spatial distribution of carnivores, due to their close association with humans (BOITANI et al., 2017). There are records that dogs exhibit generalist feeding habits in many ecosystems (BUTLER and DU TOIT, 2002; CAMPOS et al., 2007; KRAUZE-GRYZ and GRYZ, 2014), as well as the use of space (TORRES and PRADO, 2010; KRAUZE-GRYZ and GRYZ, 2014). In this way, dogs exert an interference effect on the home range on native fauna (VANAK and GOMPER,

*Corresponding author:
e-mail: jrau@ulagos.cl

©2022 Authors. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>)

2002; VANAK et al., 2014), affecting resource use according to their ecological requirements.

Although there is background information regarding the adaptation of carnivores to urban environments (GESE and BEKOFF, 2004), this process is restricted to species whose spatial flexibility allows their establishment and success (BATEMAN and FLEMING, 2012). This may be determined by the feasibility to subsidize carnivores with food of anthropogenic origin (FEDRIANI et al., 2001). However, this availability of resources could negatively affect their healthy conditions (MURRAY et al., 2015). Spatial dynamics of carnivores are associated to availability of local-scale resources (WALTON et al., 2017), which suggests an inverse association between home range of these species and the productivity of a locality. Thus, when there is low food availability, individuals are forced to make greater movements in search of food (ŠÁLEK et al., 2015). In parallel, seasonality plays an important role in carnivores' spatial dynamics, since it modulates the occurrence of their prey over time (BORROR et al., 1989; HANSSON and HENTONNEN, 1988). Therefore, in temperate forests, seasonal changes in prey consumption are to be expected in response to fluctuations in their availability. In this sense, peri-urban environments can be considered as habitats with low prey diversity (FERNÁNDEZ and SIMONETTI, 2013; KLIMANT et al., 2017), which limits the energetic requirements of carnivores (GITTLEMAN and HARVEY, 1982; CARBONE and GITTLEMAN, 2002). Thus, when considering this context, it is expected that seasonality will generate a change in carnivores in relation to the spectrum of prey consumed.

In south-central Chile, carnivores are partially asso-

ciated with the native forest (MURÚA, 1996), a habitat that has undergone a deep change in a significant proportion by forestry plantations and agroecosystems (ECHEVERRÍA et al., 2008). One of these species is the chilla fox (*Lycalopex griseus*), a canid widely distributed throughout Chile (DEL SOLAR and RAU, 2004). This fox, in addition to presenting great dietary flexibility (MARTÍNEZ et al., 1993; JAKSIC, 1997; ZÚÑIGA et al., 2008; MUÑOZ-PEDREROS et al., 2018), is found in many habitats throughout this country (IRIARTE and JAKSIC, 2012). This canid has also generalist habits in the use of space (GUERRERO et al., 2006; ZÚÑIGA et al., 2009). However, there is an information gap about the space use of this species in urbanized environments (SILVA-RODRÍGUEZ et al., 2020), as well as its seasonal variations.

The objective of this study is to compare the seasonal diet and use of space between chilla fox and domestic dogs in a peri-urban environment of south-central Chile. Through the collection of feces, the diet of this canid and its spatial distribution through the available habitats was assessed. This was compared with recordings of domestic dog, an exotic carnivore widely distributed in this site. The seasonal differentiation of its trophic diversity is tested, as well its variation in the use of space in habitats through the seasons of the year. In addition, the hypothesis about spatial segregation between the chilla fox and domestic dog was tested, which would be reflected both in the type of food consumed, as well in habitat use.

Materials and methods

Study area

Cerro Ñielol Natural Monument (38°43'S-72°35'W) is a 88 ha protected area in south-central Chile, which is adjacent to the city of Temuco (Fig. 1). It has an average altitude of 200 m asl, being a part of the Huimpil-Ñielol mountain range, with a perhumid Mediterranean-type climate (DI CASTRI and HAJEK, 1976). The landscape is characterized by a deciduous forest, mainly represented by the roble-laurel-lingue formation (*Nothofago-Perseetum*; OBERDORFER, 1960). Three habitat types dominate the area: native forest; forest plantations of *Pinus radiata*; and scrubland, all included for the current data collection.

Sample collection and laboratory analysis

From December 2019 until December 2020, the trails of the protected area and its surroundings were traveled biweekly in search of feces from chilla foxes (the only fox observed in the study area) and dogs. This period included the following seasons: summer (December–March), fall (March–June), winter (June–August), and spring (September–December). A line of trails with a length of 4 km was considered, covering an area of 200 hectares. Chilla fox feces were recognized by morphological criteria (CHAME et al., 2003; MUÑOZ-PEDREROS, 2010), which allowed to establish a differentiation with respect to the puma (*Puma concolor*), the other locally detected carnivore, and domestic dog, whose feces' size and color are clearly distinguishable (these latter are larger and darker). Another criterion used was the permanent sighting of the species in the study area (ZÚÑIGA et al., 2008). Samples were placed in paper bags, labeled and stored for later analysis.

In the laboratory, feces of both carnivores were dried



Fig. 1. Study area. A) General plane; B) Regional scale; C) Local scale. Lines indicate the area where the sampling was carried out. Source: Google Earth.

at 60 °C and then manually separated to obtain the remains of indigestible prey, such as mammalian hair and bones, as well as bird feathers and bones and arthropod elytra. These remains were identified based on keys (DAY, 1966; CHEHEBAR and MARTIN, 1989; PEARSON, 1995), counting them according to their observed proportion with respect to the total obtained (RAU, 2009).

Analysis with ecological indexes and statistical tests

The observed diet of both species was quantified using a trophic diversity index (β ; LEVINS 1968), which consists in: $\beta = 1/\sum(p_i)^2$, where p_i is the occurrence of the prey i in the diet of the species. This index allows determining the use of resources based on the total of items recorded. Standard deviation of this index was estimated using the Jackknife method (JAKSIC and MEDEL, 1987). In parallel, standardized niche width was calculated (B_{STA} ; COLWELL and FUTUYMA, 1971), which consists in $B_{STA} = (B_{OBS}-B_{MIN})/(B_{MAX}-B_{MIN})$, where B_{OBS} is the observed niche breadth, B_{MIN} is the minimum possible niche breadth (1), and B_{MAX} is the maximum possible niche breadth. This index facilitates the contrast between seasons due to differences in food items through these periods. To compare prey diversity across seasons, Hutchenson procedure was used (HUTCHESON, 1970), which is analogous to a T-test. To avoid the incidence of type-I errors as a consequence of multiple comparisons, Bonferroni correction was performed (HOLM, 1979). The proportion in the consumption of each item was compared across seasons to determine if there were variations among these periods, for which the arithmetic mean of the frequencies obtained for each case was considered as the expected value (ZÚÑIGA et al., 2021).

The biomass calculation of the prey consumed by

chilla fox was carried out through geometric mean (JAKSIC and BRAKER, 1983), an indicator that was estimated for the four sampling seasons. In parallel, the trophic isocline method was used (KRUUK and DE KOCH, 1980, adapted by RAU, 2009), which allows determining the importance of each prey in the trophic spectrum of the predator. This analysis was performed for the total of prey obtained in the whole sampling period. 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).

Collected feces were also used to evaluate habitat use, which was carried out by comparing frequencies of recordings in each of the habitats sampled. The proportion of habitats was obtained through the GIS treatment of digital images using ArcView 3.2 software and its Spatial Analyst 2.0 extension. Thus, the sampled area corresponded to 53% scrubland, 19% plantations, and 28% native forest. To determine if the frequency of recordings observed in the habitats differed from that which would be expected by chance, a chi-square (χ^2) goodness-of-fit test was used (SOKAL and ROHLF, 1995). In cases where comparisons were significant, Bonferroni confidence intervals were estimated (BYERS et al., 1984), to determine the type of habitat selection exerted by these canids (negative, neutral or positive). Seasonal variations in habitat use were determined by Kruskal-Wallis analyses tests (SOKAL and ROHLF, 1995).

Feces of both canids (chilla fox and domestic dog) were counted alongside 100 m sections ($n = 40$) of the trails traveled. The associations between the recordings of species were established through Pearson's correlations (SOKAL and ROHLF, 1995; NEALE and SACKS, 2001), which assumes the correlation coefficient would allow determining the type of spatial

Table 1. Dietary composition of chilla fox in the study area, through the sampled seasons. Numbers in rows indicates the observed abundance of prey consumed and their percentage

Prey	Summer	Fall	Winter	Spring
Mammals				
Rodents, Cricetidae				
<i>Abrothrix longipilis</i>	1 (2.63)	3 (15)	6 (17.64)	2 (7.14)
<i>Abrothrix olivaceus</i>	1 (2.63)	–	–	–
<i>Oligoryzomys longicaudatus</i>	–	–	2 (5.88)	–
Rodents, Muridae				
<i>Rattus norvegicus</i>	–	–	7 (20.58)	2 (7.14)
<i>Rattus rattus</i>	4 (13.33)	–	12 (35.29)	7 (25)
Rodents, Echymidae				
<i>Myocastor coypus</i>	1 (2.63)	–	–	1 (3.57)
Lagomorpha				
<i>Lepus europaeus</i>	3 (10)	7 (35)	4(11.76)	1 (3.57)
Birds				
Unidentified birds	5 (13.15)	6 (30)	2 (5.88)	2 (7.14)
Reptiles				
<i>Liolaemus sp.</i>	–	1 (5)	–	–
Arthropoda				
Unidentified insects	14 (36.84)	–	–	11 (39.28)
Vegetables				
Vegetal tissues	4 (10.52)	3 (15)	1 (2.94)	2 (7.14)
Seeds	5 (13.15)	–	–	–
Garbage	1	–	1	–
Total scats	10	11	16	11
Dietary breadth (β)	4.97 + 3.22	3.84 + 1.39	4.55 + 2.02	4.17 + 2.64
Standardized niche (B_{sta})	0.49	0.71	0.59	0.45

association of both species based on the frequency of their respective recordings. Data were normalized through logarithm of recordings ($X + 1$; NEALE and SACKS, 2001).

Frequencies of recordings of both species were compared at the habitat level, where the overlap was estimated using the Pianka's index (PIANKA, 1973), and the significance of the comparisons was obtained by the procedure already indicated by Hutcheson (HUTCHESON, 1970).

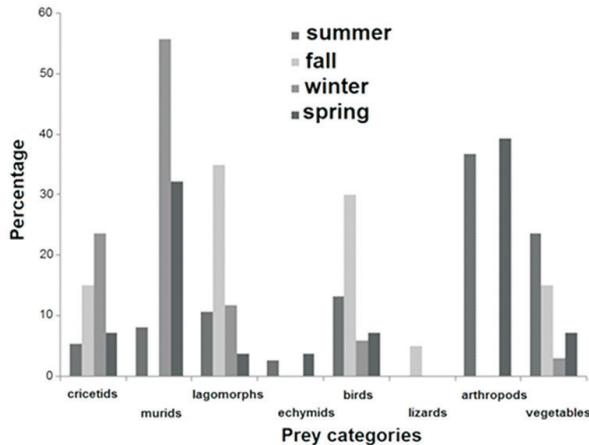


Fig. 2. Frequency of prey consumption by *Lycalopex griseus* in the study area through the sampled seasons.

Results

A total of 140 feces (48 from chilla fox and 92 from dogs) were collected, with small variations in diet composition between seasons (Table 1). However, there were not significant differences in both canids in these periods (Kruskal-Wallis test, $H = 0.628$, $p = 0.882$; 6.432 , $p = 0.075$; for chilla fox and domestic dog, respectively; d.f. in all cases: 3). In dietary terms, the trophic spectrum of chilla fox was composed by seven prey categories (cricetids, murids, lagomorphs, echymids, birds, reptiles and arthropods), highlighting the consumption of the first two seasons, followed by lagomorphs (hares), birds and arthropods (Fig. 2). Additionally, garbage fragments were found in two occasions (plastic waste), which were not incorporated into dietary analyses because these do not constitute part of a food resource.

The highest prey diversity (β) of chilla fox was observed in summer, followed by winter. Significant differences were observed when summer was compared with fall ($T = 3.98$, $p = 0.0003$), fall with winter ($T = 3.19$, $p = 0.0027$), and summer with spring ($T = 6.06$, $p < 0.0001$). In terms of frequency of consumption of each prey type, significant differences were observed throughout these periods in all cases (Chi-square test, $p < 0.0001$), except for European hare, *Lepus europaeus* ($p = 0.0591$). On the other hand, dog diet had a high proportion of food from anthropogenic sources, such as commercial dog food (>90%), with a minimal proportion of rodents (Muridae), which allowed to establish a clear dietary differentiation with respect to chilla fox, without having to carry out subsequent analyses.

In relation to the representation of biomass, the geometric means obtained were 17.92, 255.72, 131.94 and 18.88 grams for summer, fall, winter and spring, respectively. In terms of importance, it was observed that lagomorphs occupied the upper intermediate isocline (between 20% and 50%; Fig.

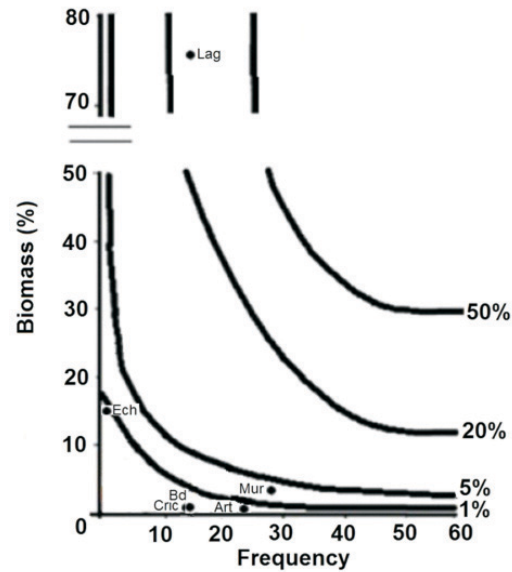


Fig. 3. Trophic isoclines for prey consumed by *Lycalopex griseus* in the study area. Art, Arthropods; Bd, Birds; Cric, Cricetids; Ech, Echymids; Lag, Lagomorphs; Mur, Murids.

3), while murids occupied the isocline that is between 1% and 5%. Cricetids, birds and arthropods were placed in the lowest isocline, less than 1%. Reptiles, due to their low representation both in terms of frequency and biomass, were not included in the analysis. Due to the characteristics of dog food (see previous paragraph), it was impossible to quantify the biomass to perform the same analysis.

Regarding to spatial habits, a seasonal variation in the proportion of use was observed for each species, with a predominance of scrublands and native forest (Fig. 4). Significant differences were observed for chilla fox in winter ($\chi^2 = 11.10$, $p = 0.0039$, d.f.: 2) and dogs in spring ($\chi^2 = 116.93$, $p < 0.0001$). In both cases, nevertheless, selectivity was not observed for any type of habitat, according to Bonferroni confidence intervals (Table 2). In addition, no changes were observed in the frequencies of use across seasons in scrublands ($H = 3.41$, $p = 0.2124$), plantations ($H = 2.46$, $p = 0.4022$), and forest ($H = 3.21$, $p = 0.2835$). In relation to overlap in the habitat use by chilla foxes and dogs, highest and significant values were obtained in summer and spring ($S = 0.95$; $T =$

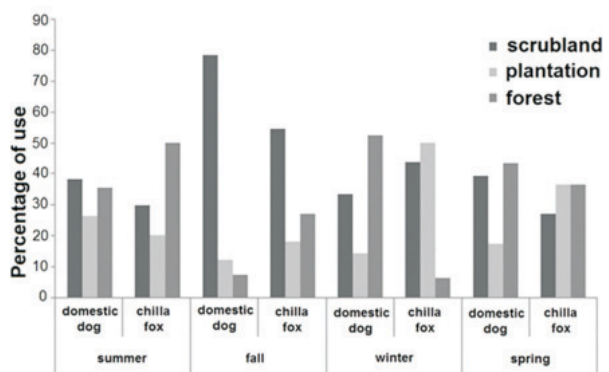


Fig. 4. Proportion of habitat use by chilla fox and domestic dog in the study area through sampled seasons.

Table 2. Frequency of habitat use of chilla fox and domestic dog according to Bonferroni's confidence intervals. These comparisons were performed in the seasons (winter for chilla fox, spring for domestic dog) where a different pattern of chance was observed, according to goodness-of-fit tests.

Species	Habitat	Intervals of confidence	p-value
Chilla fox	Scrubland	0.141–0.734 (=)	0.520
	Plantation	0.201–0.799 (=)	0.190
	Forest	0–0.207 (=)	0.280
Domestic dog	Scrubland	0.148–0.635 (=)	0.520
	Plantation	0–0.363 (=)	0.190
	Forest	0.187–0.682 (=)	0.200

6.36, $p < 0.0001$; $S = 0.92$, $T = 3.71$, $p = 0.001$, respectively). No significant differences were observed in the rest of seasons ($S = 0.92$; $T = 1.42$, $p = 0.1685$, $S = 0.58$, $T = 1.19$, $p = 0.2423$ for fall and winter, respectively). Moreover, no associations were found in the frequency of recordings in the trails through the seasons ($r = -0.083$, $p = 0.731$; $r = -0.208$, $p = 0.378$, for summer, fall, winter and spring, respectively).

Discussion

The trophic diversity observed of the chilla fox differs from that reported in forests at the same latitude (MARTÍNEZ et al., 1993; ZÚNIGA et al., 2008), which suggests a change in the local composition of prey in the study area. Previous reports indicate that the diet of this canid is based on small mammals, mainly native rodents, in habitats of high vegetation cover (SIMONETTI, 1989). However, this habitat type was not well represented in our study area. The low cover of arboreal vegetation in the vicinity of the protected area, could result in the absence of native rodents and a predominance of lagomorphs (hares), a fact that has been reported in Mediterranean environments of Central Chile (FERNÁNDEZ and SIMONETTI, 2013). The high proportion of lagomorphs (hares) in the trophic spectrum of the chilla fox is also noteworthy, considering its condition as an exotic and invasive species in the study area (JAKSIC et al., 2002), which suggests a modification of their trophic preferences. On the other hand, the consumption of garbage is similar to that reported in peri-urban environments in the Northern Hemisphere (JANKOWIAK et al., 2016), which suggests a progressive incorporation of anthropogenic food in the trophic spectrum of this canid.

The differences observed in the dietary diversity of chilla fox among sampled seasons would be explained mainly by the reproductive characteristics of the prey, which would modulate its abundance throughout these periods (HANSKI et al., 2001). In the case of fall and winter, a high frequency of consumption of native rodents was observed, which is consistent with that reported in forests of southern Chile, where the abundance of these mammals reaches its peak (GONZÁLEZ and MURÚA, 1983). In contrast, there are reports that murids have irregular reproductive periods throughout the year (KING et al., 1996), which is consistent with the highest capture rate observed in winter and spring by foxes. In the case of hares, there are reports in the Northern hemisphere of a marked seasonality in their reproductive patterns, which occurs mainly in winter (BANFIELD, 1974). This fact is consistent with the results obtained in the study area where, together with fall, the highest relative frequencies of consumption were observed. On the other hand, the seasonal pattern in the consumption of

echymids (*Myocastor coypus*) must be observed with caution, due to the similarities on size between this rodent and chilla fox (MUÑOZ-PEDREROS and YÁÑEZ, 2009). Indeed, scavenging is likely due to bigger carnivores in the study area, and predation of *M. coypus* by chilla fox is still to be confirmed. This fact is due to the presence of puma in the study area, which has showed reports of consumption of *M. coypus* (ZÚNIGA and MUÑOZ-PEDREROS, 2014). In consideration of this, it is important to quantify the population changes of prey used by the chilla fox in the study area across seasons, which would allow determining the degree of selectivity that this canid exerts on them according to the temporal variations (JAKSIC, 1989).

Regarding the effect of prey biomass on the trophic spectrum of chilla fox, it was observed that hares were located in the upper position of the isoclines. This shows the importance that this item occupied in dietary terms. This finding is consistent with what was observed in agroecosystems (ZÚNIGA et al., 2018; ZÚNIGA et al., 2021), which suggests that this prey is acquiring more relevance as the environment is transforming (SIMONETTI, 1986). The incorporation of murids in the intermediate position of the isoclines is consistent with the aforementioned study of agroecosystems, which indicating that this group also presents importance in the diet of chilla fox, with a decrease of native prey (NOVARO et al., 2000). On the other hand, the geometric mean values of prey in general terms are lower than those reported in agroecosystems (ZÚNIGA et al., 2021), which suggests a low availability of prey in peri-urban habitats, with limitations to obtain their energetic requirements (SILVA et al., 2005).

The absence of an association between the abundance of dog and fox feces of dogs was surprising, due to the documented negative impact of dogs on the use of space by chilla fox (SILVA-RODRÍGUEZ et al., 2010a). Considering the great flexibility in habitat use that dogs can perform through the landscape (MEEK, 1999; PASCHOAL et al., 2018), this finding should be taken with caution. This can be explained by two reasons. First that the use of feces alone would not account for the interaction of chilla foxes with domestic dogs. In this way, its use combined with other types of signs, such as tracks, could reinforce the use of space by species in the study area (BAREA-AZCÓN et al., 2007). On the other hand, it is proposed that a similarity in the use of habitat by both species would be compensated by a reduction in the overlap of their activity patterns, a situation that has been observed with urban parks in the Northern Hemisphere (MELLA-MÉNDEZ et al., 2019). This mechanism would limit the likelihood of interference among species, which however must be tested to determine if it is applicable in the study area. A critical issue in this study is related with the low number of feces, which were lower than those observed in forested environments, despite their sampling efforts being similar (ZÚNI-

GA et al., 2008). This means that the effect the urban mosaic would affect the availability of preys, and therefore their spatial patterns. In a similar way, recordings of chilla foxes in agroecosystems were low in all seasons sampled (ZÚNIGA et al., 2021), which was explained by the homogenization of resources present in this environment (BENTON et al., 2003).

The seasonal variations in the habitat use by foxes (GOLDYN et al., 2003; ZÚNIGA et al., 2009), could be explained by the temporary fluctuations in the availability of prey (RANDA et al., 2009; WALTON et al., 2017). In this way, the use of scrubland by chilla fox could be associated with the greater abundance of European hares. Hares are mainly found in this habitat, with a lesser occurrence in plantations, and in a minimal proportion in native forest (A.H. Zúñiga, personal observation). As such, under a scenario of reduction of prey availability (mainly in spring and summer), would imply the need for a great effort of displacement for obtain food, with the subsequent increase in interaction with humans (SILVA-RODÍGUEZ et al., 2010b).

An additional aspect that would partially explain the spatial pattern of chilla foxes in the study area is related to the frequent presence of humans, mainly due to recreational and sports activities. This fact was reported as one of the most important factors that affects the occurrence of carnivores, with evasive behaviors in spatio-temporal terms (MOREIRA et al., 2015; BAKER and LIBERG, 2018). Additionally, human visitors often bring their dogs to the study area, which would cause an additional effect on the avoidance effects on chilla foxes. Despite the fact that the COVID-19 pandemic has restricted human mobility, with likely positive effects on wildlife (SILVA-RODÍGUEZ et al., 2020), disturbance by people had been continuous in the study area, regardless of movement regulations. This fact would result in a pressure on wildlife of different degree compared to the period prior to the pandemic, which only be appreciable according to changes observed through long-term records.

In conclusion, a predominance of exotic prey was observed in general terms in the trophic spectrum of the chilla fox, which could be associated with seasonal variations of the population size of the preys. Although avoidance behavior of this wild canid in relation to the domestic dog was not observed, the continuous presence of the latter indicates that the observed pattern should be reinforced with complementary records. Systematic monitoring is necessary to indicate changes in the fox population as response to anthropic pressures (human and dog presence) over time.

Acknowledgements

The authors thank to two reviewers who helped to improve this manuscript. Peter Lewis and Christopher Anderson corrected the language of the text.

References

AMAYA, J.N.G., ALSINA, M. S., BRANDANI, A.A., 1979. Ecología de la liebre europea (*Lepus europaeus* P.) II. Reproducción y peso corporal de un área de San Carlos de Bariloche [Ecology of the European hare (*Lepus europaeus* P.) II. Reproduction and body weight of an area of San Carlos de Bariloche]. Informe técnico – Estación Experimental Regional Agropecuaria Rafaela, No. 9.

Bariloche, Argentina. 36 p.

BAKER, A.D., LEBERG, P.L., 2018. Impacts of human recreation on carnivores in protected areas. *Plos One*, 13 (4): e0195436. <https://doi.org/10.1371/journal.pone.0195436>

BANFIELD, A., 1974. *Mammals of Canada*. Toronto: University of Toronto Press. 438 p.

BAREA-AZCÓN, J.M., VIRGÓS, E., BALLESTEROS-DUPERÓN, MOLEÓN, M., CHIROSA, M., 2007. Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. *Biodiversity and Conservation*, 16: 1213–1230. <https://doi.org/10.1007/s10531-006-9114-x>

BATEMAN, P.W., FLEMING, P.A., 2012. Big city life: carnivores in human environments. *Journal of Zoology*, 287 (1): 1–23. <https://doi.org/10.1111/j.1469-7998.2011.00887.x>

BENTON, T.G., VICKERY, J.A., WILSON, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, 18 (4): 182–188. [https://doi.org/10.1016/S0169-5347\(03\)00011-9](https://doi.org/10.1016/S0169-5347(03)00011-9)

BOITANI, L., FRANCISCI, F., CIUCCI, P., ANDREOLI, G., 2017. The ecology and behavior of feral dogs: a case study of Central Italy. In SERPELLI, J. (ed.). *The domestic dog: its evolution, behavior, and interactions with people*. Cambridge: Cambridge University Press, p. 342–348.

BORROR, D.J., TRIPLEHORN, C.A., JOHNSON, N.F., 1992. *Study of insects*. Orlando: Saunders College Publishing. 875 p.

BUTLER, J.R.A., DU TOIT, J.T., 2002. Diet of free-ranging domestic dogs (*Canis familiaris*) in rural Zimbabwe: implications for wild scavengers on the periphery of wildlife reserves. *Animal Conservation* 5 (1): 29–37. <https://doi.org/10.1017/S136794300200104X>

BYERS, C.R., STEINHORST, R.K., KRAUSMAN, P.R., 1984. Clarification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management*, 48 (3): 1050–1053. <https://doi.org/10.2307/3801467>

CAMPOS, C.B., ESTEVES, C.F., FERRAZ, K.M.P.M., CRAWSHAW, P.G., VERDADE, L.M., 2007. Diet of free-roaming cats and dogs in a suburban and rural environment, southeastern Brazil. *Journal of Zoology*, 273 (1): 14–20. <https://doi.org/10.1111/j.1469-7998.2007.00291.x>

CARBONE, C., GITTLEMAN, J., 2002. A common rule for the scaling of carnivore density. *Science*, 295 (5663): 2273–2276. <https://www.science.org/doi/10.1126/science.1067994>

CHAME, M., 2003. Terrestrial mammal feces: a morphometric summary and description. *Memórias do Instituto Oswaldo Cruz*, 98, Suppl. 1: 71–94. <https://doi.org/10.1590/S0074-02762003000900014>

CHEHÉBAR, C., MARTIN, S., 1989. Guía para el reconocimiento microscópico de los pelos de los mamíferos [Guide for the microscopic recognition of mammalian hairs]. *Doñana Acta Vertebrata*, 16: 247–291.

COLWELL, R., FUTUYMA, J., 1971. On the measurement of the niche breadth and overlap. *Ecology*, 52 (4): 567–572. <https://doi.org/10.2307/1934144>

CROOKS, K.R., 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology*, 16 (2): 488–502. <https://doi.org/10.1046/j.1523-1739.2002.00386.x>

DAY, M.G., 1966. Identification of hair and feather remain in the gut and feces of stoat and weasels. *Journal of Zoology*, 18: 315–326. <https://doi.org/10.1111/j.1469>

- 7998.1966.tb02948.x
- DEL SOLAR, G.R., RAU, J., 2004. Pseudalopex griseus. In SILLERO-ZUBIRI, C., HOFFMANN, M., MACDONALD, D. (eds). *Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan*. Oxford: IUCN The World Conservation Union, p. 56–63.
- DI CASTRI, E., HAJEK, E., 1976. *Bioclimatología de Chile* [Bioclimatology of Chile]. Santiago: Ediciones Universidad Católica de Chile. 163 p.
- EHEVERRÍA, C., COOMES, D., HALL, M., NEWTON, A., 2008. Spatially explicit models to analyze forest loss and fragmentation between 1976 and 2020 in southern Chile. *Ecological Modelling*, 212 (3-4): 439–449. <https://doi.org/10.1016/j.ecolmodel.2007.10.045>
- FEDRIANI, J., FULLER, T., SAUVAJOT, R., 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography*, 24 (3): 325–331. <https://doi.org/10.1111/j.1600-0587.2001.tb00205.x>
- FERNÁNDEZ, I., SIMONETTI, J.A., 2013. Small mammal assemblages in fragmented shrublands of urban areas of Central Chile. *Urban Ecosystems*, 16 (2): 377–387. <https://doi.org/10.1007/s11252-012-0272-1>
- GESE, E., BEKOFF, M., 2004. M. Coyote *Canis latrans* Say, 1823. In SILLERO-ZUBIRI, C., HOFFMANN, M., MACDONALD, D. (eds). *Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan*. Oxford: IUCN The World Conservation Union, p. 81–87.
- GITTLEMAN, J., HARVEY, P.H., 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, 10 (1): 57–63. <https://doi.org/10.1007/BF00296396>
- GOLDYN, B., HROMADA, M., SURMACKI, A., TRYJANOWSKI, P., 2003. Habitat use and diet of the red fox *Vulpes vulpes* in an agricultural landscape in Poland. *Zeitschrift für Jagdwissenschaft*, 49 (3): 1–10. <https://doi.org/10.1007/BF02189737>
- GONZÁLEZ, L., MURÚA, R., 1983. Características del periodo reproductivo de tres roedores cricétidos del bosque higrófilo templado [Characteristics of the reproductive period of three cricetid rodents from the temperate hygrophilous forest]. *Anales del Museo de Historia Natural*, 16: 87–99.
- GUERRERO, C., ESPINOZA, L., NIEMEYER, H.M., SIMONETTI, J.A., 2006. Using fecal profiles of bile acids to assess habitat use by threatened carnivores in the Maulino forests of central Chile. *Revista Chilena de Historia Natural*, 79 (1): 89–95. <http://dx.doi.org/10.4067/S0716-078X2006000100008>
- HAIRSTON, N., SMITH, F.E., SLOBODKIN, L.B., 1960. Community structure, population control, and predation. *American Naturalist*, 94: 421–425. <https://doi.org/10.1086/282415>
- HANSKI, I., HENTONNEN, H., KÖRPIÄKI, E., OKSANEN, L., TURCHIN, P., 2001. Small-rodents dynamic and predation. *Ecology*, 82 (6): 1505–1520. [https://doi.org/10.1890/0012-9658\(2001\)082\[1505:SRDAP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1505:SRDAP]2.0.CO;2)
- HANSSON, L., HENTONNEN, H., 1988. Rodent dynamics and community process. *Trends of Ecology and Evolution*, 3 (8): 195–200. [https://doi.org/10.1016/0169-5347\(88\)90006-7](https://doi.org/10.1016/0169-5347(88)90006-7)
- HASWELL, P.M., JONES, K.A., KUSAK, J., HAYWARD, M.W., 2018. Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. *Oecologia*, 187 (1): 573–583. <https://doi.org/10.1007/s00442-018-4133-3>
- HOLM, A., 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6 (2): 65–70. [cit. 2021-10-14]. <https://www.jstor.org/stable/4615733>
- HUTCHESON, K., 1970. A test for comparing diversities based on Shannon formula. *Journal of Theoretical Biology*, 29 (1): 151–154. [https://doi.org/10.1016/0022-5193\(70\)90124-4](https://doi.org/10.1016/0022-5193(70)90124-4)
- IRIARTE, A., JAKSIC, F., 2012. *Los carnívoros de Chile* [Carnívoros of Chile]. Santiago: Flora & Fauna CASEB Ediciones. 257 p.
- JAKSIC, F., 1989. Opportunist, selective, and other often-confused terms in predation literature. *Revista Chilena de Historia Natural*, 62 (1): 7–8.
- JAKSIC, F., 1997. *Ecología de los vertebrados de Chile* [Ecology of the vertebrates of Chile]. Santiago: Ediciones Universidad Católica de Chile. 262 p.
- JAKSIC, F., BRAKER, E., 1983. Food-niche relationships and guild structure of birds of prey: competition vs. opportunism. *Canadian Journal of Zoology*, 61 (10): 2230–2241. <https://doi.org/10.1139/z83-295>
- JAKSIC, F., MEDEL, R., 1987. El acuchillamiento de datos como método de obtención de intervalos de confianza y de prueba de hipótesis para índices ecológicos [The jackknifing data as a method of obtaining confidence intervals and hypothesis testings for ecological indices.] *Medio Ambiente*, 8: 95–103.
- JAKSIC, F.M., IRIARTE, A., JIMÉNEZ, J.E., MARTÍNEZ, D.R., 2002. Invaders without frontiers: cross-border invasions of exotic mammals. *Biological Invasions*, 4: 157–173. <https://doi.org/10.1023/A:1020576709964>
- JANKOWIAK, L., MALECHA, A.W., KRAWCZYK, A.J., 2016. Garbage in the diet of carnivores in an agricultural area. *European Journal of Ecology*, 2: 81–86. <https://doi.org/10.1515/eje-2016-0009>
- KING, C.M., INNES, J.G., FLUX, M., KIMBERLEY, M.O., LEATHWICK, J.R., WILLIAMS, D.S., 1996. Distribution and abundance of small mammals in relation to habitat in Pureora National Forest Park. *New Zealand Journal of Ecology*, 21 (2): 215–240.
- KRAUZE-GRYZ, D., GRYZ, J., 2014. Free-ranging domestic dogs (*Canis familiaris*) in Central Poland: density, penetration range and diet composition. *Polish Journal of Ecology*, 62 (1): 183–193. <https://doi.org/10.3161/104.062.0101>
- KLIMANT, P., KLIMANTOVÁ, A., BALÁŽ, I., JAKAB, I., TULIS, F., RYBANSKÝ, L., VADEL, L., KRUMPALOVÁ, Z., 2017. Small mammals in an urban area: habitat preferences and urban-rural gradient in Nitra City, Slovakia. *Polish Journal of Ecology*, 65: 144–157. <https://doi.org/10.3161/15052249PJE2017.65.1.013>
- KRUUK, H., DE KOCK, L., 1980. Food and habitat of badgers (*Meles meles* L.) of Monte Baldo, northern Italy. *Zeitschrift für Säugetierkunde*, 46 (5): 295–301.
- LEVINS, R., 1968. *Evolution in a changing environments*. New York: Princeton University Press. 120 p.
- LUCK, G.W., 2007. A review of the relationships between population human density and biodiversity. *Biological Reviews*, 82: 607–645. <https://doi.org/10.1111/j.1469-185X.2007.00028.x>
- MARTÍNEZ, D.R., RAU, J.R., MURÚA, R.E., TILLERÍA, M.S., 1993. Depredación selectiva de roedores por zorros chilla (*Pseudalopex griseus*) en la pluviselva valdiviana, Chile [Selective predation of rodents by chilla foxes (*Pseudalopex griseus*) in the Valdivian rainforest, Chile]. *Revista Chilena de Historia Natural*, 66 (4): 419–426.
- MEEK, P.D., 1999. The movement, roaming behaviour and

- home-range of free-roaming domestic dogs, *Canis lupus familiaris*, in coastal New South Wales. *Wildlife Research*, 26 (6): 847–855. <https://doi.org/10.1071/WR97101>
- MELLA-MÉNDEZ I., FLORES-PEREDO, R., PÉREZ-TORRES, J., HERNÁNDEZ-GONZÁLEZ, S., GONZÁLEZ-URIBE, D.U., BOLÍVAR-CIMÉ, B.S., 2019. Activity patterns and temporal niche partitioning of medium-sized wild mammals in urban parks of Xalapa, Mexico. *Urban Ecosystems*, 22 (6): 1061–1070. <https://doi.org/10.1007/s11252-019-00878-2>
- MOREIRA-ARCE, D., VERGARA, P.M., BOUTIN, S., 2015. Diurnal human activity and introduced species affect occurrence of carnivores in a human-dominated landscape. *PLoS One*, 10: 1–10. <https://doi.org/10.1371/journal.pone.0137854>
- MUÑOZ, A., MURÚA, R., 1990. Efectos de la reforestación de *Pinus radiata* sobre la diversidad y abundancia de micromamíferos en un agroecosistema de Chile Central [Effects of reforestation of *Pinus radiata* on the diversity and abundance of small mammals in an agroecosystem of Central Chile.] *Turrialba*, 39: 143–150.
- MUÑOZ-PEDREROS, A., 2010. *Huellas y signos de mamíferos de Chile* [Tracks and signs of mammals from Chile]. Valdivia: CEA Ediciones. 112 p.
- MUÑOZ-PEDREROS, A., YÁÑEZ, J., 2009. *Mamíferos de Chile* [Mammals of Chile]. Valdivia: CEA Ediciones. 573 p.
- MUÑOZ-PEDREROS, A., YÁÑEZ, J., NORAMBUENA, H., ZÚÑIGA, A., 2018. Diet, dietary selectivity and density of south american grey fox, *Lycalopex griseus*, in Central Chile. *Integrative Zoology*, 13 (1): 46–57. <https://doi.org/10.1111/1749-4877.12260>
- MURRAY, M., EDWARDS, M.A., ABERCROMBIE, B., ST. CLAIR, C.C., 2015. Poor health is associated with use of anthropogenic resources in an urban carnivore. *Proceedings of the Royal Society B*, 282: 201500009. <https://doi.org/10.1098/rspb.2015.0009>
- MURÚA, R., 1996. Comunidades de mamíferos en el bosque nativo de Chile [Communities of mammals in the native forest of Chile]. In ARMESTO, J.J., VILLAGRÁN, C., ARROYO, M.K. (eds.). *Ecología de los bosques nativos de Chile*. Santiago: Editorial Universitaria, Santiago, p. 113–133.
- NEALE, J., SACKS, B., 2001. Food habits and space use of gray foxes in relation to sympatric coyotes and bobcats. *Canadian Journal of Zoology*, 79 (10): 1794–1800. <https://doi.org/10.1139/z01-140>
- NORAMBUENA, H., RIQUELME, J., 2014. *Profesor Dr. Francisco Behn Kuhn (1910-1976) biografía y catálogo de su colección de aves chilenas* [Professor Dr. Francisco Behn Kuhn (1910-1976) biography and catalog of his collection of Chilean birds]. Valdivia: CEA Ediciones. 152 p.
- NOVARO, A., FUNES, M., WALKER, S., 2000. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. *Biological Conservation*, 73 (1): 143–150. [https://doi.org/10.1016/S0006-3207\(99\)00065-8](https://doi.org/10.1016/S0006-3207(99)00065-8)
- ONBERDORFER, F., 1960. *Pflanzensoziologische Studien in Chile. Ein Vergleich mit Europa* [Phytosociological studies in Chile. A comparison with Europe]. Flora et Vegetatio Mundi, 2: Weinheim: Cramer. 208 p.
- PASCHOAL, A.M.O., MASSARA, R.L., BAILEY, L.L., DOHERTY, P.F., SANTOS, P.M., PAGLIA, A.P., HIRSCH, A., CHIARELLO, A.G., 2018. Anthropogenic disturbances drive domestic dog use of Atlantic forest protected areas. *Tropical Conservation Science*, 11: 1–14. <https://doi.org/10.1177/1940082918789833>
- PEARSON, O., 1995. Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanin National Park, southern Argentina. *Mastozoología Neotropical*, 2: 99–148.
- PIANKA, E., 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4: 53–74. <https://doi.org/10.1146/annurev.es.04.110173.000413>
- RANDA, L.A., COOPER, D.M., MESERVE, P.L., YUNGER, J.A., 2009. Prey switching of sympatric canids in response to variable prey abundance. *Journal of Mammalogy*, 90 (3): 594–603. <https://doi.org/10.1644/08-MAMM-A-092R1.1>
- RATCHKE, B., PLACEY, E., 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, 16: 179–214. <https://doi.org/10.1146/annurev.es.16.110185.001143>
- RAU, J., 2009. Métodos de ecología trófica [Methods of trophic ecology]. In MUÑOZ-PEDREROS, A., YÁÑEZ, J. (eds). *Mamíferos de Chile*. Valdivia: CEA Ediciones, p. 495–506.
- ROSALINO, L.M., ROSA, S., SANTOS-REIS, M., 2010. The role of carnivores as Mediterranean seed dispersers. *Annales Zoologici Fenici*, 47 (3): 195–205. <https://doi.org/10.5735/086.047.0304>
- ŠÁLEK, M., DRAHNÍKOVÁ, L., TKADLEC, E., 2015. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. *Mammalian Review*, 45 (1): 1–14. <https://doi.org/10.1111/mam.12027>
- SCHELL, C.J., STANTON, L.A., YOUNG, J.K., ANGELONI, L.M., LAMBERT, J.E., BRECK, S.W., MURRAY, M.H., 2021. The evolutionary consequences of human-wildlife conflict in cities. *Evolutionary Applications*, 14 (1): 178–197. <https://doi.org/10.1111/eva.13131>
- SCHUETTE, P., WAGNER, A.P., WAGNER, M.E., CREEL, S., 2013. Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation*, 158: 301–312. <https://doi.org/10.1016/j.biocon.2012.08.008>
- 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 (2): 239–246. <http://dx.doi.org/10.4067/S0716-078X2005000200007>
- SILVA-RODRÍGUEZ, E., ORTEGA-SOLÍS, G., JIMÉNEZ, J.E., 2010a. Conservation and ecological implications of the use of space by chilla foxes and free-ranging dogs in a human-dominated landscape in southern Chile. *Austral Ecology*, 35 (7): 765–777. <https://doi.org/10.1111/j.1442-9993.2009.02083.x>
- SILVA-RODRÍGUEZ, E., SOTO-GAMBOA, M., ORTEGA-SOLÍS, G., JIMÉNEZ, J.E., 2010b. Foxes, people and hens: human dimensions of a conflict area in a rural area of southern Chile. *Revista Chilena de Historia Natural*, 82 (3): 375–386. <http://dx.doi.org/10.4067/S0716-078X2009000300005>
- SILVA-RODRÍGUEZ, E., GÁLVEZ, N., SWAN, G.J.F., CUSACK, J. J., MOREIRA-ARCE, D., 2020. Urban life in times of COVID-19: What can infer from novel carnivore records in urban areas? *Science of Total Environment*, 765: 142713. <https://doi.org/10.1016/j.scitotenv.2020.142713>
- SIMONETTI, J., 1986. Human-induced dietary shift in *Dusicyon culpaeus*. *Mammalia*, 50: 406–408.
- SIMONETTI, J., 1989. Microhabitat use by small mammals in Central Chile. *Oikos*, 56 (3): 309–318. <https://doi.org/10.2307/3565615>

- SOKAL, R.R., ROHLF, F.J., 1995. *Biometry*. New York: W.H. Freeman and Company. 887 p.
- TORRES, P.C., PRADO, C.I., 2010. Domestic dogs in a fragmented landscape in the Brazilian Atlantic Forest: abundance, habitat use and caring by owners. *Brazilian Journal of Biology*, 70 (4): 987–994. DOI: 10.1590/S1519-69842010000500010
- VANAK, A.T., GOMPPER, M.E., 2002. Dogs *Canis familiaris* as carnivores: their role and function in intraguild competition. *Mammal Review*, 39 (4): 265–283. <https://doi.org/10.1111/j.1365-2907.2009.00148.x>
- VANAK, A.T., DICKMAN, C.R., SILVA-RODRÍGUEZ, E.A., BUTLER, J.R.A., RITCHIE, E.G., 2014. Top-dogs and under-dogs: competition between dogs and sympatric carnivores. In GOMPPER, M.E. (ed.). *Free-ranging dogs and wildlife conservation*. Oxford: Oxford University Press. p. 69-93.
- WALTON, Z., SAMELIUS, G., ODDEN, M., WILLEBRAND, T., 2017. Variation in home range size of red foxes *Vulpes vulpes* along a gradient of productivity and human landscape alteration. *Plos One*, 12 (4): e0172591. <https://doi.org/10.1371/journal.pone.0175291>
- ZHAO, S., DA, L., TANG, Z., FANG, H., SONG, K., FANG, J., 2006. Ecological consequences of rapid urban expansion: Shanghai, China. *Frontiers in Ecology and the Environment*, 4 (7): 341–346. [https://doi.org/10.1890/1540-9295\(2006\)004\[0341:ECORUE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2006)004[0341:ECORUE]2.0.CO;2)
- ZÚÑIGA, A.H., MUÑOZ-PEDREROS, A., 2014. Hábitos alimentarios de Puma concolor (Carnivora, Felidae) en bosques fragmentados del sur de Chile [Food habits of Puma concolor in fragmented forests of southern Chile]. *Mastozoología Neotropical*, 21 (1): 157–161.
- ZÚÑIGA, A., MUÑOZ-PEDREROS, A., FIERRO, A., 2008. Diet of *Lycalopex griseus* (Gray, 1837) (Mammalia: Canidae) in the intermediate depression intermedia of southern Chile. *Gayana*, 72 (1): 113–116. <http://dx.doi.org/10.4067/S0717-65382008000100013>
- ZÚÑIGA, A., MUÑOZ-PEDREROS, A., FIERRO, A., 2009. Habitat use of four terrestrial carnivores in southern Chile. *Gayana*, 73 (2): 200–210. <http://dx.doi.org/10.4067/S0717-65382009000200004>
- ZÚÑIGA, A.H., FUENZALIDA, V., SANDOVAL, R., 2018. Diet of South American grey foxes *Lycalopex griseus* in an agroecosystem of southern-central Chile. *Therya*, 9: 179–183. <https://doi.org/10.12933/therya-18-574>
- ZÚÑIGA, A.H., FUENZALIDA, V., SANDOVAL, R., ENCINA, F., 2021. Seasonal variation in the diet of two predators in an agroecosystem in southern-central Chile. *Animal Biodiversity and Conservation*, 44 (1): 89–102. <https://doi.org/10.32800/abc.2021.44.0089>

Received November 2, 2021

Accepted May 20, 2022