Seasonal variation in the diet of two predators in an agroecosystem in southern-central Chile

A. H. Zúñiga, V. Fuenzalida, R. Sandoval, F. Encina

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Abstract

Seasonal variation in the diet of two predators in an agroecosystem in southern–central Chile. In ecosystems, seasonal fluctuations in the availability of resources can promote effects on species with similar trophic requirements, increasing the probability of interspecific competition. This scenario becomes more evident in human–dominated landscapes where homogenization of space can contribute to the shortage of resources, modifying species feeding behavior to an uncertain degree. Understanding how these species modify their feeding habits within the context of habitat transformation is of special interest. We evaluated the diversity of prey and overlap for two predators, the chilla fox *Lycalopex griseus* and the barn owl *Tyto alba*, during three seasons in 2018 (winter, spring and summer). The study was based on the analysis of feces and pellets in a landscape with agricultural predominance in Southern–central Chile. We found the chilla fox had a generalist dietary profile, feeding on a broad spectrum of prey, with predominance of lagomorphs and, to a lesser extent, rodents. In contrast, the diet of the barn owl mainly consisted of small rodents, with little variation across seasons. Analyses of dietary overlap showed fluctuations during the periods surveyed, with a maximum value in winter and a minimum value in spring. Variations in the consumption of prey based on their size could facilitate their coexistence in the study area.

Key words: Barn owl, Chilla fox, Diet overlap, Feeding behavior, Non-invasive methods, Trophic isoclines

Resumen

Variación estacional en la dieta de dos depredadores en un agroecosistema en el centro y sur de Chile. En los ecosistemas, las fluctuaciones estacionales en la disponibilidad de recursos pueden tener efectos en especies con requerimientos tróficos similares, lo cual aumenta la probabilidad de que surja la competencia interespecífica. Esta situación se hace más evidente en ambientes antropizados, donde la homogeneización del espacio puede agudizar la escasez de recursos y modificar el comportamiento alimentario en un grado incierto. De esta manera, resulta de especial interés entender cómo estas especies modifican sus hábitos alimentarios en un contexto de transformación del hábitat. Evaluamos la diversidad de presas y el solapamiento de dos depredadores, el zorro chilla, Lycalopex griseus, y la lechuza blanca o lechuza común, Tyto alba, durante tres estaciones en 2018 (invierno, primavera y verano). Se utilizaron heces y egagrópilas recolectadas en un paisaje con predominancia agrícola en el centro y sur de Chile. En el caso del zorro chilla, se observó un perfil trófico generalista, ya que consumió una amplia variedad de presas, en la que predominaron los lagomorfos y en menor medida, los roedores. En cambio, la lechuza concentró una gran proporción de su perfil alimentario a los pequeños roedores, con pequeñas variaciones entre estaciones. El análisis del solapamiento de las dietas mostró variaciones durante los periodos estudiados, con un valor máximo en invierno y uno mínimo en primavera. La variación en el consumo de presas en función de su tamaño facilitaría la coexistencia de ambas especies en la zona de estudio.

Palabras clave: Lechuza común o lechuza blanca, Zorro chilla, Solapamiento de la dieta, Comportamiento alimentario, Métodos no invasivos, Isoclinas tróficas



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Alfredo H. Zúñiga, Laboratorio de Ecología, Universidad de Los Lagos, Osorno, Chile.— Víctor Fuenzalida, Consultora Ambientes del Sur, Temuco, Chile.— Rodolfo Sandoval, Red de la Conservación de la Biodiversidad de Nahuelbuta, Contulmo, Chile.— Francisco Encina, Núcleo de Ciencias Ambientales, Universidad Católica de Temuco, Chile.

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

ORCID ID: A. H. Zúñiga: 0000-0002-0504-7540; V. Fuenzalida: 0000-0003-3044-9610; R. Sandoval: 0000-0002-1338-7123; F. Encina: 0000-0002-8756-8736

Introduction

Ecological communities are sets of species that coexist in a specific time and place (Morin, 2011). Within this organizational level, predators form a group of relevance whose main function is to control prey populations (Hairston et al., 1960). In general, intraguild species and, in particular, predators (Root, 1967), must minimize the co-use of resources between members to avoid effects derived from competition (Schoener, 1974; Fedriani, 1997). For this purpose, species can use several behavioral mechanisms. Food resources are relevant because they promote differentiation of diet between species through types of prey consumed (Zapata et al., 2007). The size of the predator can directly also influence prey size (Gittleman, 1985), deepening segregation. Seasonality, however, could also play a determining role in species interactions, mainly due to variations in the availability of resources. This possibility is evidenced through changes in growth and development in plant species (Rathcke and Placey, 1985) and demographic fluctuations between vertebrate prey (Meserve et al., 1999). Such variations of resources could affect the trophic response of predators, forcing them to modify their trophic spectra (Jaksic, 1989) and consequently to change the relationship of partition of resources between species, affecting their fitness (Wiens, 1977).

Transformation of original habitat has strong effects on biodiversity due to loss of resources for species and limitations on the movement of individuals through patches (Olff and Ritchie, 2002). This issue is important from the view of conservation because the increasing human impact on natural habitats affects their persistence (Crooks, 2002; Olifiers et al., 2005). One of the main ways that habitats are transformed are agroecosystems, where habitat homogenization limits the availability of resources for many species (Benton et al., 2003). Although predators modify their trophic spectrum in farmlands (Drouilly et al., 2018), the extent to which change occurs may be associated with the local composition of species and their ecological particularities, as these factors will enable their occupancy in this type of environments (Ferreira et al., 2018). Knowledge about how species respond to a changing habitat scenario and their interaction with other species in the community is therefore of special relevant to the implementation of conservation plans.

Chilean native forest is characterized by its unique representation of species in a wide latitudinal distribution, with a high degree of endemism (Armesto et al., 1995). Among the predators that occur in this habitat, chilla fox (*Lycalopex griseus*) is one of the three extant canids with a wide distribution, ranging from Arica to Tierra del Fuego, at altitudes that vary from sea level to 3,000 m a.s.l. (Iriarte and Jaksic, 2012). This canid has a generalist trophic behavior that includes small vertebrates and arthropods (Simonetti et al., 1984; Martínez et al., 1993; Zúñiga et al., 2008; Muñoz—Pedreros et al., 2018). On the other hand, the barn owl (*Tyto alba*) is a nocturnal raptor of the family Tytonidae (Pavez, 2004) and its subspecies *tuidara* is widely represented in Chile.This raptor's diet is

mainly carnivorous, with rodents making up the bulk of its food source (Carmona and Rivadeneira, 2006; Muñoz–Pedreros et al., 2016). Although these two species coexist across a broad geographic continuum, little is known about their trophic interaction, their seasonal dynamics and flexibility, and the potential co—use of resources (Jaksic et al., 1996; Correa and Roa, 2005). The purpose of this study was to compare the diet of these two predators in central—southern Chile in a seasonal context. We tested the hypothesis that the trophic spectrum would change for both species at both seasonal and interspecific levels as a way of differentiating the use of resources.

Material and methods

The agroecosystem where the study was peformed is located 20 km. east of Mulchén (37° 49' 42" S -721° 4' 51" W), an urban center in central-southern Chile, with an altitude ranging from 120 to 150 m a.s.l. The climate is humid (Di Castri and Hajek, 1976), with a maximum mean temperature of 25 °C in summer and a minimum temperature of 4 °C in winter (Weather Spark, 2020). Rainfall fluctuates between a minimum mean of 21 mm in summer and a maximum mean of 151 mm in winter (Weather Spark, 2020). The vegetation consists of temperate deciduous forest (Gajardo, 1994). The dominant trees species are of the genus Nothofagus, mainly roble (Nothofagus obliqua) and coigüe (Nothofagus dombeyi). Crops in the area are mainly Avena barbata, Lupinus sp. Triticum sp. and Zea mays, with 62% of the total area surveyed (fig. 1). Mosaics of exotic plantations of Eucalyptus globulus and Pinus radiata make up 28% of the total area; prairies and shrublands account for a further 6%, and native forest for 4%.

Feces and pellets were collected along 1 km line segments during winter and spring 2018 and summer 2019. Feces from chilla foxes were identified using morphometric criteria (Chame, 2003; Muñoz-Pedreros, 2010) and confirmed through the use of camera traps (Kays and Slauson, 2008). Six cameras were placed in the study area, at a distance of 500 m from each other (Zúñiga et al., 2017). In the case of owl pellets, although their recognition was also made by morphological patterns (Muñoz-Pedreros and Rau, 2004), their identification was reinforced through direct observation in a group of trees used by the individuals as a roost. In the transect where these trees are present, the presence of the fox has also been recorded. Feces and pellets were measured, weighed and stored in paper bags for later analyses in the laboratory.

In the laboratory, the samples (feces and pellet were dried at 60 °C and examined manually to determine prey. The criteria to recognize rodents was the morphological pattern of skulls and shape of cuticle of hairs (Day, 1966; Reise, 1973; Pearson, 1995), and for birds it was was feathers (Day, 1966). Reference collections (property of 'Ambientes del Sur consultores') were used for the remaining. The trophic analysis for both species was based on frequencies of relative occurrence of each prey in relation to

the total observed (Rau, 2000), providing an index of trophic diversity (Levins, 1968). This index (B) is based on the formula B = $1/(\sum pi^2)$, where pi is the relative frequency of the prey in the diet. This number fluctuates between 0 and n (n, the number of categories of prey), reflecting the degree of uniformity of prey consumption in relation to the total number of categories observed. Standard deviation of this index was obtained using the Jackknife method (Jaksic and Medel, 1987). Additionally, we calculated a standardized index (Colwell and Futuyma, 1971), which fluctuated between 0 and 1, according to the degree of homogeneity in resources used (0, no homogeneity; 1, total homogeneity). This index allows a better comparison between seasons, assuming the variation of resources during these periods. We assessed the variation in the proportion of each category of prey according to season through the goodness-of-fit test (Sokal and Rohlf 1995), where the average consumption of each category was considered as the expected proportion for the comparisons, due to uneven sample size between seasons.

To quantify the co–use of resources by both species, we used the dietary overlap index (Pianka, 1973). This index fluctuates between 0 and 1, according to the degree of similarity of consumption of prey (0, no overlap; 1, total overlap). Seasonal variations in the diet of the two predators and the effect of the interaction of one species on the other on their respective diets were analyzed by a hierarchical agglomerative clustering, using Bray–Curtis as an index of similarity. SIMPROF tests were performed to identify groups in these sources of variation. (Clarke et al., 2014). Additionally, multivariate analysis of variant (Permanova) was carried out to test differences between groups (Quinn and Keough, 2002).

To evaluate the effect of the biomass of prey on the trophic spectrum of the two predators, we calculated the geometric mean of the prey (Jaksic and Baker, 1983). Likewise, trophic isoclines were applied (Kruuk and De Kock, 1980), allowing us to determine the importance of each prey based on its location in a graphic layout. This analysis was performed taking all seasons into account. In both cases (geometric mean and isoclines), weights of prey were obtained from Muñoz—Pedreros and Gil (2009) for the case of mammals, and from Norambuena and Riquelme (2014) for birds.

Results

A total of 53 feces and 101 pellets were collected over the study period (table 1). Diet for chilla fox consisted of eight categories: small mammals (cricetid and murid rodents), lagomorphs (*Lepus europaeus*), echimyds (*Myocastor coypus*), reptiles (lizards), birds (Passeriformes), insects, and vegetable matter. Categories varied according to season (fig. 2). When diversity of prey was compared between seasons, the proportions of items varied for seven groups (fig. 3). Differences were non–significant when winter was compared with spring (Pair–wise tests, T = 1.464, p = 0.06), but significant in the other comparisons

(T = 2.428, T = 2.656 for winter vs. summer and spring vs. summer, respectively; p = 0.001 in both cases).

For the barn owl, only six categories of prey were observed, with families of small mammals (Cricetidae and Muridae) predominating and and more pronounced than in the diet of the chilla fox. In terms of diversity, summer was the season with greatest magnitude for chilla fox (table 1). When diversity of prey was compared between seasons, barn owl showed four groups of prey in all seasons (fig. 3), with significant differences between them (Permanova test, Pseudo–F = 5.261; p = 0.001). The proportion of prey differed slightly in both predators in relation to frequency expected across seasons. While in the case of barn owl all categories of prey showed this trend (table 2), in the case of chilla fox only one category of prey was consumed in a random way.

Regarding the differentiation of prey in terms of biomass, during winter and spring the chilla fox (193.17, 485.86 in winter and spring, respectively) showed higher values of geometric mean than barn owl (58.2, 22.73 in winter and spring, respectively). However, in summer there was a change in this pattern; chilla fox had the lowest value for this parameter (23.61, for chilla fox and 36.21 for barn owl). When the weights of prey were analyzed through trophic isoclines, for chilla fox, the lagomorphs were placed above the upper isocline (fig. 4), while the echymids were placed in an intermediate isocline, and small mammals (murids and cricetids) were placed in the lowest isocline. In contrast, for the barn owl we found that two groups, murids and cricetids, were the most highly represented prey located in the intermediate isocline, while birds and arthropods were placed in the lowest isocline (fig. 5). Reptiles were not incorporated in this layout due to their low frequency in all seasons,

The dietary overlap for the different seasons was respectively 0.6, 0.27 and 0.46 for winter, spring,and summer . In these periods, we found a trend of segregation around lagomorphs and rodents. In winter, seven groups of prey consumption were observed, (fig. 6); Pseudo–F = 3.190, p = 0.011), as in spring (Pseudo–F = 7.281, p = 0.001), while in summer, six groups were present (Pseudo–F = 15.873, p = 0.001).

Discussion

The dietary composition for both predators differed in relation to sites with less transformed landscape, where native rodents and marsupials were the most common prey (Martínez et al., 1993; Zúñiga et al., 2008; Muñoz–Pedreros et al., 2016). This finding could be explained by the high degree of habitat loss in the study area, where environmental homogeneity would affect the occurrence of the two species. Both species are present in sites with less human intervention (Muñoz–Pedreros et al., 1990), and their spatial habits are linked to a greater structural complexity (Murúa and González, 1982; Vásquez, 1996). It can be expected that local diversity of prey is affected, with low abundances of native species, such as rodents (Fernández and Simonetti, 2013),

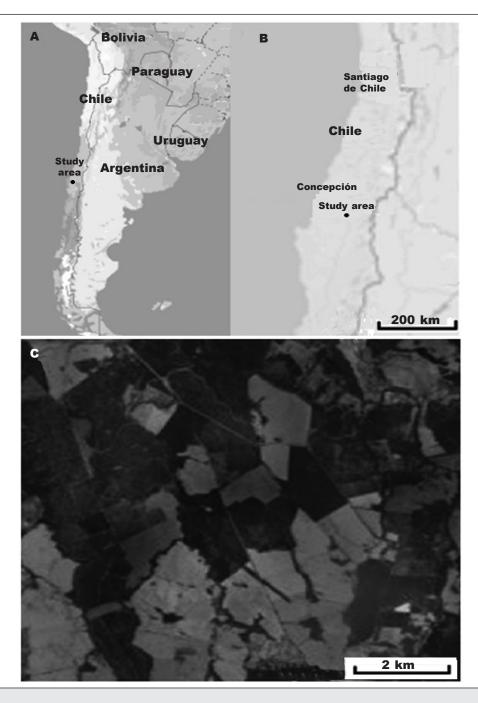


Fig. 1. Study area: A, sub-continental scale; B, regional scale; C, local scale.

Fig. 1. Zona de estudio: A, escala subcontinental; B, escala regional; C, escala local.

and an increase in exotic species, such as murids and lagomorphs (Jaksic et al., 2002). Despite this, patches of native forest scattered throughout the study area could sustain an important source of specialist prey species. This would allow both predators to maintain a diverse profile of food sources, and it emphasizes the importance of conserving these environments in the long term.

The dietary pattern of both species showed diversity across season. Their respective frequency of consumption which would likely be explained by differences in the reproductive patterns of prey. This has been reported in fall for rodents (González and Murúa, 1983) and in spring for birds and insects (Daan et al., 1989; Peña, 1987). It can therefore be expected that the rate of predation will be greater

Table 1. Dietary composition of both predators through the sampled seasons. The columns indicates observed abundance of each prey and their percentage.

Tabla 1. Composición de la dieta de ambos depredadores durante las estaciones estudiadas. En las columnas se indican la abundancia observada de cada presa y su porcentaje.

	Predators						
	Chilla fox				Barn owl		
Prey	Winter	Spring	Summer	Winter	Spring	Summer	
Mammals							
Rodents, Cricetidae							
Abrothrix longipilis	2 (6.89)	1 (3.84)	6 (11.53)	5 (19.23)	7 (13.46)	45 (32.37	
Abrothtix olivaceus	1 (3.44)	_	1 (1.92)	2 (7.69)	6 (11.53)	13 (9.35)	
Oligoryzomys longicaudatus	7 (24.13)	1 (3.84)	1 (1.92)	5 (19.23)	8 (15.38)	21 (15.10)	
Irenomys tarsalis	_	_	-	1 (3.84)	-	_	
Phyllotis darwini	_	_	_	_	-	6 (4.31)	
Rodents, Muridae							
Rattus norvegicus	_	_	-	4 (15.38)	5 (9.61)	10 (7.19)	
Rattus rattus	4 (13.79)	2 (7.69)	7 (13.46)	7 (26.92)	8 (15.38)	25 (17.98	
Rodents, Echymidae							
Myocastor coypus	1 (3.44)	4 (15.38)	_	_	_	_	
Lagomorpha							
Lepus europaeus	8 (27.58)	9 (34.61)	7 (13.46)	_	1 (1.92)	1 (0,71)	
Birds							
Unidentified birds	7 (26.92)	7 (26.92)	8 (15.38)	2 (7.69)	4 (7.69)	5 (3.59)	
Reptiles							
Liolaemus sp.	_	2 (7.69)	_	_	2 (3.84)	_	
Insecta							
Cratomelus armatus	_	_	5 (9.61)	_	10 (19.23)	9 (6.4)	
Brachysternus viridis	_	_	_	_	1 (1.92)	_	
Unidentified insect	_	_	13 (25)	_	_	2 (1.4)	
Vegetables							
Vegetal tissue	-	_	4 (7.6)	-	_	2 (1.43)	
Total scats/pellets	18	18	17	26	27	48	
Dietary breadth (β)	5.8±1.54	4.33±1.77	6.59±1.37	5.82±1.43	8.24±1.08	5.50±2.05	
Standardized niche (Bsta)	0.58	0.55	0.69	0.80	0.65	0.45	

during these seasons. Likewise, the non–random pattern of frequencies of consumption observed in the goodness–of–fit tests illustrated the population changes of the respective types of prey. This finding should be taken with caution, however, and further studies on the demographic pattern of these species in human dominated landscapes are needed. In the case of chilla fox, the high consumption of cricetids in winter increased even further in summer, suggesting continuity in their reproductive dynamics throughout

the seasons. This possibility could be explained by interannual variations in population sizes, where demographic dynamics of rodents can fluctuate year to year (Murúa et al., 1986), expanding periods of greatest abundance, and allowing their greater capture by predators. On the other hand, murids have a broad spatial pattern, with intra–annual reproductive dynamics that would facilitate their consumption over the seasons (King et al., 1996; Douangboupha et al., 2009). Their low frequency of consumption, however,

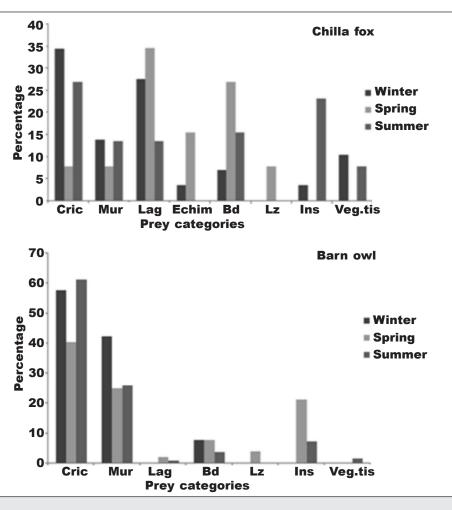


Fig. 2. Percentage representation of the prey captured by chilla fox *Lycalopex griseus* and barn owl *Tyto alba* in the study area, through the sampled seasons, year 2019: Cric, cricetids; Mur, murids; Lag, lagomorphs; Bd, birds; Lz, Lizards; Ins, insects; Veg.tis, vegetable tissues

Fig. 2. Representación del porcentaje de las presas capturadas por el zorro chilla Lycalopex griseus y la lechuza común Tyto alba en la zona de estudio, durante las estaciones estudiadas del año 2019: Cric, cricétidos; Mur, múridos; Lag, lagomorfors; Bd, aves; Lz, lagartos; Ins, insectos; Veg.tis, tejidos vegetales.

could be attributed to changes in the use of space, minimizing the likelihood of encounters.

The consumption of lagamorphs was greater than previously detected (Zúñiga et al., 2018a), suggesting the progressive incorporation of this group into the dietary spectrum with replacement of native prey (Simonetti, 1986; Novaro et al., 2000). This pattern has also been found in other fox species, where periods of trong population growth of hares was linked to high rates of consumption by red foxes (*Vulpes vulpes*) and lower rates of predation on smaller mammals (Goszczyński and Wasileski, 1992). The absence of statistical differences in the frequency of consumption between seasons suggests a certain degree of regular consumption, with a proportion that did not vary along across seasons (Jaksic, 1989). Nevertheless, this observation should be examined

with caution because it is necessary to monitor their abundance. It is important to note that apart from cougar (predators that are occasionally detected in the study area) records of other mammal predators that capture lagomorphs are lacking. Predation pressure on lagomorphs could be low due to the low number of predators, which would account for a low impact on its population size and allowing chilla fox to consume them with frequency across the the seasons. Reports on the demographic fluctuation of hares during inter—annual periods (Wasilewski, 1991; Sokos et al., 2016) makes it necessary to systematically monitor hare populations so as to determine how the trophic response of chilla fox is affected.

Seasonal variation in the diet of the barn owl also showed changes in the composition of prey, although their dependence on small mammals was

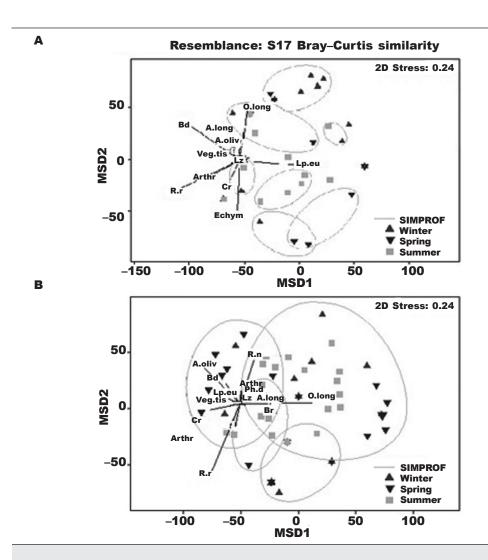


Fig. 3. Dissimilarities represented by Metric multidimensional scaling (MDS) between the types of prey consumed seasonally by chilla fox *Lycalopex griseus* (A) and barn owl *Tyto alba* (B): A.long, *A. longipilis*; A.oliv, *A. olivaceus*; Arthr, arthropods; Bd, birds; Br, *Brachisternus viridis*; Cr, *Cratomelus armatus*; Echym, Echymids; Lp.eu, *Lepus europaeus*; Lz, lizards; O.long, *Oligoryzomys longicaudatus*; Ph.d, *Phyllotis darwini*; R.n, *Rattus norvegicus*; R.r, *Rattus rattus*; Veg.tis, vegetable tissue.

Fig. 3. Diferencias representadas mediante el escalamiento multidimensional métrico (MDS en su sigla en inglés) entre los tipos de presa consumidos de forma estacional por el zorro chilla Lycalopex griseus (A) y la lechuza común Tyto alba (B): A.long, A. longipilis; A.oliv, A. olivaceus; Arthr, artrópodos; Bd, aves; Br, Brachisternus viridis; Cr, Cratomelus armatus; Echym, equímidos; Lp.eu, Lepus europaeus; Lz, lagartos; O.long, Oligoryzomys longicaudatus; Ph.d, Phyllotis darwini; R.n, Rattus norvegicus; R.r, Rattus rattus; Veg.tis, Tejido vegetal.

more marked, as evidenced in the high frequency of capture. Even though barn owl consumption of cricetidae was consistent with previous reports (Correa and Roa, 2005; Zúñiga et al., 2018b), differences were observed in terms of diversity across seasons. These differences could be explained by the incorporation of other groups of cricetids associated with native forest. This is the case of the mice Chilean *Irenomys tarsalis* and *Phyllotis darwini*, which are in the limit of southern distribution (Muñoz–Pedreros

and Gil, 2009). However, their abundances reflect a low contribution to the total dietary spectrum. It is therefore necessary to determine the population dynamics of these two species to understand their real contribution across seasons. On the other hand, the appearance of murids in the diet would be associated with opportunistic feeding behavior on small rodents due to the occurrence of this group in sites with low forest cover (Teta et al., 2012). The low consumption of hares would be explained by their size. The fact

Table 2. Values of chi–square analysis (χ^2) and their respective statistical significance (p) for comparisons of frequencies of prey consumption through the seasons surveyed.

Tabla 2. Valores del análisis de la χ^2 y su significación estadística (p) respectiva para comparaciones de frecuencias de consumo de presas durante las estaciones estudiadas.

	Chi	lla fox	Ва	Barn owl	
	χ^2	р	χ^2	р	
Cricetids	17.47	0.0002	53.33	< 0.0001	
Murids	15.23	0.0005	35.67	< 0.0001	
Lagomorphs	1.81	0.404	121.65	< 0.0001	
Echymids	47.57	< 0.0001	_	-	
Birds	17.17	0.0002	61.47	< 0.0001	
Arthropods	104.94	< 0.0001	73.65	< 0.0001	

that they are usually larger than this raptor (Pavez, 2004) suggests an age-based segregation for their capture, with juveniles being more vulnerable, as has been reported for rabbits (*Oryctolagus cuniculus*) in Central Chile (Simonetti and Fuentes, 1983).

Differences in the co—use of resources between the two predators across the seasons account for changes in responses used under a scenario of fluctuation of resources, where prey size appeared to be an important factor to minimize trophic overlap. Likewise, although the relatively high trophic overlap observed in winter suggests that small mammals were a critical resource for both species, consumption of larger prey seems to favor the partitioning of resources. The presence of lagomorphs in the upper isocline in the case of chilla fox highlights the importance of this prey in

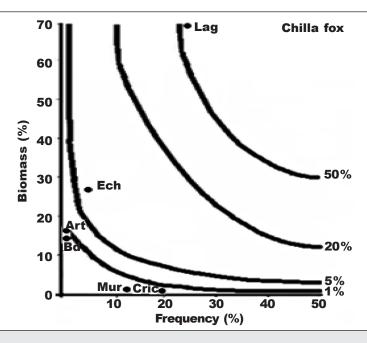


Fig. 4. Trophic isoclines for prey consumed by chilla fox *Lycalopex griseus* in the study area: Art, arthropods; Bd, birds; Cric, cricetids; Ech, echymids; Lag, lagomorphs; Mur, murids.

Fig. 4. Isoclinas tróficas de las presas consumidas por el zorro chilla Lycalopex griseus en la zona de estudio: Art, artrópodos; Bd, aves; Cric, cricétidos; Ech, equímidos; Lag, lagomorfos; Mur, múridos.

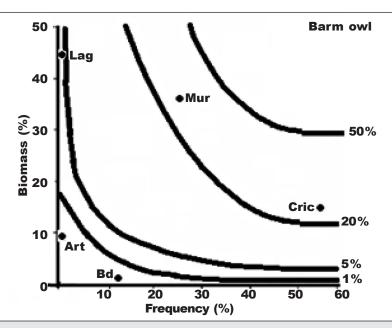


Fig. 5. Trophic isoclines for prey consumed by Barn owl *Tyto alba* in the study area: Art, arthropods; Bd, birds; Cric, cricetids; Lag, lagomorphs; Mur, murids.

Fig. 5. Isoclinas tróficas de las presas consumidas por la lechuza común Tyto alba en la zona de estudio: Art, artrópodos; Bd, aves; Cric, cricétidos; Lag, lagomorfos; Mur, múridos.

the trophic spectrum, considering that the weight of *L*. europaeus is greater than the rest. On other hand, the presence of Myocastor coypus, whose size is about to 10 kg (Muñoz-Pedreros and Gil 2009), similar to chilla fox, suggests that these records would be the resultof scavenging. Such scavenging can be explained by the occasional presence of Puma concolor (60 kg) in the study area, which has consumption reports of M. coypus (Iriarte and Jaksic, 2012; Zúñiga and Muñoz-Pedreros, 2014), contributing therefore to the food subsidy of other predators (Wilson and Wollkowich, 2011). In the case of the barn owl, the presence of both murid and cricetid rodents in the intermediate isocline accounts for the importance of both these groups in the diet, despite their different spatial habits. This can be explained due to the energy requirements of the barn owl -a minimum of 55g/day (Hamilton and Neill, 1981)- and its flexibility to capture rodents, with variations in selectivity of species according to seasonal availability (Tores et al., 2005). It should also be noted, however, that although both predators consumed arthropods, the taxonomic level achieved may be underrepresentative of the supply in the environment (Greene and Jaksic, 1983); caution is therefore called for regarding the diversity in types of prey (Peña, 1987).

The use of space is a key aspect in the ecological differentiation of the two predators. The lower number of feces of chilla fox collected in relation to barn owl pellets suggests that this canid uses the agroecosystem in a marginal way, with extensive roaming in

search of food in sites adjacent to the study area. This possibility is supported by reports that account for a low frequency of use of this habitat, in relation to native forest and commercial plantations (Zúñiga et al., 2009) and their home range (Silva–Rodríguez et al., 2010). In contrast, barn owl have a greater degree of territoriality than chilla fox because their home range smaller (Tomé and Valkarna, 2001; Hafdzi et al., 2003). Particularities about the type of movement associated with their hunting activities (Massa et al., 2015) could favor a finer degree of differentiation between the two predators.

The low geometric mean observed for chilla fox in summer has its minimum value in relation to other seasons, showing noticeable decrease in the size of the prey consumed. This could be due to low availability of large prey, compensated only by a high consumption of arthropods. This illustrates the different strategies of the two predators. This diet is considered as suboptimal for the species because its low biomass contribution would not support its energy requirements, as has been reported for its congeneric culpeo fox, Lycalopex culpaeus (Silva et al., 2005). The low abundance of rodents suggests the forced displacement of chilla fox towards patches with greater availability of resources. Considering that the study area is a mosaic of agricultural landscape with forest plantations and native forest, there is a high probability that these canids may converge with domestic dogs. which could interfere in their spatio-temporal patterns (Silva-Rodríguez et al., 2010). Knowledge about the

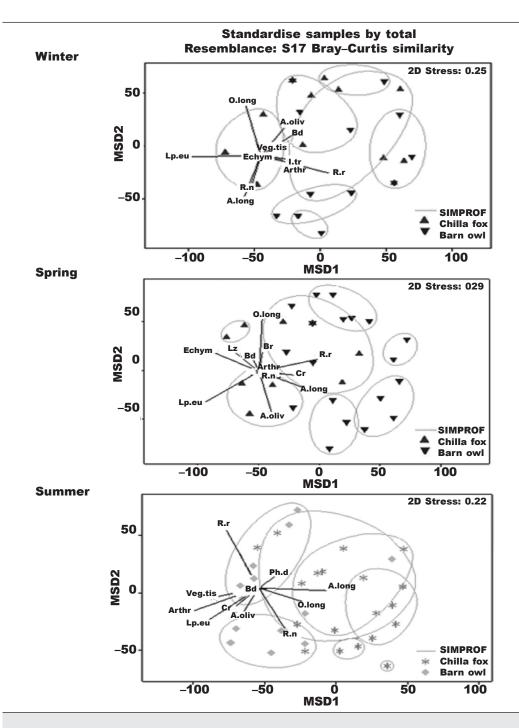


Fig. 6. Dissimilarities represented by Metric multidimensional scaling (MDS) between the types of prey consumed by chilla fox *Lycalopex griseus* and barn owl *Tyto alba* (both species together) in the study area, across the seasons surveyed: A.long, *A. longipilis*; A.oliv, *A. olivaceus*; Arthr, arthropods; Bd, birds; Br, *Brachisternus viridis*; Cr, *Cratomelus armatus*; Echym, echymids; I.tr, *I. tarsalis*; Lp.eu, *Lepus europaeus*; Lz, lizards; O.long, *Oligoryzomys longicaudatus*; Ph.d, *Phyllotis darwini*; R.n, *Rattus norvegicus*; R.r, *Rattus rattus*; Veg.tis, vegetable tissue.

Fig. 6. Diferencias representadas mediante el escalamiento multidimensional métrico (MDS en su sigla en inglés) entre los tipos de presa consumidos por el zorro chilla Lycalopex griseus y la lechuza común Tyto alba (ambas especies juntas) en la zona de estudio, en las estaciones estudiadas: A.long, A. longipilis; A.oliv, A. olivaceus; Arthr, arthropods; Bd, birds; Br, Brachisternus viridis; Cr, Cratomelus armatus; Echym, echymids; I.tr, I. tarsalis; Lp.eu, Lepus europaeus; Lz, lizards; O.long, Oligoryzomys longicaudatus; Ph.d, Phyllotis darwini; R.n, Rattus norvegicus; R.r, Rattus rattus; Veg.tis, tejido vegetal.

spatial ecology in this area, considering the potential conflict due to the proximity to human settlements, is of special importance for the implementation of conservation strategies. In conclusion, although the two studied species shared a high proportion of prey species, their rate of consumption varied over the seasons in the study period. Differences in abundance of prey, added to the particularities of the predators' use of space, resulted in variations in the trophic overlapping. Future research should focus on whether the selectivity pattern differs between the two species.

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References

- Armesto, J., Villagrán, C., Arroyo, M. K., 1995. *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago de Chile.
- Benton, T. G., Vickery, J. A., Wilson, J. D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, 18: 182–188.
- Carmona, E. R., Rivadeneira, M. M., 2006. Food habits of the barn owl *Tyto alba* in the National Reserve Pampa del Tamarugal, Atacama Desert, North Chile. *Journal of Natural History*, 40: 473–483.
- Chame, M., 2003. Terrestrial mammal feces: a morphometric summary and description. *Memoriás do Instituto Oswaldo Cruz*, 98: 71–94.
- Clarke, K., Gorley, R., Somerfield, P., Warwick, R., 2014. Changes in marine communities: an approach to statistical analysis and interpretation. Primer–E Ltd. Lutton, Ivybridge.
- Colwell, R., Futuyma, J., 1971. On the measurement of niche breadth and overlap. *Ecology*, 52: 567–572.
- Correa, P., Roa, R., 2005. Relaciones tróficas entre Oncifelis guigna, Lycalopex culpaeus, Lycalopex griseus y Tyto alba en un ambiente fragmentado de la zona central de Chile. Mastozoología Neotropical, 12: 57–60.
- Crooks, K. R., 2002. Relative sensibilities of mammalian carnivores to habitat fragmentation. Conservation Biology, 16: 488–502.
- Daan, S., Dijkstra, C., Drent, R., Meijer, T., 1989. Food supply and the annual timing of avian reproduction.
 In: Proceedings 19th International Ornithology Congress: 392–407 (H. Ouellet, Ed.). Ottawa, Canada.
- 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.
- Di Castri, F., Hajek, E., 1976. *Bioclimatología de Chile*. Ediciones Universidad Católica de Chile, Santiago de Chile.
- Douangboupha, B., Brown, P. R., Khamphoukeo, K., Paplin, K., Singleton, G. R., 2009. Population dynamics of Rodent prey species in upland farmings of Lao PDR. *Kasetsart Journal*, 43: 125–131.

Drouilly, M., Nattrass, N., O'Riain, M. J., 2018. Dietary niche relationships among predators on farmland and a protected area. *Journal of Wildlife Management*, 82: 507–518.

- Fedriani, J. M., 1997. Relaciones interespecíficas entre el lince ibérico, Lynx pardinus, el zorro, Vulpes vulpes, y el tejón, Meles meles, en el Parque Nacional Doñana. Tesis doctoral, Universidad de Sevilla.
- Fernández, I., Simonetti, J., 2013. Small mammal assemblages in fragmented shrublands of urban areas of Central Chile. *Urban Ecosystems*, 16: 377–387.
- Ferreira, A. L., Peres, C. A., Cassano, C. R., 2018. Use of agroecosystem matrix habitats by mammalian carnivores (Carnivora): a global–scale analysis. *Mammal Review*, 48: 312–327.
- Gajardo, R., 1994. La vegetación natural de Chile, clasificación y distribución geográfica. Editorial Universitaria, Santiago de Chile.
- Gittleman, J., 1985. Carnivore body size: ecological and taxonomical correlates. *Oecologia*, 67: 540–554.
- González, L., Murúa, R., 1983. Características del periodo reproductivo de tres roedores cricétidos del bosque higrófilo templado. *Anales del Museo de Historia Natural*, 16: 87–99.
- Goszczyński, J., Wasileski, R., 1992. Predation of foxes on a hare population in central Poland. *Acta Theriologica*, 31: 329–338.
- Greene, H. W., Jaksic, F. M., 1983. Food–niche relationships among sympatric predators: effects of level of prey identification. Oikos, 40: 151–154.
- Hafdizi, M. N., Hamzah, M. H., Jamaluddin, 2003. Ranging behavior of *Tyto alba* in ricefield from radio telemetry studies. *Journal of Malasyan Biology*, 32: 47–51.
- Hairston, N. G., Smith, F. E., Slobodkin, L. B., 1960. Community structure, population control, and competition. *American Naturalist*, 94: 421–425.
- Hamilton, K. L., Neill, R. L., 1981. Food habits and bioenergetics of a pair of barn owls and owlets. *American Midland Naturalist*, 106: 1–9.
- Iriarte, J. A., Jaksic, F., 2012. Los carnívoros de Chile. Flora and Fauna/CASEB Ediciones, Santiago de Chile.
- Jaksic, F. M., 1989. Opportunist, selective, and other often–confused terms in the predation literature. Revista Chilena de Historia Natural, 62: 7–8.
- Jaksic, F., Braker, F., 1983. Food–niche relationships and guild structure of birds of prey: competition vs. opportunism. *Canadian Journal of Zoology*, 61: 2230–2241.
- Jaksic, F. M., Iriarte, J. A., Jiménez, J. E., Martínez, D. R., 2002. Invaders without frontiers: cross–border invasions of exotic mammals. *Biological Invasions*, 4: 157–173.
- 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. *Medio Ambiente*, 8: 95–103.
- Jaksic, F. M., Silva, S. I, Meserve, P. L., Gutiérrez, J. R., 1996. A long–term study of vertebrate responses to an El Niño (ENSO) disturbance in western

- South America. Oikos, 78: 351-354.
- 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.
- 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, 20: 215–240.
- Kruuk, H., De Kock, L., 1980. Food and habitat of badgers (*Meles meles* L.) on Monte Baldo, northern Italy. *Zeitschrift fur Saugertierkunde*, 46: 295–301.
- Levins, R., 1968. *Evolution in changing environments*. Princeton University Press, New Jersey.
- Martínez, D. R, Rau, J. R., Murúa, R. E., Tillería, M., 1993. Depredación selectiva de roedores por zorros chillas (*Pseudalopex griseus*) en la pluviselva valdiviana, Chile. *Revista Chilena de Historia Natural*, 66: 419–426.
- Massa, C., Gabelli, F. M., Cueto, G. R., 2015. Using GPS tracking to determine movement patterns and foraging habitat of the common barn–owl (*Tyto alba*). *Hornero*, 30: 7–12.
- Meserve, P. L., Martínez, D. R., Rau, J. R., Murúa, R., Lang, B. K., Muñoz–Pedreros, A., 1999. Comparative demography and diversity of small mammals in precordilleran temperate rainforests of Southern Chile. *Journal of Mammalogy*, 80: 880–890.
- Morin, P., 2011. *Community Ecology*. Wiley–Blackwell, Sussex.
- Muñoz-Pedreros, A., 2010. Huellas y signos de mamíferos de Chile. CEA Ediciones, Valdivia.
- Muñoz-Pedreros, A., Gil, C., 2009. Orden rodentia. In: *Mamíferos de Chile*: 93–157 (A. Muñoz-Pedreros, J. Yáñez, Eds.). CEA Ediciones, Valdivia.
- Muñoz-Pedreros, A., Gil, C., Yáñez, J., Rau, J. R., Möller, P., 2016. Trophic ecology of two raptors, Barn owl (*Tyto alba*) and White-tailed kite (*Elanus leuc*urus), and possible implications for biological control of hantavirus reservoir in Chile. *The Wilson Journal of Ornithology*, 128: 391–403.
- Muñoz-Pedreros, A., Murúa, R., González, L., 1990. Nicho ecológico de micromamíferos en un agroecosistema forestal de Chile Central. Revista Chilena de Historia Natural, 63: 267–277.
- Muñoz-Pedreros, A., Rau, J., 2004. Estudios de egagrópilas en aves rapaces. In: Aves rapaces de Chile: 265-279 (A. Muñoz-Pedreros, J. Yáñez, Eds.), CEA Ediciones, Valdivia.
- Muñoz-Pedreros, A., Yáñez, J., Norambuena, H. V., Zúñiga, A., 2018. Diet, dietary selectivity and density of South american grey fox, Lycalopex griseus, in Central Chile. Integrative Zoology, 13: 46–57.
- Murúa, R., González, L., 1982. Microhabitat selection in two Chilean cricetid rodents. *Oecologia*, 52: 12–15.
- Murúa, R., González, L. A., Meserve, P. L., 1986. Population ecology of *Oryzomys longicaudatus philipii* (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.
- Novaro, A., Funes, M. C., Walker, R. S., 2000. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. *Biological Conservation*, 73: 143–150.
- Olff, H., Ritchie, M. E., 2002. Fragmented nature: consequences for biodiversity. *Landscape and Urban Planning*, 58: 83–92.
- Olifiers, N., Gentile, R., Fiszon, J. T., 2005. Relation between small–mammal species composition and anthropic variables in the Brazilian Atlantic forest. *Brazilian Journal of Biology*, 65: 495–501.
- Pavez, E., 2004. Descripción de las aves rapaces chilenas. In: Aves rapaces de Chile: 29–103 (A. Muñoz–Pedreros, J. Yáñez., Eds.). CEA Ediciones, Valdivia.
- Pearson, O., 1995. Annotated keys on near Nahuel Huapi National Park on near Lanin National Park, Southern Argentina. *Mastozoología Neotropical*, 2: 99–148.
- Peña, L., 1987. *Introducción al estudio de los insectos de Chile*. Editorial Universitaria, Santiago de Chile.
- Quinn, G. P., Keough, M. J., 2002. Experimental design and data analysis for biologists. Cambridge University Press, New York.
- Pianka, E., 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics*, 4: 53–74.
- Rathcke, B., Placey, E., 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, 16: 179–214.
- Rau, J., 2000. Métodos de ecología trófica. In: *Mamíferos de Chile*: 397–406 (A. Muñoz–Pedreros, J. Yáñez, Eds.). CEA Ediciones, Valdivia, Chile.
- Reise, D., 1973. Claves para la determinación de los cráneos de marsupiales y roedores chilenos. *Gayana*, 27: 1–20.
- Root, R. B., 1967. The niche exploitation pattern in the blue–gray gnatcatcher. *Ecological Monographs*, 37: 317–350.
- Schoener, T. W., 1974. Resource partitioning in ecological communities. *Science*, 185: 27–39, Doi: 10.1126/science.185.4145.27
- 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.
- Silva–Rodríguez, E. A., Ortega–Solís, G., Jiménez, J. E., 2010. Conservation and ecological implications of the use of space by chilla foxes and free–ranging dogs in a human–dominated landscape in southern ecology. *Austral Ecology*, 35: 765–777.
- Simonetti, J. A., 1986. Human–induced dietary shift in *Dusicyon culpaeus*. *Mammalia*, 50: 406–408.
- Simonetti, J. A., Fuentes, E. R., 1983. Microhabitat use by European rabbits (*Oryctolagus cuniculus*) in Central Chile: are adults and juvenile pattern the same? *Oecologia*, 54: 55–57.
- Simonetti, J. A., Poiani, A., Raedeke, K. J., 1984. Food habits of *Dusicyon griseus* in Northern Chile. *Journal of Mammalogy*, 65: 515–517.
- Sokal, R. R., Rohlf, F. J., 1995. 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.

- Teta, P., C. Hercolini, C., Cueto, G., 2012. Variation on the diet of the western barn owls (*Tyto alba*) along an urban–rural gradient. *The Wilson Journal of Ornithology*, 124: 589–596, Doi: 10.2307/23324567
- Tomé, R., Valkarna, J., 2001. Seasonal variation in the abundance and habitat use of barn owls *Tyto alba* on lowland farmland. *Ornis Fennica*, 78: 109–118.
- Tores, M., Motro, Y., Motro, U., Yom–Tov, Y., 2005. The barn owl a selective opportunistic predator. *Israel Journal of Zoology*, 51: 349–360.
- Vásquez, R. A., 1996. Patch utilization by three species of Chilean rodents differing in body- size and mode of locomotion. *Ecology*, 77: 2343–2351.
- Wasilewski, M., 1991. Population dynamics of the European hare *Lepus europaeus* Pallas, 1778 in Central Poland. *Acta Theriologica*, 36: 267–274.
- Weather Spark, 2020. *El clima promedio de Mulchén*, https://es.weatherspark.com/y/25133/Clima-promedio-en-Mulch%C3%A9n-Chile-durante-todo-el-a%C3%B1o [Accessed on July 1st, 2020].
- Wiens, J., 1977. On the competition and variable environments. *American Scientist*, 65: 590–597.

Wilson, E. E., Wollkowich, E. M., 2011. Scavenging: how carnivore and carrion structure communities. *Trends in Ecology and Evolution*, 26: 129–135.

- Zapata, S. C., Travaini, A., Ferreras, P., Delibes, M., 2007. Analysis of trophic structure of two carnivore assemblages by means of guild identification. *European Journal of Wildlife Research*, 53: 276–286.
- Zúñiga, A., 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., Muñoz-Pedreros, A., Fierro, A., 2008. Dieta de *Lycalopex griseus* (Gray, 1837) (Mammalia: Canidae) en la depresión intermedia del sur de Chile. *Gayana*, 72: 113–116.
- 2009. Uso de hábitat de cuatro carnívoros terrestres en el sur de Chile. Gayana, 73: 200–210.
- Zúñiga, A. H., Fuenzalida, V., Sandoval, R., 2018a. Diet of South american grey fox *Lycalopex griseus* in an agroecosystem of southern central Chile. *Therya*, 9: 179–183.
- 2018b. Hábitos alimentarios de la lechuza blanca Tyto alba en un agroecosistema del centro–sur de Chile. Ecología en Bolivia, 53: 7–15.
- 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.