



Commentary

Ecology of the culpeo (*Lycalopex culpaeus*): a synthesis of existing knowledge

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Abstract

We conducted an extensive review of the existing literature on the culpeo to improve our understanding of its ecology, natural history and conservation, and to identify gaps in current knowledge. For resources published before 1988, we used the synthesis made by Medel and Jaksic (1988). For studies published from 1988 onwards, we carried out a literature searching in the Scopus, Web of Knowledge and Google Scholar databases, considering all of the generic names used to define the species. We found 96 scientific articles. Most of the studies focused on diet, conflicts with the species in livestock areas, and on the use of space and habitat. We found that the description of subspecies is incomplete and that subspecies' geographic distribution is not well known. There are also few published studies on genetic issues, population dynamics and conservation concerns. It is remarkable that vast regions in South America where culpeos live still lack basic information on the species. Diet studies describe a marked trend towards resource selection at the local level, which supports the view of the culpeo as a facultative trophic specialist. In addition, it has been confirmed that in the high Andes, the culpeo can behave as a top predator and that it is an important seed disperser in arid environments. There is no sufficient information to precisely assess the species' conservation status in most regions. The species has been listed as "Vulnerable" in Ecuador and Colombia. Direct persecution and habitat transformation are the most critical threats that the species faces in many countries, although other threats such as climate change could also have severe consequences for the culpeo on a global scale.

Introduction

The culpeo (*Lycalopex culpaeus*), also called Andean fox, red fox or páramo wolf, is the second-largest canid in the South American continent, with adults weighing up to 14 kg (Jiménez et al., 1995; Jiménez and Novaro, 2004). Body size presents sexual dimorphism, with males being larger than females (Johnson and Franklin, 1994a,b; Novaro, 1997a; Travaini et al., 2000a). The culpeo is a solitary canid except in the breeding season when both sexes take care of the cubs (Johnson and Franklin, 1994a). They generally have one litter per year of three to five cubs. These become sexually mature adults at seven months of age (Crespo and de Carlo, 1963). There are few records on population sex ratio: for Argentina, Crespo and de Carlo (1963) found a ratio of 0.69 females per male, while (Novaro, 1995) reported a ratio of 0.92 per male.

The culpeo is present from southern Colombia to Tierra del Fuego, following the Andes range (Fig. 1). Globally, the International Union for Conservation of Nature and Natural Resources (IUCN) has classified the culpeo as "Least Concern". However, the degree of threat differs among countries (Lucherini, 2016) and is listed as "Vulnerable" in some of them, such as Ecuador and Colombia (Tirira, 2011; MADT, 2014). However, field studies of the culpeo are concentrated in a few regions of its wide distribution range (see Fig. 1), and there are vast geographical areas for which there is no data on the species. We also show that information on its ecology is sometimes unclear and contradictory (for example, concerning distribution patterns, see below), which may reflect a significant degree of plasticity in the ecology of

the culpeo or just a lack of knowledge. In any case, the lack of information and geographical bias make it difficult to have a good picture of the species' biology and correctly assess the status of its populations and their conservation threats.

The main goal of this work is to compile the existing information for the species throughout its range, to derive from the most informative reports new general patterns in the ecology, behavior and conservation status of the culpeo. Finally, we identify the most critical knowledge gaps and propose new research lines to better understand the biology of the species and its management implications.

Methods

We conducted a systematic review of the existing literature for the species, including scientific articles, book chapters and relevant web resources. For the research information published before 1988, we used the report by Medel and Jaksic (1988), and for that one published between 1988 and 2019, we used "Web of Knowledge", "Google Scholar" and "Scopus" search engines. Bibliographic searches included the terms: culpeo, *Lycalopex culpaeus*, Andean fox, red fox, páramo wolf, as well as *Dusicyon culpaeus* and *Pseudalopex culpaeus* (i.e. the two names that have been used to describe the species before).

Then, those articles focused mainly on culpeos were classified according to dealt topics into five basic categories: biometric studies (those reporting body measurements), diet studies (those describing food items), ecology studies (those related to habitat use, activity patterns, interactions and population dynamics), taxonomy and evolution studies (those considering evolutionary issues), and finally conservation studies (those related to threats and conservation concerns). Given

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Table 1 – Number of articles focused on the culpeo (*Lycalopex culpaeus*), published between 1988 and 2019, providing information for each ecoregion and country.

Ecoregion	N. articles per ecoregion
Atacama desert	2
Beni sabana	1
Bolivian montane dry forests	1
Bolivian Yungas	1
Central Andean puna/dry/wet puna	11
Chilean Matorral	17
Cordillera Central páramo	2
Dry Chaco	3
Low Monte	3
Magellanic subpolar forests	8
Northern Andean páramo	1
Northwest Andean montane forests	5
Patagonian steppe	14
Sechura desert	2
Ucayali moist forests	1
Valdivian temperate forests	18

Country	N. articles per country
Argentina	39
Bolivia	9
Chile	38
Colombia	2
Ecuador	8
Peru	4

that several articles dealt with various topics, each study could be classified into more than one category. In addition, we calculated the number of articles providing information for each country, topic category and ecoregion (this last, according to Olson et al., 2001).

To identify different diet types of culpeos, we performed a cluster analysis with the main trophic groups described in the literature. Previously, we selected a set of 17 reports providing enough data for 19 representative independent samples (i.e. sites or habitat types). To be selected for analyses, sample sizes had to be higher than 30 (Lozano et al., 2006). Moreover, diet data were recalculated to relative frequency of prey (RF) and expressed as a percentage to allow for comparisons among studies. Prey items were grouped into the following ten trophic groups: invertebrates, herptiles (reptiles and amphibians), birds, eggs, small mammals (weighing less than 300 g), lagomorphs, big rodents, large herbivores (deer, camelids and livestock), edentates (i.e. armadillos), and carnivorous species (i.e. carnivores and meat-eating marsupials). Finally, we used Kruskal-Wallis tests to test for differences in the consumption of the main trophic groups among biomes. Statistical analyses were performed using Statistica 10 (StatSoft, 2011).

Results

In total, we found 109 scientific publications (96 being articles and the rest grey literature), most of them from Argentina and Chile (Tab. 1). A complete list of the 96 revised articles, with information on the country, topics covered, ecoregions, biomes and habitat types (according to authors), can be found in Tab. S1 (Supplementary Material). Articles are shown in Fig. 1 arranged according to the geographical origin of the studied samples and the main topics considered. Their study regions are not evenly represented and there are vast regions with scarce information, especially in the northernmost areas of the culpeo range and the corresponding countries (Tab. 1, Fig. 1).

Regarding the topics dealt with in the articles, diet and ecology studies were the most abundant. Diet studies (40 articles) comprised descriptive and comparative diet reports, as well as others discussing the role of culpeo as a seed disperser (Fig. 1). A similar number of studies on culpeo ecology (40 articles) were found describing the use of habitat and space, ecological interactions and population variation. There are

also studies (28 articles) that relate to the conservation of the species, focusing mainly on conflicts that arise from the interaction of culpeos with livestock. Furthermore, there are some studies on taxonomy and evolution of South American canids (11 articles) and only a few biometric studies (7 articles).

Regarding ecoregions, culpeos have been mainly studied in Valdivian temperate forests, Chilean Matorral and Patagonian steppes (Tab. 1). There are a moderate number of studies in the Puna and Magellanic subpolar forests compared to other ecoregions. With all, the number of studies is very low (less than 6) for the majority of South American ecoregions (see Tab 1).

Geographical distribution and taxonomy

The culpeo is distributed across South America, covering a wide latitudinal gradient (see Fig. 1) that goes from southern Colombia (Ramírez-Chaves et al., 2013) through the Andean mountain range to the Patagonian plains of Tierra del Fuego in Argentina (Cabrera and Yepes, 1960; Langguth, 1975; Novak and Paradiso, 1983; Redford and Eisenberg, 1992), also reaching the islands of the far south (Markham, 1971). It is also present on the Pacific and Atlantic coasts of Peru and Chile (Jaksic et al., 1980, 1992; Meserve et al., 1987; Medel and Jaksic, 1988; Marquet et al., 1993; MINAM, 2011), reaching 4800 meters above sea level (m a.s.l.) in the Andes (Jiménez et al., 2008). The presence of the species in eastern Patagonia is considered recent, favored by the abundance of introduced European hares (*Lepus europeus*) and sheep (Zapata et al., 2005), as well as by the low density of pumas (*Puma concolor*) (Lucherini and Zapata, 2012).

The average size of adult specimens varies throughout the range. In southern Peru, females weigh between 4–5 kg and males around 9 kg

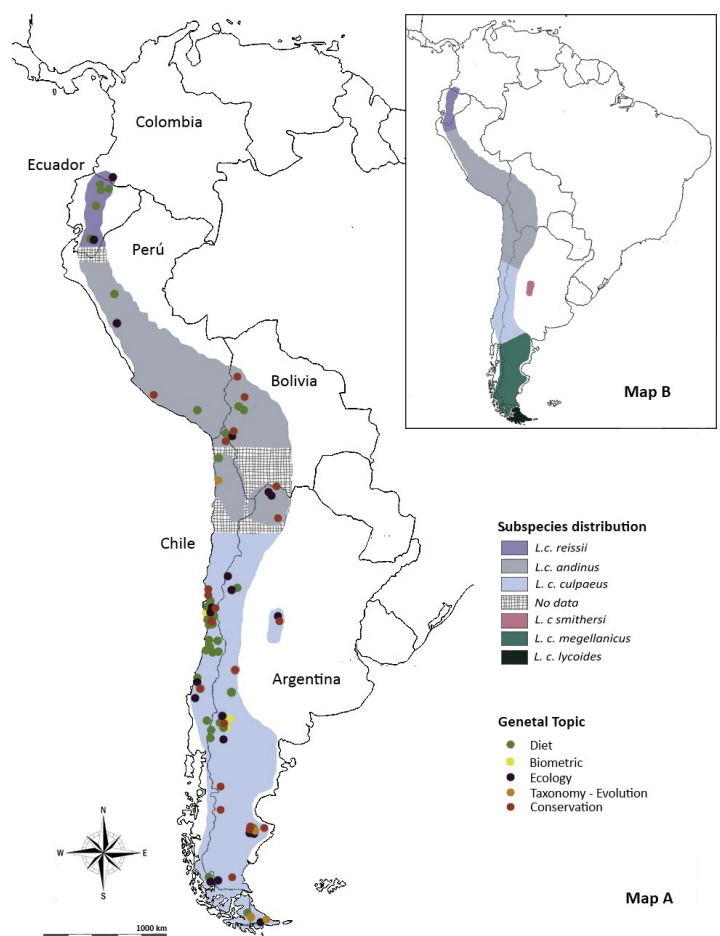


Figure 1 – Map of the proposed distribution of culpeo subspecies based on studies by Guzmán et al. (2009) (Map A), and distribution area for the species defined by Lucherini (2016) (Map B). The location of the area where the studies published were conducted between 1988 and 2019 as well as the type of study, are also shown in Map A.

(Person 1951, in MINAM, 2011), and in northern Chile the average adult weight is only 4–6 kg (Jiménez et al., 1995; Jiménez and Novaro, 2004), apparently increasing towards the southernmost latitudes (Fuentes and Jaksic, 1979). It has been suggested that size variation in the culpeo varies with regional prey availability, shrinking with decreasing prey availability (Meserve et al., 1987). It has also been proposed that the size increase towards the south of its distribution may be an evolutionary response to the partition of resources (that is, avoidance of interspecific competition) in those areas where the culpeo is sympatric with the chilla (*Lycalopex griseus*) (Fuentes and Jaksic, 1979; Meserve et al., 1987; Johnson, 1992). However, it could also be the result of adaptations to the cold weather conditions of southern regions and high-altitude ecosystems (Jiménez et al., 1995, see also Novaro, 1997a). Nevertheless, it has been shown that skull size follows the Bergmann's rule, and that the spatial differentiation of populations can be driven at the same time by environmental factors and neutral evolutionary processes (see Martínez et al., 2018).

Currently, there is a high diversity of canids in South America, totaling 11 species (Wilson and Mittermeier, 2009). The genus *Lycalopex* radiated fast and recently, with a common ancestor living between 1–1.6 million years ago (Perini et al., 2010; Tchaicka et al., 2016). Phylogenetic analyses and molecular data have estimated that the culpeo and the chilla diverged only 350000 years ago (Tchaicka et al., 2016). Adaptations to climatic variations and interspecific competition seem to be the main driver of the diversification of the group (De Moura Bubadué et al., 2016). Thus, factors such as glacier expansion and retraction (Perini et al., 2010), variation in the extent of solitary hunting behavior, opportunistic behavior, and a great diversity of resources could explain the diversification of this group of carnivores, which was not affected by the collapse of ungulate populations that occurred on the continent during the Pleistocene (Berta, 1987).

On the culpeo genus

The culpeo was described by Molina (1782) and named as *Canis culpaeus*, without establishing a holotype nor referencing the material studied (see Guzmán et al., 2009). Two centuries later, Burmeister added the genera *Lycalopex* and *Pseudalopex* to the South American canid species. Berta (1987) relied on the fossil record and cladistic analysis to assign the culpeo species to the genus *Pseudalopex*, which is now considered a paraphyletic group. Later, Zunino et al. (1995) used morphological criteria, to reclassify the species and grouped the genera *Pseudalopex* and *Lycalopex* into a single monophyletic clade where the term *Lycalopex* had priority. These conclusions were later supported by phylogenetic analyses applied to a large number of carnivorous species as well as by recent DNA-based molecular studies (Bininda-Emonds et al., 1999; Zrzavý and Řičánková, 2004; Chaves et al., 2012; Rodríguez-Castro et al., 2018).

Other studies (see Thomas 1914, Cabrera 1958, in Wozencraft, 2005) classified the culpeo in the genus of *Dusicyon* (Smith 1839), although this genus is considered distantly related to *Lycalopex* by several authors (Bininda-Emonds et al., 1999; Slater et al., 2009; Austin et al., 2013). However, Perini et al. (2010) still suggest that *L. culpaeus* and the extinct guará (*Dusicyon australis*) may be congeneric species, in which case the generic name *Dusicyon* would be more appropriate for culpeo.

Culpeo subspecies

Within the species *L. culpaeus*, dental and cranial morphological criteria (see also for ontogenetic issues Segura and Prevosti, 2012; Segura, 2013), as well as coat colour, have been used to differentiate subspecies often with few type specimens (Novaro, 1997a; Guzmán et al., 2009). In the taxonomic listing of Cabrera (1931) six subspecies of culpeo were recorded and proposed. The work of Wozencraft (2005), based on morphometric and distribution criteria, supports the existence of the same six subspecies (see Fig. 1):

1. *L. c. culpaeus*, is presumably the subspecies described by Molina (1782), although there is no type specimen. It is commonly called culpeo fox or red fox. The skull and snout are longer than the rest

of the subspecies (Novaro, 1997a). The coat is a bright orange-brown around the head, feet and legs that turns grey on the body and upper part of the tail (Osgood 1943, in Novaro, 1997a). It is present in Chile and Argentina.

2. *L. c. andinus* (Thomas 1914), the altiplano culpeo fox or puna red fox, presents a slender and shorter snout than *L. c. culpaeus*. With a coat similar to *L. c. culpaeus*, but paler, with the head, legs and feet looking ochre instead of orange (Osgood 1943, in Novaro, 1997a). It is present in Peru, Bolivia, Chile and Argentina.
3. *L. c. reissii* (Hilzheimer 1906), the páramo wolf, sierra wolf, or Ecuadorian culpeo fox, has a more robust appearance presenting a dense reddish coat on the head, neck and extremities, whitish on the belly, and a grey and black coat in the back. The tail is thick and long (Garzón et al., 2017). The skull is similar to *L. c. andinus*, although body coat patterns differ. It is present in Colombia, Ecuador and Peru.
4. *L. c. smithersi* (Thomas 1914), is characterized by a uniform reddish coloration. There are specimens of yellowish cream or bay, their appearance is thinner and the tail is finer (OParques Nacionales Argentina, 2021). It is present in Argentina. It is distributed across the Sierras Grandes of the province of Córdoba, possibly occupying nearby mountain ranges (see Pía, 2011).
5. *L. c. magellanicus* (Gray 1837), is characterized by its southern distribution, in the continental Magellanic region, and by the cranial differences found in the few specimens collected. This subspecies seems to have a larger skull than *L. c. culpaeus*, with a relatively narrower cranial cavity, although a revision including more specimens would be necessary (Markham, 1971).
6. *L. c. lycoides* was proposed as a subspecies based on the conclusions that Lönnberg (1919) drew from two skulls whose place of collection is unknown. It is restricted to two islands of the archipelago of Tierra de Fuego of Chile and Argentina (Philippi, 1896). It appears to be larger and with a relatively narrow cranial cavity compared to *L. c. magellanicus*. The recommendations are the same as for the latter (Osgood, 1943; Markham, 1971). The so-called Fuegian dog, which accompanied the inhabitants of the archipelago, seems to be descended from these culpeos (Petrih and Fugassa, 2013).

Indeed, these subspecies are not recognized today unanimously. The results of dendrocranial analysis (Guzmán et al., 2009), and mitochondrial DNA variation from specimens from Chile and Argentina (Yahnke et al., 1996), suggest that the populations of northern Chile would correspond to the subspecies *L. c. andinus*, while the rest of the populations studied (*L. c. lycoides*, *L. c. magellanicus* and *L. c. smithersi*) would only correspond to the subspecies *L. c. culpaeus*. In fact, the Integrated Taxonomic Information System (ITIS, 2016) currently recognizes only the three subspecies accepted by Guzmán et al. (2009). Finally, the most recent analyses show six genetically differentiated populations of culpeos in South America, which coincide with the six subspecies defined above (Martínez et al., 2018).

Subspecies distribution

The distribution of the six subspecies of culpeo has been coarsely mapped (Cabrera, 1931; Novaro, 1997a). The most isolated populations have a well-defined distribution. *L. c. lycoides* is restricted to the Tierra de Fuego archipelago while *L. c. smithersi* occupies the mountains of Córdoba. However, the limits of the subspecies along the Andes mountain range are not well defined. The boundary between *L. c. reissii* and *L. c. andinus* would be in the northern region of Peru. The boundary between *L. c. andinus* and *L. c. magellanicus* differs according to the authors. According to Novaro (1997a), *L. c. andinus* reaches the region corresponding to the provinces of the same latitude of Valparaíso in central Chile and Mendoza in Argentina. However, Guzmán et al. (2009) propose that the populations of northwestern Argentina correspond to *L. c. culpaeus*, while those of northern Chile at the same latitude belong to *L. c. andinus* (Fig. 1). In addition, these authors attribute the specimens from central-southern Chile (Metropolitan, Valparaíso, Maule and Biobío regions) to *L. c. culpaeus* and not to *L.*

c. andinus, the boundary between the two species being much farther north than that proposed by Novaro (1997a).

It is interesting to highlight that the regional distribution proposed by Guzmán et al. (2009) for the culpeo subspecies coincides with that of the guanaco subspecies (*Lama guanicoe*, as defined by genetic analysis; see Gonzalez et al., 2006). This coincidence could suggest a convergence in the forces that separated the populations of both species of vertebrates, favouring the appearance of new subspecies in the same areas. Still, further work is required to finely resolve the limits between the culpeo subspecies (see Fig. 1).

As compared to other studies, Guzmán et al. (2009) is based on verifiable empirical data and on an exhaustive geographical sampling. Other studies generate confusion, which is evident in some webpages dealing with biodiversity. For example, we can find the Global Biodiversity Information Facility (GBIF, 2018), which refers to the subspecies recognized by Wozencraft (2005) that present totally mixed distribution areas, with *L. c. andinus* individuals occurring in practically all regions.

Nevertheless, there is a need to carry out more systematic studies on the species' distribution, biometrical differences between subspecies (establishing and clearly describing the type specimens) and their phylogenetic relations (Martínez et al., 2018). In addition to the variation in body size, possible subspecies could present other important local adaptations given the large differences of potential subspecies in the habitats used and environmental conditions endured, which could in turn, have conservation implications. Finally, determining the final number of subspecies of the culpeo and their geographical distribution (see Martínez et al., 2018) would be a valuable tool to better understand the biology of the species as well as the conservation status of its populations.

Habitat

The culpeo is considered a generalist in habitat use given that it can be found in a large variety of environments (Cofre and Marquet, 1999). It also can occupy humanized habitats (Salvatori et al., 1999) and areas dedicated to livestock (Johnson and Franklin, 1994b; Novaro et al., 2000a,b; Pía, 2013), where its abundance can be high, even similar to that of well-preserved areas (Pía et al., 2003). Culpeo populations can reach high altitudes, up to 4800 m a.s.l. (Jiménez et al., 2008), such as the high steppes of the Andes and the puna's grasslands and rocky areas of Argentina (Pía et al., 2003; Walker et al., 2007; Tellaeche et al., 2014; Palacios et al., 2012; Cuyckens et al., 2015) and Chile (Marquet et al., 1993; Johnson and Franklin, 1994a,b; Pacheco et al., 2004). The species also inhabits very humid areas such as the high mountain 'páramos' (i.e. a moor-like habitat) of Peru (Romo, 1995), Ecuador (Zapata-Ríos and Branch, 2016; Guntiñas et al., 2019) and Colombia (Ramírez-Chaves et al., 2013).

In relation to types of habitats, it is known that the culpeo occupies high and mid mountain range semi-arid ecosystems formed by arid steppes and semi-desert scrublands in Argentina and Bolivia (Olarie et al., 2009; Maldonado et al., 2014), Ecuador (Trujillo and Trujillo, 2007; Tirira, 2011), Peru (Cornejo Farfán and Jiménez Milón, 2001) and Chile (Castro et al., 1994; Jaksic et al., 1980; Meserve et al., 1987; Marquet et al., 1993; Arim and Jaksic, 2005; Guzmán-Sandoval et al., 2007; Lucherini et al., 2009). It is present in different forest and scrub formations of temperate regions at low altitude in Argentina (Novaro et al., 2000a; Jiménez and Novaro, 2004; Gantchoff and Belant, 2016) and Chile (Iriarte et al., 1989; Acosta-Jamett and Simonetti, 2004). The species also occupies the coastal forests of *Nothofagus* in the subantarctic region (Gómez et al., 2010; Monteverde and Piudo, 2011). Some individuals have been found in Amazon-like rain forests at low altitudes (Jiménez et al., 2008; Ordóñez-Delgado et al., 2018), although several authors suggest that culpeos would occupy adjacent areas truly (MINAM, 2011).

It has been described that in Ecuador, the culpeo is linked to the so-called páramos in high altitude ecosystems, with records starting at 2600 m a.s.l. (Tirira, 2011; Guntiñas et al., 2019). However, in this country the species has been poorly studied, and new records are in-

creasingly frequent in lower altitude ecosystems (Ordóñez-Delgado et al., 2018), and even in dry forests (Trujillo and Trujillo, 2007). This lack of knowledge on the fine distribution, use of habitat and basic biology of the culpeo in Ecuador is probably a reflection of what can be happening in other large regions of South America.

Habitat selection

Considering the wide range of habitats contained in the large distribution range of culpeos, there are few studies on habitat selection and as expected the results are very different. For example, Pía (2011) described that the culpeo was positively associated to grasslands in protected areas, and negatively to areas without legal protection, close to houses, or of easy access and without vegetation cover. In well-preserved areas or where nature is recovering, riverbanks were used as pathways by culpeos, whereas grazing areas with livestock, with little or no vegetation, were avoided (Pía, 2011). However, Pía et al. (2003) had shown that culpeo abundances were similar in livestock areas and well conserved lands, these latter being near national parks.

Other studies compare the use of space in native ecosystems versus forest plantations. In Argentina they found a lower occupation in pine plantations than in native forest (Lantschner et al., 2012). However, in central Chile, culpeos preferred more open areas, with less vegetation cover and close to roads, which corresponded to pine plantations (Acosta-Jamett and Simonetti, 2004). Moreover, culpeos responded positively to the harvesting of pine plantations by increasing their presence (Escudero-Páez et al., 2019). Similarly, in another area of Chile, culpeos positively selected habitats where the vegetation covers and the structural diversity of forests was lower (Moreira-Arce et al., 2016).

In well-conserved areas, mainly in high mountain ecosystems, other factors explain habitat use. In the puna type ecosystem of the extreme north of Argentina, the main factors explaining the abundance of culpeo were the distance to wetlands, and temperature-related variables (Cuyckens et al., 2015). In the páramos of Colombia (Noguera-Urbano et al., 2016) and Ecuador (Guntiñas et al., 2019) the greatest abundance of culpeos was associated with areas of high precipitation, extreme temperatures and homogeneous moor-like vegetation.

It is possible that this large variation in the use of habitat suggests that other factors play a role in determining presence and abundance in different regions. A key candidate could be prey abundance. Indeed, several authors highlight prey availability as one of the main factors determining habitat use and species abundance (Johnson and Franklin, 1994b). Cuyckens et al. (2015) explained the association of culpeos to wetlands with the presence of waterbirds that they would use as prey. Similarly, Olarte et al. (2009) suggested that the selection of an area could be explained by a high density of rodents. In Ecuador a strong relationship between the abundance of the culpeo population and the mountain tapir (*Tapirus pinchaque*) was found, so that a link between culpeo numbers and prey density was also suggested (Guntiñas et al., 2019) because tapir activity may enhance density of deer species, which are the staple prey for culpeos in the region (see Guntiñas et al., 2017).

Prey availability could explain that the density and type of vegetation cover influence the habitat selection of the culpeo among different types of vegetation and cover. Lantschner et al. (2012) concluded that greater availability of hares and rodents would explain the higher presence of culpeos in native forests than in pine plantations. Acosta-Jamett and Simonetti (2004) suggested that culpeos could benefit from the increased abundance of prey in pine plantations, since the lower vegetation cover would facilitate hunting. In addition, Simonetti et al. (2013) found in pine plantations that culpeo abundance decreased when understory was eliminated, which was related to the decrease of small prey abundance. Furthermore, Grez et al. (1998) did not observe any decrease in culpeo abundance in plantations without vegetation cover compared to those plantations with understory where small prey were not the main source of food for the canid, suggesting that the type of prey (in addition to its abundance) also plays a key role in culpeo habitat selection. Other factors, such as interaction with other predators, may also have an important influence on habitat selection and the use of space. These may

influence the culpeo, either through indirect competition for prey, competition for other resources, through direct agonistic interactions, etc.

Trophic ecology

Culpeos have a wide food spectrum that varies considerably across its distribution. It is considered an opportunistic carnivore of generalist trophic habits (Medel and Jaksic, 1988; Cornejo Farfán and Jiménez Milón, 2001; Zapata et al., 2005; Achilles, 2007; Walker et al., 2007; Carevic et al., 2019) with the flexibility to vary the diet according to environmental conditions, and to specialize in a given trophic resource (Guntiñas et al., 2017). Therefore, diet descriptions of the species vary between being considered one of the most carnivorous foxes in South America (Redford and Eisenberg, 1992; Jiménez and Novaro, 2004), to being practically insectivorous in some regions (Guzmán-Sandoval et al., 2007; Carevic et al., 2019), or at certain times of the year (Iriarte et al., 1989), with clear tendencies also to frugivory (Ebensperger et al., 1991; Cornejo Farfán and Jiménez Milón, 2001; Achilles, 2007). The culpeo diet can be affected by regional productivity variation and large-scale phenomena such as El Niño, so that in Chile, prey richness for culpeos did vary over time (i.e. years) and with precipitation (Arim and Jaksic, 2005). Recently, in the Atacama desert (Chile), a relationship between trophic niche breadth and primary productivity was also found (Carevic et al., 2019).

It is worth noting that the culpeo's dentition is more adapted to a carnivorous diet than that of other South American canids, presenting relatively longer canines (Wayne et al., 1989) and smaller molars (Kraglievich, 1930 in Jiménez and Novaro, 2004). However, the diversity of foods it exploits gives the culpeo a greater versatility than a pure diet consisting of a single exclusive group (Silva et al., 2004, 2005b).

Trophic groups

Small rodents form an essential component of the culpeo's diet, both in terms of biomass contribution (Jaksic et al., 1980; Ebensperger et al., 1991; Achilles, 2007) and in terms of frequency of occurrence (Jaksic et al., 1980; Meserve et al., 1987; Iriarte et al., 1989; Ebensperger et al., 1991; Corley et al., 1995; Novaro et al., 2000a; Pía et al., 2003; Correa and Roa, 2005; Pía, 2013). Cuis (*Cavia* sp.) are consumed in the high mountains of Argentina (Pía, 2011). However, in other studies, this group is less important than in the previous ones (Guzmán-Sandoval et al., 2007). Although it is not the main source of food usually, medium-sized or large rodent species such as rats (*Rattus* sp.), squirrels (*Sciurus* sp.) and spotted pacas (*Cuniculus paca*) also can appear in the culpeo diet (Romo, 1995; Walker et al., 2007; Guntiñas et al., 2017).

Introduced species, such as the European hare (*Lepus europeaus*) and the rabbit (*Oryctolagus cuniculus*), are relevant food sources in several locations such as Patagonia (Iriarte et al., 1989; Johnson, 1992; Johnson and Franklin, 1994b; Pía, 2013; Zúñiga and Fuenzalida, 2016), being sometimes more consumed than native fauna (Crespo and de Carlo, 1963; Jaksic, 1998; Novaro et al., 2000a; Rubio et al., 2013). It seems that the abundance of these exotic species has facilitated an expansion in the distribution range of the culpeo in Argentina (Lucherini, 2016). However, the pattern does not seem uniform, as Meserve et al. (1987) reported that in areas where hares are abundant, the diet is based on small mammals and hares are ignored as prey. Also, in areas where native wild rabbits (*Sylvilagus brasiliensis*) are present, there is a high consumption of them by culpeos (Beltrán-Ortíz et al., 2017; Guntiñas et al., 2017; Reina, 2019; Cadena-Ortíz et al., 2020).

Medium and large size herbivorous mammals can be consumed, particularly livestock, such as sheep and camelids in Chile, Argentina, Bolivia and Peru (Novaro et al., 2000a; Pía et al., 2003; Zacari and Pacheco, 2005; Iranzo et al., 2018), and sometimes can become a relevant trophic resource reaching up to a 21% of consumed biomass (Novaro et al., 2000a). Some species of small-bodied wild deer (*Mazama* and *Pudu* genera) have been described as the main trophic resource in some areas of Ecuador and northern Peru (Guntiñas et al., 2017). There are reported cases of Patagonian huemul fawns (*Hippocamelus bisulcus*) consumption in Argentina and Chile (Smith-Flueck, 2003; Corti et al., 2010). Large herbivores (i.e. livestock, camelids, deer) can be con-

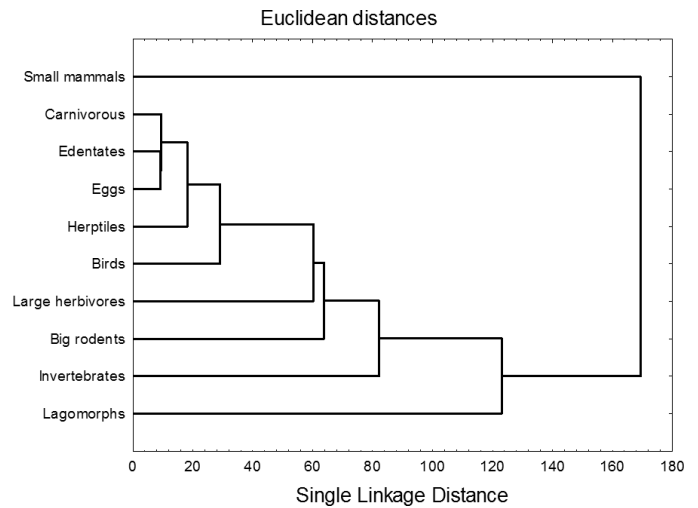


Figure 2 – Diagram describing the main diet types of the culpeo in South America, obtained from the cluster analysis (single linkage distance, Euclidean distances) performed with the ten trophic groups considered in this study [Source: Jaksic et al., 1980; Iriarte et al., 1989; Ebensperger et al., 1991; Marquet et al., 1993; Johnson and Franklin, 1994a,b; Romo, 1995; Novaro et al., 2000a; Cornejo Farfán and Jiménez Milón, 2001; Pía et al., 2003; Zapata et al., 2005; Achilles, 2007; Walker et al., 2007; Berg, 2007; Monteverde and Piudo, 2011; Palacios et al., 2012; Rubio et al., 2013; Guntiñas et al., 2017].

sumed as carrion (Novaro et al., 2000a; Palacios et al., 2012) or directly hunted (Franklin 1982, in Donadio et al., 2012; Bellati, 1992b; Novaro et al., 2000a,b; Pía et al., 2003; Zacari and Pacheco, 2005; Pía, 2013; Guntiñas et al., 2017). In Chile, Novaro et al. (2009) clearly documents culpeo attacks on young guanaco (*Lama guanicoe*), that are three times larger than the canid.

Other groups of mammals also appear in the diet of the culpeo, such as marsupials (Johnson and Franklin, 1994b; Zapata et al., 2005; Achilles, 2007; Walker et al., 2007; Palacios et al., 2012; Pía, 2013; Beltrán-Ortíz et al., 2017), other carnivorous species (Walker et al., 2007; Guntiñas et al., 2017) and some edentates (Zapata et al., 2005; Guntiñas et al., 2017). Birds and reptiles, with some exceptions (see Cuyckens et al., 2015 for birds; and Romo, 1995; Achilles, 2007; Carevic et al., 2019 for reptiles), are not an important food resource in the culpeo diet (Ebensperger et al., 1991; Romo, 1995; Pía et al., 2003; Achilles, 2007; Guzmán-Sandoval et al., 2007).

Invertebrates, and especially coleoptera, are an important food resource in regions of Chile (Ebensperger et al., 1991; Correa and Roa, 2005; Guzmán-Sandoval et al., 2007; Palacios et al., 2012; Carevic et al., 2019), Peru (Cornejo Farfán and Jiménez Milón, 2001) and Argentina (Zapata et al., 2005). This item appears in lower proportions in other studies (Iriarte et al., 1989; Ebensperger et al., 1991; Achilles, 2007; Walker et al., 2007; Beltrán-Ortíz et al., 2017), and are completely absent in others (Pía, 2013).

Overall, the results of the cluster analysis of the ten groups of prey, show six main types of diet for the culpeo (see Fig. 2). There is a first type of diet, very different from the others, based on small mammals. The two next types of diet, clearly differentiated, are based on lagomorphs and invertebrates. Big rodents and large herbivores form the other two sufficiently differentiated types of diet. Finally, there is a diverse type of diet, including the consumption of birds, herptiles, eggs, edentates and carnivorous species. In relation to small mammals, there was no difference in their consumption among biomes ($H_{(4,N=19)}=1.003$, $p=0.91$). Biomes also had no influence on the consumption of lagomorphs ($H_{(4,N=19)}=8.59$, $p=0.07$) and invertebrates ($H_{(4,N=19)}=2.37$, $p=0.67$). In the case of big rodents, the highest value of consumption appeared in temperate grasslands ($H_{(4,N=19)}=11.22$, $p<0.05$). In montane grasslands and temperate grasslands took place the highest consumptions of large herbivores ($H_{(4,N=19)}=11.31$, $p<0.05$). Graphical results from Kruskal-Wallis tests can be found in Fig. S2 (Supplementary Material).

High fruit intake has been described at certain times of the year (Jaksic, 1998; Castro et al., 1994; Romo, 1995; Cornejo Farfán and Jiménez

Milón, 2001; Silva et al., 2005a; Trujillo and Trujillo, 2007). Castro et al. (1994) observed that fruit consumption increased in periods where the density of small mammals was less than 10 individuals/ha, and Corley et al. (1995) found a negative correlation in the consumption of insects (coleoptera) and plants. The high intake of fruits by culpeos led to the suspicion that the species is an important seed disperser. At least, the efficiency of the culpeo as disperser has been proven for carob trees (*Propollis flexuosa* and *P. pallida*) (Cornejo Farfán and Jiménez Milón, 2001; Maldonado et al., 2014), as well as for the pepper (*Schinus molle*) (Castro et al., 1994). Fruits from bromeliads (*Greigia sphacellata*) (Achilles, 2007), ericaceae fruits (genus *Vaccinium*) (Romo, 1995) and trees (e.g. *Prunus cerasus*, *Malus domestica*) (Bravo et al., 2019), are also abundant in the diet of culpeo, but this canid's role as seed disperser has not been proven for these plants. In fact, some authors suggested that culpeos would not be an efficient disperser for all species (Bustamante et al., 1992; León-Lobos and Kalin-Arroyo, 1994; Silva et al., 2005a). The efficiency of seed dispersion by culpeos probably depends on the involved plant species, but further research is needed to confirm this.

Trophic resources selection

There are several studies, carried out in different places and habitats, that compare the consumption of prey with its availability. A study from Argentinian Patagonia found a higher consumption of hares and sheep than expected according to their density and biomass availability, while carrion, calves, rodents and birds were consumed less often than expected (Novaro et al., 2000a). A study from the semi-arid scrubland of the Chilean matorral found trophic selectivity by culpeos towards the brushtail mouse (*Octodon degus*), even during periods of extremely low rodent abundance (Martínez et al., 1993). Jaksic et al. (1992) observed in the Chilean matorral that, in the face of a reduction in the abundance of micromammals, the culpeo did not increase its diet breadth as might otherwise have been expected. Ebensperger et al. (1991) observed that in the Chilean matorral, the culpeo consumed smaller prey than would have been expected given this predator's size, while Jiménez and Novaro (2004) observed a broad selection towards the largest small mammals available.

According to Meserve et al. (1987) and Iriarte et al. (1989), the key to understanding trophic selection is not the abundance of prey, but the microhabitat space use of the prey (e.g. the use of open areas in scrub-

lands) as well as its size. In agreement with this, Corley et al. (1995) conducted a study on prey vulnerability based on its morphology and behavior. The most abundant mouse species, the jerbo mouse (*Eligmodontia typus*), was not the most consumed, which is attributed to a more effective escape strategy seemingly due to its long hind legs. Therefore, as it happens with other predator species (e.g. Barja, 2009; Piñeiro and Barja, 2011), prey selection by the culpeo can depend on prey abundance and on other drivers of prey availability, such as accessibility to the predator, which is affected in turn by habitat type, prey use of the space, prey morphology and behavior, etc.

Although diet is one of the most studied aspects of culpeo biology, there are still many South America regions where no information is available. As previously mentioned, there are trophic groups that being highly abundant in different environments can be important in some of them, but not in others. Regarding whether the species is a dietary generalist, or follows a facultative trophic specialist strategy (see Gun-tiñas et al., 2017), it would be worthwhile to carry out more diet studies that consider the availability of different food resources and how they vary, as well as studies on prey selection and how it changes with varying environmental factors.

Spatial ecology

Population density

Data on culpeo population densities are only available from studies carried out in Argentina and Chile. Density values rarely exceeded one specimen per square kilometer (very similar to chilla densities in Tierra del Fuego; Wilson and Mittermeier, 2009), varying between 0.2 and 2.6 individuals/km² (Tab. 2). Some studies show that culpeo increases its population density in response to an increase in rodent densities (Falero 1987, in Romo, 1995), but others found no decrease in the abundance of culpeos after a drastic decrease of their prey (Martínez et al., 1993). Nevertheless, the variation in density values is similar to that of other canid species of similar size, depending in general on prey availability, habitat type or anthropogenic pressure (Wilson and Mittermeier, 2009).

On the other hand, Pía et al. (2003) found in the dry Chaco similar densities in a natural protected park area and a livestock zone. Even higher densities are recorded in areas under intense hunting pressure than in non-hunting areas in Patagonian steppes (Novaro et al., 2000b,

Table 2 – Culpeo densities reported in different studies, and field methods employed detailed by study areas and countries.

Densities		Method	Study area	Country	Source
culpeos/km ² ±SE	scats/km				
0.7		Intensive trapping	North-west Patagonia	Argentina	Crespo and de Carlo (1963) (in Bellati and von Thungen, 1990)
1.9		—	North-west Patagonia	Argentina	Rabinovich et al. (1987) (in Bellati and von Thungen, 1990)
1.2		Telemetry	Torres del Paine	Chile	Johnson (1992) (in Jiménez, 1993)
		—	North-central	Chile	Jiménez (1993) (in Lucherini, 2016)
2.6					In ravines of study site
0.3					Throughout the study site
		Linear transect	North-west Patagonia	Argentina	Novaro et al. (2000b)
in 1993: 0.77±0.50					in non-hunting area
in 1994: 0.82±0.64					
in 1993: 1.31±0.76					in hunting area
in 1994: 1.07±0.72					
0.2±1.3					in the total area
1.3		Based on sightings	Torres del Paine	Chile	J. Rau pers. comm. (In Jiménez and Novaro, 2004)
		Scent stations	North-west Patagonia	Argentina	Novaro et al. (2005)
0.49±0.12					in four hunting ranches
0.31±0.09					in two non-hunting ranches
		Linear transect		Argentina	Pía et al. (2003)
	1.01		Quebrada del Condorito National Park		in National Park
	0.87		Sierras Grandes of Córdoba		in a ranch

2005) (see Tab. 2). This could be explained by a model of source-sink population dynamics, in which there are non-hunting areas surrounding hunting zones that provide dispersant individuals that colonize areas where they compensate the high mortality due to culpeo harvesting (Novaro et al., 2005).

Regarding temporal variation in density, in 30 years the density of culpeos doubled in a region of Argentinian Patagonia where hunting took place (Crespo and de Carlo, 1963; Novaro et al., 2000b). However, in Torres del Paine National Park (Chile), density values remained stable for approximately ten years (Johnson, 1992, in Jiménez and Novaro, 2004). These data could suggest that in protected areas, population densities remain constant over time as compared with areas where the culpeo is persecuted or hunted. However, data on this matter are still very scarce, and more work is needed focused on population dynamics before general conclusions can be drawn.

Home range

The scarce available data indicate that culpeo home ranges varies from 6 km² to 9 km² for females, and from 2 to 10 km² in the case of males (see Tab. 3). The culpeo home range is smaller than that of the maned wolf (*Chrysocyon brachyurus*), which is between 25 and 59 km² (Wilson and Mittermeier, 2009)). The culpeo home range seems to be similar to that of the Hoary fox (*Lycalopex vetulus*) (i.e. 4.5 km²), and overall it is larger than those of the other South American canids. For example, chilla home range is around 2 km², Pampas fox (*Lycalopex gymnocercus*) home range is 0.45 km², and Darwin's fox (*Lycalopex fulvipes*) home range is 1.6 km² (Wilson and Mittermeier, 2009).

As for the differences between the sexes, there is divergence in the studies: in Patagonian steppes of Argentina Novaro et al. (2000a) observed that the territories of males were larger. On the contrary, in the Chilean matorral (semi-arid scrubland), Salvatori et al. (1999) found that the territories of males were three times smaller than those of females (Tab. 3). For their part, Johnson and Franklin (1994a) did not observe any differences between the sexes in Magellanic forests. The same territory can be shared by related individuals (Novaro et al., 2000a), and the boundaries of male territories can overlap (Johnson and Franklin, 1994a).

Radio-tracking studies have shown that anthropogenically modified areas in Argentina were part of the territories of adult individuals. Moreover, it was common that culpeos would abandon territories due to the scarcity of prey (Novaro et al., 2000a), which was also observed in the scrubland of central Chile (Salvatori et al., 1999). Dispersion distance of young culpeos has been estimated between 12 and 90 km (Novaro et al., 2005), while seasonal displacements of up to 15 km were associated with the movements of their main prey (Crespo and de Carlo, 1963).

Activity patterns

Studies of culpeo activity patterns are mostly based on camera-trapping campaigns, direct sightings, and studies that take into account the behavior of prey whose remains were found within culpeo scats. Overall, there is a certain disparity in the results, and there are also extensive geographical regions where there is no information on the topic. Until now, camera-trapping studies showed that in areas of Argentina, Chile and Bolivia, there is a bias (65% of records) towards nocturnal activity

(Walker et al., 2007; Lucherini et al., 2009; Tellaeche et al., 2014). Indeed, in many regions culpeos are considered mainly nocturnal. While moon light did not seem to affect the activity of the culpeo (Lucherini et al., 2009), peaks of activity have been recorded at different times of the night (Monteverde and Piudo, 2011). More nocturnal activity has also been reported in males than in females (Salvatori et al., 1999). However, most studies based on direct sightings and diet components show diurnal behaviour of the species to some extent and suggested a mainly twilight activity (Jaksic et al., 1980; Iriarte et al., 1989; Martínez et al., 1993; Johnson and Franklin, 1994a; Salvatori et al., 1999; Walker et al., 2007; Lucherini et al., 2009; Olarte et al., 2009; Stucchi and Figueroa, 2010).

The factors that influence the activity patterns of the species have been the subject to debate. Traditionally, it has been considered that nocturnal activity could be influenced by human harassment (Lucherini and Zapata, 2012; Olarte et al., 2009). However, nocturnal activity has also been observed in protected areas lacking hunting pressure (Monteverde and Piudo, 2011), as well as diurnal activity in areas where the culpeo is hunted (Iriarte et al., 1989). Some authors suggest that culpeo activity may be related to patterns of prey activity and availability (Johnson and Franklin, 1994b; Salvatori et al., 1999), or to the interaction with other predators due to temporal niche segregation and competition avoidance (Lucherini et al., 2009; Monteverde and Piudo, 2011). Furthermore, Monteverde and Piudo (2011) mentioned seasonal differences in activity patterns, suggesting an increase in activity during the feeding period of cubs. Nevertheless, more studies are needed to clarify activity patterns of the culpeo in its entire range.

Interspecific relations

The culpeo shares space with many predator species in its wide distribution range in South America. However, most of the existing data collected has to do with interactions with chillas (also called South American grey foxes) and pumas.

Chilla (*Lycalopex griseus*)

One of the best studied interactions to date is the relationship of the culpeo with the chilla, a closely related species that currently co-occurs in large areas of Argentina, Chile and Peru. An allopatric distribution between both species is observed throughout the Andean mountain range. Culpeos and chillas are found in sympatry only to the south of its range, where there is less opportunity for altitudinal segregation as the Andes decreases in elevation towards southern Chile (Fuentes and Jaksic, 1979). For central Chile, Fuentes and Jaksic (1979) and Jaksic et al. (1980) suggested that allopatric distribution could be a consequence of competitive exclusion determined by the similarity in sizes of both predators and potential prey. Where the geographical range of both species overlap, like in Patagonia, processes of niche differentiation could explain the observed distribution patterns (Travaini et al., 2001; Bolkovic and Ramadori, 2006).

In relation to the use of space, in regions of Chile and Argentina there are areas where the territories of both species did not overlap (Johnson and Franklin, 1994a), while in others a common use of space has been observed (Jiménez et al., 1996; Travaini et al., 2001, 2013). In Argentina, Travaini et al. (2001) suggest that there is avoidance and probably a habitat and resource partitioning between the two canids.

Table 3 – Home range data provided in different studies. MCP: minimum convex polygon, HME: harmonic mean estimators, Kernel: Kernel method, NA: no data available.

Home Range (km ² ±SE)			Method	Source
General	Female	Male		
	8.2±0.6	10.2±1.5	—	Novaro (1997a) (in Pacheco et al., 2004)
3.5±0.6			100% MCP	Johnson and Franklin (1994a)
7.7±1.4			95% HME	Johnson and Franklin (1994a)
4.65	8.94	3.31	100% MCP	Salvatori et al. (1999)
4.86	9.43	3.37	95% HME	Salvatori et al. (1999)
3.24	6.24	2.24	95% Kernel	Salvatori et al. (1999)

Results from scent stations show that the culpeo occupied steppe habitats and steppe-forest ecotone areas, while the chilla was only present in the steppe (Bolkovic and Ramadori, 2006). In southern Chile, culpeos selected forested areas of *Nothofagus* and dense scrub habitats, while chillas occupied transition habitats formed by mid-cover scrublands at higher altitudes (Johnson and Franklin, 1994a). The culpeos would select those areas because of the higher densities of European hares and small rodents, or because they provide more shelter (Johnson and Franklin, 1994a). However, in the same region, both species coincided in selecting forest habitats with low structural diversity (Moreira-Arce et al., 2016).

There are significant differences in the diet of both canids (Johnson and Franklin, 1994b). Johnson (1992) had found that culpeos consumed larger prey than chillas and that the degree of trophic overlap was low. In general, culpeos consume more European hares than chillas (Jaksic et al., 1980; Zapata et al., 2005; Palacios et al., 2012). Indeed, the two species can potentially consume the same type of prey, and the degree of diet overlap varies seasonally (Fuentes and Jaksic, 1979; Zapata et al., 2005). All these authors suggest that the culpeo would exclude the chilla from habitats with presence of high quality prey, thus describing a competitive relationship between the two canids in which the culpeo would be the strong competitor, displacing the smaller chilla.

Puma (*Puma concolor*)

The culpeo shares almost its entire range with one of the large felids and top predators of South America, the puma, which can prey on culpeos (Pacheco et al., 2004; Novaro et al., 2005). There are only studies in Argentina that address their interactions, where it was found that the culpeo decreased its abundance as the density of pumas increased (Novaro and Walker, 2005). Pía (2013) observed that the culpeo avoided rocky outcrops that were important for pumas, suggesting that the puma presence altered the canid's use of space.

Cuyckens et al. (2015), using models of biological interactions, could not find evidence that the culpeo distribution was influenced by the puma. These authors also concluded that in Argentina there is not much mutual influence between different predator species, after observing the distribution patterns of the Andean cat (*Leopardus jacobita*), the Pampas cat (*Leopardus colocolo*), the puma and the culpeo. By contrast, other authors associate the expansion of the culpeo's distribution area in Patagonia with a decrease in puma densities (Lucherini and Zapata, 2012). It is possible that culpeos prey on young or small puma specimens, since sometimes remains of puma appear in the excrements of the canid (e.g. Guntiñas et al., 2017). Therefore, the culpeo-puma interaction seem complex to unravel at the moment and probably depends on the ecological context of each place (e.g. the degree of competition in a given area, the density of prey, the density of the predators themselves, the degree and intensity of human interference, etc), requiring further research in this field.

Other interactions

Culpeos can be affected by the presence of feral dogs in their territories. Indeed, in Cayambe-Coca National Park (Ecuador) the abundance of culpeos decreased, they becoming more nocturnal in the areas where dogs were present Zapata-Ríos and Branch, 2016. Further, in Argentina culpeo deaths by dogs have also been recorded (Novaro et al., 2005), and there is empirical evidence of similar events in the páramos of the Cotopaxi volcano in Ecuador, where different individuals are being monitored with radio collars (Yáñez, pers. comm.). In addition, transmission of diseases from dogs is also possible (Acosta-Jamett et al., 2015; Veintimilla, 2015).

There are similarities between the diet of the culpeo and that of different species of felids. In high altitude deserts in Argentina, there is an overlap of resources between the culpeo and both the Andean and the Pampas cats (Walker et al., 2007). The three species consumed the same prey (mainly rodents, birds and hares) but in different proportions: the culpeo was the most generalist, adding to its diet a significant number of invertebrates as well as carrion. In Argentinian Patagonia, a trophic overlap between the culpeo and the Geoffroy cat (*Leopardus*

geoffroyi) was also observed (Palacios et al., 2012), the culpeo diet being less specialized in rodents (with greater consumption of hares and arthropods) than that of the feline.

Similarities in diets suggest some degree of competition among the different species of carnivores. This competition could decrease in some cases due to the partition of resources, the culpeo being more generalist than felines (Walker et al., 2007; Cuyckens et al., 2015). In other cases, interference competition could partly explain the presence in the diet of carnivorous species, reaching up to 10% of total prey, as described for culpeos living in the high Andes' páramos (Guntiñas et al., 2017). This high consumption clearly shows the top-predator behavior of culpeos (although the puma, the other Andean top-predator, can also prey on culpeos), and could be a key factor in regulating the populations of smaller carnivores in high-Andean ecosystems. Therefore, more studies are needed to analyze the interactions of culpeos with other predators and on the functioning of the ecosystem as a whole, where cascading effects may occur (Ripple et al., 2014).

Pathogens and parasites

In Argentina, the nematodes *Physaloptera clausa*, *Toxocara leonina* and *Protospirura numidica creceticola* were found in 4% of the culpeo excrements analyzed (Stein et al., 1994). Decades ago in the same region, *Toxocara canis* and *Echinococcus patagonicus* were also described (Crespo and de Carlo, 1963). The presence of *Neospora*, *Leptospira*, *Toxoplasma*, *Brucella* and canine parvovirus was determined through serological analysis of 28 culpeo samples (Martino et al., 2004). In the same country, *Echinococcus granulosus* was also detected in culpeos (Schantz et al., 1972). Ticks *Amblyomma tigrinum* and fleas *Pulex irritans* were observed in captured culpeos (Millan et al., 2019).

In the puna of Peru, *E. granulosus* was detected in the intestine of shepherd dogs, but not in 20 analyzed culpeos, which were positive to *Taenia hydatigena*, *T. multiceps*, *Mesocostoides lineatus*, *Dipylidium caninum*, *Uncinaria stenocephala* and *Oncicola canis* (Moro et al., 1998). Also in Peru, *Corynosoma obtusens*, an acantocephalon linked to marine species, was found in the intestines of two culpeos (Tantaleán et al., 2007). In Bolivian yungas, scat analysis determined the presence of cestode eggs (*Taemia* sp., probably *T. hydatigena*), nematodes (*Toxocara* sp., *Trichuris* sp., Ancylostomatidae family and Strongylida order) as well as *Coccidium* oocysts (Ayala-Aguilar et al., 2013).

In the humid páramos of Ecuador, Veintimilla (2015) described the existence of the parasites *Trichuris vulpis* and *Ancylostoma caninum*, the latter also present in the dogs from the same area. The serological analysis of 9 culpeo specimens was negative for distemper virus and *Leptospira*, but positive for *Brucella canis*. Given the possible presence of *Brucella*, the cause of brucellosis (a contagious disease that causes spontaneous abortions in the infected female), Veintimilla (2015) highlighted the need for more studies and pointed out that the incidence of this bacterium could have important consequences in wild animal populations.

In Chile, the presence of *Linguatula serrata* was reported in culpeos (Alvarez, 1960). An outbreak of canine distemper virus with epidemic characteristics was reported in 2003 in wild fox populations in different regions of the Valdivian coast, particularly in Fray Jorge National Park and Puerto Velero (Moreira and Stutzin, 2005). In subsequent studies, Acosta-Jamett et al. (2011, 2015) detected a seroprevalence of the virus in culpeos and chillas, and for the first time of canine parvovirus. Culpeos living near human settlements also had a higher prevalence of distemper. It has been suggested that these culpeos would be more exposed to the viruses because of the proximity and likelihood of contacting domestic dogs. Given the severity of distemper in wild carnivore populations (Funk et al., 2001), more studies should be conducted to understand the dynamics of infection among dogs and wild canids.

Conservation concerns

The International Union for Conservation of Nature (IUCN) lists the culpeo as a "Least Concern" species, given that the population trend seems stable at the continental scale, populations are not severely

fragmented and no sharp population declines have been reported (Lucherini, 2016). However, at regional and local levels, the culpeo has been listed under different categories of threat. For example, in Argentina it has been included in the last National Red List as “Least Concern” (Pía et al., 2019), and the real status of the populations is not known, with the consequent uncertainty regarding its assessment and the future of the species in the country. On the one hand, there are populations in Tierra del Fuego that show a clear negative trend, as in Bosques Petrificados Natural Monument (Lucherini and Zapata, 2012), a possible consequence of the use of poison and the increase in puma densities (Lucherini and Zapata, 2012). Indeed, the two endemic subspecies of culpeos (*L. c. lycooides* and *L. c. smithersi*) have been listed as “Endangered”. In addition, it has been calculated that only 14% of protected areas are large enough to sustain viable populations of culpeos (Jiménez and Novaro, 2004). On the other hand, the culpeo has extended its range to arid Patagonia, which indicates that other populations are increasing. In this sense, expanding populations could counteract the decline of others, thus keeping the population trend stable and the corresponding conservation status of the culpeo at national scale.

In Chile, the species falls under two different categories (MMA, 2007). The restricted population in the forests of the southern island of Tierra del Fuego, attributed to the subspecies *L. c. lycooides*, is classified as “Vulnerable”. The rest of the populations, which are attributed to the subspecies *L. c. culpaeus*, are considered as “Least Concern”. In Peru, it is listed as a “Least Concern” species in CITES Appendix II (MINAM, 2011), while in Bolivia the culpeo is not included in the Red List of threatened species (Aguirre et al., 2009).

Finally, the situation of the culpeo in the northern part of its distribution is less clear. In Colombia, it has been declared as a “Vulnerable” species due to the supposed decrease of its population (MADT, 2014), although there are claims that the key population parameters and population dynamics of the culpeo in the country are unknown, and that there are reasons to believe it is actually abundant (Ramírez-Chaves et al., 2013). In Ecuador the culpeo was also listed as “Vulnerable” (Tirira, 2011), due to the suspected regression of its populations, although there are no reliable data over time. To obtain data on culpeo population trends in the country some studies are being carrying out in several key populations for the species, as for example the pilot project for long-term monitoring of wildlife in the so-called Sangay-Podocarpus Connectivity Corridor, in southern Ecuador (Cisneros et al., 2020).

Direct persecution

Human activity is one of the main drivers of culpeos mortality. Until the 1990s, culpeos were heavily hunted for their skins (Crespo and de Carlo, 1963; Travaini et al., 2003). Also, different parts of their body are used as traditional medicine remedies in Argentina and Bolivia (Barbarán, 2004). It is also known that adult and juvenile culpeos can be killed by dogs (Novaro et al., 2005), and there are also cases of road traffic accidents (Novaro et al., 2005; Pía, 2011), although the importance of these threats has not been quantified. However, one of the main problems is related to livestock activity.

The culpeo enters in conflict with human populations when it hunts domestic species such as lambs and goats (Bellati and von Thungen, 1990; Novaro et al., 2000b; Pía et al., 2003; Muñoz, 2017). In some areas (such as central Patagonia) the culpeo is considered the main predator of livestock, even more harmful than pumas (Llanos et al., 2019). Livestock losses determine a negative perception of the species on the part of the farmers, which causes the culpeo to be persecuted legally and/or illegally (Bellati, 1992a; Travaini et al., 2000b; Lucherini and Merino, 2008; Gáspero et al., 2018). Culpeos are heavily hunted with traps, dogs and poison in certain regions, where up to 75% of the local population can be eliminated each year (Novaro, 1995). In Peru, Chile, Bolivia, and some regions of Argentina, hunting of culpeos is now permitted as a predator control strategy to reduce damage to livestock (Lucherini, 2016; Gáspero et al., 2018). In Ecuador, carrion poisoning to control livestock predators illegally, especially feral dogs, is

also killing culpeos (A. Yáñez, *pers. comm.*). Certainly, the use of poison is widespread, and it is one of the methods preferred by farmers to control carnivores (Gáspero et al., 2018).

However, the control of culpeo populations has triggered a controversial debate concerning its efficacy and necessity (see for a global discussion Treves et al., 2016; Lozano et al., 2019). Farmers usually perceive high rates of livestock mortality due to predation by carnivores. For example, in northwest Patagonia (Argentina) around the 8% (ranging between 0% and 43%) of sheep and goat losses are attributed to culpeos (Gáspero et al., 2018). However, Bellati and von Thungen (1990), through sheep necropsies in Argentinean Patagonia, found that 47% of deaths were not actually caused by predation and concluded that losses of lambs not related to culpeo are very high. Similar conclusions were obtained in the highlands of Bolivia (Zacari and Pacheco, 2005), where the losses of camelids due to health problems were between 2.3 and 6.4 times greater than those produced by carnivores. In addition, there are attacks on livestock by dogs (Montecino-Latorre and San Martín, 2019) that are erroneously attributed also to culpeos (Aliaga-Rossel et al., 2012).

The response of the culpeo populations to these control actions is unclear across all regions. Argentina is probably the country where most effort has been made to characterize the population trends of the canid. Since the 1980s, systematic monitoring programs of canine populations have been implemented in some areas (Von Thünen, 1991; Novaro et al., 1996, 2000b). This has allowed gaining an understanding of population dynamics in environments under hunting pressure. For example, Novaro (1995) and (Novaro et al., 2005) claimed that in the different Argentinean regions the culpeo has not disappeared due to the existence of a source-sink dynamics. This type of dynamics is common to other canine species populations, such as the European red fox (*Vulpes vulpes*) in Europe (Rushton et al., 2006), or the black-backed jackal (*Canis mesomelas*) in South Africa (Minnie et al., 2016), which often renders lethal control efforts useless (Treves et al., 2016; Lozano et al., 2019).

In Argentina, an attractive management plan for canids (Bolkovic and Ramadori, 2006) contemplated reducing the pressure on culpeos and avoiding attacks on livestock. The plan proposed the introduction of guard dogs in the ranches affected by carnivore predation (see also Novaro et al., 2017). This measure is usually effective at preventing attacks on livestock (Von Thünen, 1998; Bolkovic and Ramadori, 2006; Eklund et al., 2017), especially when it is in combination with others (see Lozano et al., 2019). Furthermore, Travaini et al. (2001, 2013) observed that culpeos avoided areas where new elements producing strange stimuli were installed in the environment. So, they proposed to use these repellent elements to keep culpeos away from the ranches. Indeed, there is an ongoing strong trend to recommend non-lethal methods to be applied in livestock areas for reducing predation by carnivores (Novaro et al., 2017; Llanos et al., 2019).

Habitat disturbance

Although habitat loss is a major threat to many species (e.g. Pimm et al., 1995), some authors claim that this should not be the case for the culpeo in regions affected by habitat loss, as this canid appears to be highly adaptable to changes in the landscape (see Acosta-Jamett and Simonetti, 2004; Jiménez et al., 2008). However, an increasing number of studies disagree with this view. In Peru, overgrazing and mining have been catalogued as threats to culpeo populations (Villegas and Ortega, 2010, in MINAM, 2011). In addition, areas with scarce plant cover, and close to human presence, can be risk zones (where culpeos can be easily found and killed) or barriers to the movement of culpeos (Pía, 2011). In some regions, such as northwestern Argentina (Cuyckens et al., 2015) and the high Andes of Ecuador (Gutiérrez et al., 2019), culpeos appear associated with high mountain ecological conditions, which could indicate specific local adaptations and thus, a limited capacity of response to environmental changes in those areas.

Conclusions

The culpeo is a canid that uses a wide variety of trophic and spatial resources, and it is found in various ecosystems of South America. Behavioral patterns are driven by a number of factors, with prey availability and interactions with other carnivores as being one of the most important. Nevertheless, it is evident that at a local scale there is a marked tendency towards trophic resources selection, so that culpeos appear to be facultative trophic specialists more than simple generalists. Moreover, the culpeo behaves in some high Andean areas as a top predator, and it is a seed disperser in arid environments, so that plays a key role in the functioning of ecosystems.

The culpeo's conservation status differs among regions, depending on the degree of knowledge about its populations in each country. In general, there is not enough information to draw clear conclusions on its conservation status or population trends. It seems that direct persecution and habitat alteration (such as that caused by mining or grazing) are the most obvious threats faced by the species, although transmission of pathogens and widespread landscape changes due to global ecological drivers (such as the effects of climate change) are factors that could also affect the species. The existence of a network of Protected Areas has a demonstrated beneficial effect on the conservation of culpeos.

Argentina and Chile have so far led the research effort on the species. Studies are being carried out in relation to the dynamics of populations under hunting pressure in Argentina, and on the dynamics of contagion and prevalence of pathogens in Chile. However, additional information is appearing on diet or other aspects of the culpeo ecology in different regions of the continent. Nevertheless, there is still much to be known about the species throughout its extensive geographical distribution, so that the information we have today is surely no more than the tip of the iceberg.

In particular, more research effort on the culpeo's biology is urgently needed in countries such as Peru, Ecuador and Colombia, as well as in their respective ecoregions. The fine-scale distribution of the species as well as the distribution limits of each subspecies still remain to be well established. We need to know how the culpeo interacts with other species in their habitats, and more details about the potential role of the culpeo as a regulator of ecosystems. An effort should be made to characterize country-level population trends based on a better characterization of regional population dynamics and of population density drivers. Finally, real threats to culpeo populations must be identified, and we have to find evidence-based solutions for alleviating the conflict of the culpeo with livestock. ☞

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Complete list of the articles reviewed.

Figure S2 Graphical results from Kruskal-Wallis tests.