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Ecology of the culpeo (*Lycalopex culpaeus*): a review of knowledge and current gaps

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ABSTRACT

A deep review of the existing literature on the culpeo ecology is carried out, using scientific articles, book chapters and web resources. For information published before 1988, the synthesis made by a previous report was used. For subsequent information, bibliographic searches were carried out through the main servers, considering all of the generic names used to define the species so far. From this update, new general patterns on ecology, behavior and conservation concerns about culpeos are described. Gaps in current knowledge have been identified and new lines of research are proposed.

Most of the studies focused on diet, conflicts with the species in livestock areas, and on the use of space and habitat. We found an incomplete, poor justification for all of the proposed subspecies and their supposed geographical distribution, as well as a scarcity of studies on genetic issues, population dynamics and conservation concerns. It is remarkable that vast regions in South America holding culpeos lacked basic information on the species.

Diet studies describe a marked trend towards resources 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 is also a top predator that may regulate carnivorous communities, as well as that in arid environments culpeos can act as important seed dispersers.

The assessment of the conservation status of the species differs among regions, although there is no sufficient information to reach clear conclusions in most cases. Even so, in Ecuador and Colombia the species has been listed as ‘Vulnerable’. Direct persecution and habitat alteration are considered to be the most important threats that the species is facing in many countries, although other risk factors such as climate change could also have serious consequences for the canid at the global scale.

Keywords: Andean fox, canids, carnivore ecology, Neotropical region, top predator, wolves

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 & Novaro 2004). Body size presents sexual dimorphism with males being larger than females (Johnson & Franklin 1994a,b, Novaro 1997a, Travaini et al. 2000a). There is variation in the coat, which is usually dense, of reddish and grayish tones, with a dense tail with black hairs at the tip and sometimes also at the base.

The culpeo is a solitary canid except in the breeding season, when both sexes take care of the cubs (Jonhson & Frankling 1994a). They generally have one litter per year of three to five cubs. These become sexually mature adults at seven months of age (Crespo & 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, although detectability rates might differ between sexes. With respect to life expectancy, the longest-lived specimen reported in the wild reached 11 years old (Novaro 1997b, in Jiménez & Novaro 2004).

The International Union for Conservation of Nature and Natural Resources (IUCN) has classified the culpeo as of '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, and there are vast geographical areas for which there is no data on the species. In addition, information on its ecology is sometimes unclear and contradictory, which may reflect a large degree of plasticity in the ecology of the culpeo, or just an important lack of knowledge. In any case, the lack of information and its geographical bias make it difficult have a good picture of the biology of the species, and to correctly assess the status of its populations and their conservation threats.

The main goal of this work is to compile the existing ecological information for the species throughout its range, integrating the new results with results available in previous documents (Jiménez & Novaro 2004). From this expanded information framework, new general patterns of ecology, behavior and conservation status of the culpeo are suggested. Finally, we identify the most important knowledge gaps and propose new lines of research that are needed to better understand the biology of the species and its management implications.

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 Jacsik (1988), and for that one published between 1988 and 2018 we used 'Web of Knowledge', 'Google Scholar' and 'Scopus' research 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. two generic names that have been used to describe the species before).

In total we found 93 scientific publications (80 being articles), most of them from Argentina and Chile. There are vast regions with scarce information, especially in the northernmost areas of the range (Fig. 1). Regarding the topics dealt with in the articles, diet studies were the most abundant comprising descriptive and comparative diet studies, as well as others discussing the role of culpeo as a seed disperser (Fig. 1). There are also numerous studies that relate to the conservation of the species, focusing mainly on conflicts that arise from the interaction of culpeos with livestock. A number of studies on culpeo ecology are found describing the use of habitat and space. Furthermore, there are few biometric studies, and also some studies on taxonomy and evolution of south American canids. Finally, half of the studies come from protected areas (National Parks, etc), and the other half come from human-altered areas.

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 & Yepes 1960, Langguth 1975, Novak & Paradiso 1983, Redford & Eisenberg 1992), also reaching the islands of the far south (Brent 1971). It is also present on the Pacific and Atlantic coasts of Peru and Chile (Jaksić et al. 1980, 1992, Meserve et al. 1987, Medel

& Jaksić 1988, Marquet et al. 1993, MINAM 2011), reaching 4,800 meters above sea level (masl) in the Andes (Jiménez et al. 2008). The presence of the species in eastern Patagonia is considered recent, favored by the presence of hares and sheep (Zapata et al. 2005), as well as by the low density of pumas (*Puma concolor*) (Jiménez et al. 2016).

The average size of adult specimens varies throughout the range. In southern Peru, females weigh between 4-5 kg and males around 9 kg (Person 1951, in MINAM 2011), and in northern Chile the average adult weight is only 4-6 kg (Jiménez et al. 1995, Jiménez & 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 grey fox (*Lycalopex griseus*) (Fuentes & Jaksic 1979, Meserve et al. 1987, Jonshon 1992). 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 Novaro 1997a).

Currently, there is a high diversity of canids in South America, totaling 11 species (IUCN 2017). 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 (*L. culpaeus*) and the grey fox (*L. griseus*) diverged only 350,000 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 et al. 2017). 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, Burmuister 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 (see Bininda-Emonds et al. 1999, Zrzavý & Ricankova 2004). Moreover, recent DNA-based molecular studies are used to differentiate the species of the genus recognized currently (Chaves et al. 2011, Rodríguez-Castro et al. 2018).

Other studies (see Thomas 1914, Cabrera 1958, in Wozencraft 2005) classified the culpeo in the extinct 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 *Lycalopex culpaeus*, dental and cranial morphological criteria, as well as coat colour have been used to differentiate subspecies, often with few type specimens (Novaro 1997a, Guzmán et al. 2009). Thus, in the taxonomic listing of Cabrera (1931) six subspecies of culpeo were recorded and proposed. The works of Novaro (1997a) and Wozencraft (2005), based on morphometric and distribution criteria, support the existence of the same six subspecies (see also 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. reissi* (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 hair 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 (SIB 2018). It is present in Argentina. It is distributed across the Sierras Grandes of the province of Córdoba, possibly occupying nearby mountain ranges (see Pia 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 (Markhan 1970).

6) *L.c. lycoides* was proposed as a subspecies based on the conclusions that Lônnberg (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, Markhan 1970).

Indeed, these subspecies are not recognized today unanimously. From specimens from Chile and Argentina, the results of dendrocranial analysis (Guzmán et al. 2009) and mitochondrial DNA variation (Yanhe 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*. For *L.c. reissii* no genetic studies or morphological analyses have been developed after its initial description (see Guzmán et al. 2009). Finally, the Integrated Taxonomic Information System (ITIS 2016) currently recognizes only the three subspecies accepted by Guzmán et al (2009) (see Fig. 1).

Subespecies distribution

The distribution of the six subspecies of culpeo has been 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* (Figure 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 González et al. 2006). This coincidence could suggest a convergence in the forces that separate the populations of both species of vertebrates, favoring the appearance of new subspecies in the same areas. Still further work is required to finely resolve the limits between the culpeo subspecies (see Figure 1).

Overall it seems as if the work of Guzmán et al. (2009), is the only one that aims at characterizing he distribution of the subspecies of culpeo proposed for the entire range of the species. As compared to other studies, Guzman's is based on verifiable empirical data and on an exhaustive geographical sampling. Other studies generate confusion, which is evident in the taxonomic diffusion tools, where 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 present in practically all regions.

Nevertheless, there is a need to carry out more systematic studies on the distribution of the species, biometrical differences between subspecies (establishing and clearly describing the type specimens) and their phylogenetic relations. 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 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 variety of environments (Cofré & Marquet 1999). It also can occupy humanized habitats (Salvatori et al. 1999) and areas dedicated to livestock (Johnson & Franklin 1994b, Novaro et al. 2000a,b, Pía 2013), where its abundance can be high, even similar to that of well-preserved areas (Pia et al. 2003). Culpeo populations can reach high altitudes, up to 4,800 masl (Jiménez et al. 2008), such as the high steppes of the Andes and the puna's grasslands of Argentina (Pia 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 & 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 2016, Guntiñas et al. 2019) and Colombia (Ramírez 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 Bolivia (Olarte et al. 2009, Maldonado et al. 2014), Ecuador (Trujillo & Trujillo 2007, Tirira 2011), Peru (Cornejo-Farfán & Jiménez-Milón 2001) and Chile (Castro et al. 1994, Jaksić et al. 1980, Meserve et al. 1987, Martínez et al. 1993, Arim & Jaksić 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 & Novaro 2004, Gantchoff & Belant 2016) and Chile (Iriarte et al. 1989, Acosta-Jamett & Simoneti 2004). The species also occupies the coastal forests of *Nothofagus* in the subantarctic region (Gomez et al. 2010, Monteverde & Piudo 2011). Some individuals have been found in 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 (MINAN 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 2,600 masl (Tirira 2011, Guntiñas et al. 2019). However, in this region the species has been poorly studied, and new records are increasingly frequent in lower altitude ecosystems (Ordóñez-Delgado et al. 2018), and even in dry forests (e.g. Trujillo & Trujillo 2007). This lack of knowledge on the fine distribution, use of habitat and basic biology of the culpeo in Ecuador is surely 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 the results are very different. For example, Pía (2011) described that the culpeo was positively associated to grasslands under 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 & Simoneti, 2004). 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 suggests that other factors play a role in determining presence and abundance on 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 (Jonhson & Frankling 1994b). Cuyckens et al. (2015) explained the association of culpeos to wetlands with the presence of waterbirds that they would use as prey. Similarly, Oliarte 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 abundances of the culpeo 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).

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The fact that the density and type of vegetation cover influence the habitat selection of the culpeo could be explained by the prey availability variation among different types of vegetation and cover. Lantschner et al. (2012) concluded that a greater availability of hares and rodents would explain the greater presence of culpeos in native forests than in pine plantations. Acosta-Jamett and Simoneti (2004) suggested that culpeos could benefit from the increased abundance of prey in pine plantations, since the lower vegetation cover would facilitate hunting. In contrast, Simoneti et al. (2004) 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. (1993) did not observe any decrease in culpeo abundance in plantations without vegetation cover 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, territory competition, through direct agonistic interactions, etc. These type of interactions are poorly studied, with few published works. For example, in the high Andes of Ecuador it seems that culpeos behave as top predators, killing and eating other carnivorous species (Guntiñas et al. 2017). Then, it is not expectable that small or medium-sized carnivores influence culpeo's activity in high-Andean ecosystems. However, it has been shown that bigger predators than the culpeo, such as the puma, are capable to modify the use of space of the canid (Pía 2013).

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 & Jaksic 1988, Cornejo-Farfan & Jiménez-Milón 2001, Zapata et al. 2005, Achilles 2007, Walker et al. 2007) 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 & Eisenberg 1992, Jiménez & Novaro 2004), to being practically insectivorous in some regions (Guzmán-Sandoval 2007), or at certain times of the year (Iriarte et al. 1989), with clear tendencies also to frugivory (Ebensperger et al. 1991, Cornejo Farfán & Jiménez Milón 2001, Achilles 2007). The offer of prey richness for culpeos in Chile did vary over time (i.e. years) and with precipitation, so that culpeo diet can be affected by regional productivity variation and large-scale phenomena such as El Niño (Arim & Jaksić 2005).

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 & 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 would (Silva et al. 2004, 2005b).

Trophic groups

Small rodents form an important component of the culpeo's diet, both in terms of biomass contribution (Jaksic et al. 1980, Ebensperger et al. 1991, Achilles 2007) or in terms of frequency of occurrence (Jaksic et al. 1980, Meserve et al. 1987, Iriarte et al. 1989, Ebensperger et al. 1991, Colver et al. 1995, Novaro et al. 2000a, Pia et al. 2003, Correa & Roa 2005, Pia 2013). Cuis (*Cavia sp.*) are also consumed in Argentina (Pia 2011). However, in other studies this group is not so relevant (Guzman-Sandoval 2007). Although it is not the main source of food, medium-sized or large rodent species also 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 (Iriarte et al. 1989, Johnson 1992, Johnson & Franklin 1994b, Pia 2013, Zuñiga & Fuenzalida 2016), being sometimes more consumed than native fauna (Crespo & de Carlo 1963, Jaksic 1998, Novaro et al. 2000a, Rubio et al. 2013). In fact, it seems that the abundance of these exotic species has facilitated an increase 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 an area where hares were abundant, the diet was based on small mammals and hares were ignored as prey. In areas where native wild rabbits (*Sylvilagus brasiliensis*) are present a high consumption of them by culpeos is found (Beltrán-Ortíz et al. 2017, Guntiñas et al. 2017, Reina 2019, Cadena-Ortíz et al. 2020).

Medium and large size herbivorous mammals can be an important resource, particularly livestock, such as sheep and camelids in Chile, Argentina, Bolivia and Peru (Novaro et al. 2000a, Pia 2003, 2004, Zacari & Pacheco 2005, Lucherini 2016, Iranzo et al. 2018). Some species of 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 (CP 2017). Large herbivores can be consumed 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, 200b, Pia et al. 2003, Zacari & Pacheco 2005, Pia 2013, Guntiñas et al. 2017). In Chile, Novaro et al. (2009) clearly documents culpeo attacks on young vicuña (*Vicugna vicugna*), which are three times larger than the canid.

Other groups of mammals also appear in the diet of the culpeo, such as marsupials (Johnson & Franklin 1994b, Zapata et al. 2005, Achilles 2007, Walker et al. 2007, Palacios et al. 2012, Pia 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). In relation to birds and reptiles, with some exceptions (see Cuyckens et al. 2015 for birds; and Romo 1995, Achilles 2007 for reptiles), are not an important food resource in the culpeo diet (Ebensperger et al. 1991, Romo 1995, Pia et al. 2003, Achilles 2007, Guzman-Sandoval 2007).

Invertebrates, and especially coleoptera, are an important food resource in regions of Chile (Ebensperger et al. 1991, Correa & Roa 2005, Guzman-Sandoval 2007, Palacios et al. 2012), Peru (Cornejo-Farfán & Jiménez-Milón 2001) and Argentina (Zapata et al. 2005). These appear 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 (Pia 2013).

High fruit intake has been described at certain times of the year (Jaksic 1980, Castro et al. 1994, Romo 1995, Cornejo-Farfán & Jiménez-Milón 2001, Silva et al. 2005a, Trujillo & Trujillo 2007). Castro et al. (1994) observed that fruit consumption increased in periods where the presence and availability of small mammals was less than 10 individuals/ha. Colver et al. (1995) found that plant intake increased when values of trophic diversity indices were low, with a negative correlation in the consumption of coleoptera and plants. The high intake of fruits makes the culpeo an important seed disperser. The efficiency of the culpeo as disperser has been shown for carob trees (*Propollis flexuosa* and *P. pallida*) (Cornejo-Farfán & Jiménez-Milón 2001, Maldonado et al. 2014), as well as for the pepper (*Schinus molle*) (Castro et al. 1994). Bromeliad fruits (*Greigia sphacellata*) (Achilles 2007), ericaceae fruits (genus *Vaccinium*) (Romo 1995) and tree fruits (e.g. *Prunus cerasus*, *Malus domestica*) (Bravo et al. 2018), are also abundant in the diet of culpeo, but its role as seed disperser has not been shown. However, some authors suggest that culpeos would not really be an efficient disperser for all species (Bustamante et al. 1992, León-Cobos & Kalin-Arroyo 1994, Silva et al. 2005a), so that further research is needed on this important issue.

Trophic resources selection

There are several studies, carried out in different places and habitats, that compare the expected consumption of prey with its availability. A study from Argentina 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. 2000). Other study from Chile found a clear 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 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 the culpeo consumed smaller prey than would have been expected given this predator’s size, while Jiménez and Novaro (2004) observed a selection towards the largest micromammals available.

According to Meserve et al. (1987) and Iriarte et al. (1989), the key to understand trophic selection is not the abundance of prey, but the microhabitat space use of the prey (e.g. the use of open areas in scrublands) as well as its size. In agreement with this, Corley et al. (1995) conducted a study on prey vulnerability based on the morphology and behavior of prey. The most abundant mouse species, the jerbo mouse (*Eligmodontia typus*), was not the

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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 & Barja 2011), prey selection by the culpeo can depend, not only on prey abundance, but on other variables that also determine actual prey availability, such as accessibility to the predator, which is a function of type of habitat, prey use of the space, prey morphology and abilities, prey behavior, etc.

Although diet is one of the most studied aspects of culpeo biology, there are still large regions in South America where no information is available, and where studies on the diet of the species are totally lacking. 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, so we do not yet have a clear idea of the trophic ecology of culpeo at large scales. Regarding whether the species is a dietary generalist, or follows a facultative trophic specialist strategy (see Guntiñas 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 seasonally and across the species range, as well as studies on prey selection and how it changes with varying environmental factors.

SPATIAL ECOLOGY

Population density

Data on culpeo population density are only available from studies carried out in Argentina and Chile. Density values rarely exceed one specimen per square kilometer (km^2) varying between 0.2 and 2.6 individuals (Table 1). Different factors can influence this parameter. 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).

On the other hand, Pia et al. (2003) found similar densities between a natural protected park area and a livestock zone. Even higher densities are recorded in areas under intense hunting pressure (Novaro et al. 2000b, 2005) (see Table 1). 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 takes place (Crespo & de Carlo 1963, Novaro et al. 2000b). However, in Torres del Paine National Park (Chile), density values remained stable for approximately 10 years (Johnson 1992, in Jiménez & 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, emphasizing the importance of maintaining areas dedicated to conservation. 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 km^2 to 8 km^2 for females, and from 2 to 10 km^2 in the case of males (see Table 2). As for the differences between the sexes, there is divergence in the studies: in Argentina Novaro (2000) observed that the territories of males were larger. On the contrary, in Chile Salvatori et al. (1999) found that the territories of females were three times larger than those of males (Table 2). For their part, Jonshon and Frankling (1994a) did not observe any differences between the sexes. Nevertheless, the same territory can be shared by related individuals (Novaro et al. 2000a), and the boundaries of male territories can overlap (Jonshon & Frankling 1994a).

Radio-tracking studies have shown that humanized areas in Argentina were part of the territories of adult individuals, and that it was common to abandon territories due to the scarcity of prey (Novaro et al. 2000), which was also observed in 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 & de Carlo 1963).

Activity patterns

Studies of culpeo activity patterns are generally 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 show that in areas of Argentina, Chile and Bolivia, there is a bias (65% of records) towards nocturnal activity (Lucherini et al. 2009). Indeed, in many regions culpeos are considered mainly nocturnal. The same nocturnal activity patterns were also observed in other areas of Argentina (Walker et al. 2007, Tellaeche et al. 2014). 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 & 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 (Jacksic et al. 1980, Iriarte et al. 1989, Martinez et al. 1993, Johnson & Franklin 1994a, Salvatori et al. 1999, Walker et al. 2007, Lucherini et al. 2009, Olarte et al. 2009, Stucchi & Figueroa 2010) and suggested a mainly twilight activity.

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 (Jiménez et al. 2001, Olarte et al. 2009). However, nocturnal activity has also been observed in protected areas lacking hunting pressure (Monteverde & Piudo 2011), as well as diurnal activity in areas where the culpeo is hunted (Iriarte et al. 1989). Some authors suggest that their activity may be related to patterns of prey activity and availability (Johnson & Franklin 1994b, Salvatori et al. 1999), or to the interaction with other predators due to niche segregation and competition avoidance (Lucherini et al. 2009, Monteverde & Piudo 2011). Furthermore, Monteverde & Piudo (2011) mentioned seasonal differences in activity patterns, suggesting the highest 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, there is no information on the relationships it establishes with most of them. Most of the existing data collected has to do with interactions with grey foxes and pumas. The most relevant information is reviewed below.

Grey fox (*Lycalopex griseus*)

One of the best studied interactions to date is the relationship of the culpeo with the grey fox, a closely related species that currently coincides in large areas of Argentina, Chile and Peru. An allopatric distribution between both species is observed throughout the Andean mountain range. It is 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 & 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.

In relation to the use of space, in regions of Chile and Argentina there are areas where the territories of both species do not overlap (Johnson & Franklin 1994a), while in others a common use of space has been observed (Jiménez et al. 1996, Travaini et al. 2001, 2013). In Argentina, Traiviani et al. (2001) suggest that there is avoidance and probably a habitat and resource partitioning between the two canids. Results from scent stations show that the culpeo occupied steppe habitats and steppe-forest ecotone areas, while the grey fox was only present in the steppe (Bolkoviv et al. 2006). In southern Chile, culpeos selected forested areas of *Nothofagus* and dense scrub habitats, while grey foxes occupied transition habitats formed by mid-cover scrublands at higher altitudes (Johnson & Franklin 1994a). The culpeos would select those areas because of the higher densities of European hares and small rodents or because they provide more refuge (Johnson & 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 & Franklin 1994b). Johnson (1992) had found that culpeos consumed larger prey than grey foxes and that the degree of trophic overlap was low. In general, culpeos consume more hares than grey foxes (Jaksic et al. 1980, Zapata et al. 2005, Palacios et al. 2012). Indeed, the two species can potentially consume the same type of prey, with similar average weights, and the degree of diet overlap varies seasonally (Fuentes & Jaksic 1979, Zapata et al. 2005). All these authors suggest that the culpeo would exclude the grey fox 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 grey fox.

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 its interaction, where it was found that the culpeo decreases its abundance as the density of pumas increases (Novaro & Walker 2005). Pia (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), by using models of biological interactions, could not find that the culpeo distribution was influenced by the feline. 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 jacobitus*), the colocolo cat (*L. 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 (Jiménez et al. 2016). 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 & 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 (Yánez, 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 colocolo cats (Walker et al. 2007). The three species consumed the same resources (mainly rodents, birds and hares) but in different proportions: the culpeo was the most generalist, adding to its diet a great quantity 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 a 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 high consumption of predators that has been described for culpeos living in the high Andes, reaching up to 10% of total prey (Guntiñas et al. 2017). This high consumption clearly defines the culpeo as a super-predator, 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 in particular to dive into the consequences of the culpeo's activity on the population dynamics of other species as well as 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 creiceticola* were found in 4% of the culpeo excrements analyzed (Stein et al. 1994). Decades ago in the same region, *Toxocara canis* and *Echinoccocus patagonicus* were also described (Crespo & De Carlo 1936). 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* have been observed in captured culpeos (Millans et al. 2018).

In Peru, *E. granulosus* was detected in the intestine of livestock dogs, but not in 20 analyzed culpeos, which were positive to *Taenia hydatigena*, *T. multiceps*, *Mesocestoides lineatus*, *Dipylidium caninum*, *Uncinaria stenocephala* and *Oncicola canis* (Moro et al. 1998). Also in Peru, *Corynosoma obtuscens*, an acantocephalon linked to marine species, was found in the intestines of two culpeos (Tantalean et al. 2007).

In Bolivia, 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 Ecuador, Veintimilla (2015) described the existence of the parasites *Trichuris vulpis* and *Ancylostoma caninum*, the latter also present in the dogs analyzed in 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) highlights the need for more studies and points out that the incidence of this bacterium could have important consequences in wild populations. In this way, he suggests measures to minimize the possible contagion of dogs to culpeos in rural areas and in the Andean paramos.

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 Fray Jorge National Park and Puerto Velero (Moreira & Stutzin 2005). In subsequent studies, Acosta-Jamett et al. (2011, 2015) detected a seroprevalence of the virus in culpeos and grey foxes, and for the first time of canine parvovirus. In the same studies they compared the prevalence of distemper in these wild canids and dogs. City and town dogs had a higher risk of distemper compared to more rural dogs, probably due to the higher density and contact rate of dogs living in urban environments. 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 'Near Threatened' (Ojeda et al. 2012), and the real state of the populations is not known, with the consequent uncertainty regarding its assessment and the future of the species in the country. There are populations in Tierra del Fuego that show a clear negative trend, as in Bosques Petrificados Natural Monument (Lucherini & Zapata 2012), a possible consequence of the use of poison and the increase in puma densities (Lucherini & Zapata 2012). In addition, it has been calculated that only 14% of protected areas are large enough to sustain viable populations of culpeos (Jiménez & Novaro 2004).

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. lycoides*, is classified as 'Vulnerable'. The rest of the populations, which are attributed to the subspecies *L.c. culpaeus*, are considered as 'Least Concern', since a rapid recovery is observed after episodes of population decline. In Peru, it appears listed as a 'Least

Concern' species in CITES Appendix II (MINAM 2011), while in Bolivia the culpeo does not appear in the Red List of threatened species (Aguirre et al. 2009).

Finally, the situation of the culpeo in the northern part of its distribution seems less clear. In Colombia, it has been declared as a 'Vulnerable' species due to the supposed decrease of its population (MAVDT 2014), although others claim 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 catalogued as 'Vulnerable' (Tirira 2011), due to the suspected regression of its populations, although there are no reliable data over time. Currently there is a pilot project for long-term monitoring of wildlife with camera-traps in the so-called Sangay-Podocarpus Connectivity Corridor in southern Ecuador (Cisneros et al. 2020). Preliminary information on the places where there are historical records from camera trapping in this corridor suggests that the frequency of capture of culpeos and other mammals has dramatically decreased in the last five years, apparently due to the increase of feral dogs in the same areas (Cisneros, in prep.).

Direct persecution

Human activity is one of the main known causes of culpeos mortality. Until the 1990s, culpeos were heavily hunted for their skins (Crespo & De Carlo 1931, Travaini et al. 2003). Also, different parts of their body are used as 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, Pia 2011), although the importance of these problems 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 (Novaro et al. 2000b, Pia et al. 2003) and goats (Bellati & von Thurgen 1990, Muñoz 2017), as well as calves and juveniles of alpaca, vicuña and llama (Novaro et al. 2009, Zacari & Pacheco 2005, Donadio et al. 2012). These attacks, however, do not occur in all livestock regions (Palacios et al. 2012, Guntiñas et al. 2017). These losses determine a negative perception of the species on the part of the farmers (Bellati 1992a, Travaini et al.

2000b, Lucherini & Merino 2008), which causes the culpeo to be persecuted (legally or illegally) and to be heavily hunted with traps, dogs and poison in certain regions, where up to 75% of the local culpeo 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). In Ecuador, carrion poisoning to control livestock predators illegally, especially feral dogs, is also killing culpeos (Yánez, pers. comm.).

However, the control of culpeo populations has triggered a controversial debate (see for a global discussion Treves et al. 2016, Lozano et al. 2017). Bellati & von Thurgen (1990), studying cattle 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 & Pacheco 2005), where the losses of camelids due to health problems were between 2.3 and 6.4 times greater than those produced by predation. Both studies suggest that aside from current carnivore control programs, other more important drivers of livestock mortality must be considered and addressed. In addition, there are attacks on cattle by dogs (Montecino-Latorre & Martín 2018) that are erroneously attributed also to culpeos (Aliaga-Rossel et al. 2012).

The response of the canine populations to these control actions is unclear across all regions. Argentina is probably the region in which most effort has been made to characterize the population trends of the culpeo. Since the 1980s, systematic monitoring programs of canine populations have been implemented, improved and expanded (see von Thüngen 1991, Novaro et al. 1996, 2000b). This has allowed gaining an understanding of population dynamics in environments under hunting pressure. Novaro (1995) and Novaro et al. (2005) claim that in the different Argentinean regions the culpeo has not disappeared due to the existence of source-sink dynamics: in cattle ranches where there is a low hunting pressure, dispersing animals are generated (acting as source areas), which occupy the empty spaces left by the high mortality rates in the ranches where culpeos are heavily hunted (sink areas), which allows population persistence.

This type of source-sink dynamics is common to other canine species populations, such as the 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. 2017). Population models indicate that below 30% of the total surface that acts as a source area (currently 37%) the culpeo populations could not recover (Novaro et al. 2005). This emphasizes the need to know the size and the spatial disposition of the areas with and without hunting if the conservation of the species is to be ensured.

There is currently a management plan for canids in Argentina (Bolkovic & Ramadori 2006) that contemplates reducing the pressure on culpeos and avoiding attacks on livestock. One of these measures is the introduction of guard dogs in the fields, a measure that usually works well to prevent attacks on livestock (von Thüngen 1998, Bolkovic & Ramadori 2006, Eklund et al. 2017), especially when it is in combination with others (see Lozano et al. 2017). Furthermore, Travaini et al. (2001, 2013) observed that culpeos avoided areas where new elements (i.e. strange stimuli) were installed in the environment, so they propose to implement 'avoidance stations' in livestock areas.

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 fragmentation, as it appears to be highly adaptable to changes in the landscape (see Acosta-Janett & 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 & Ortega 2010, in MINAM 2011). In addition, areas with scarce plant cover, and close to human presence, can be risk zones 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 (Guntiñas 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.

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CONCLUSIONS

The culpeo is a canid that uses a wide variety of trophic and spatial resources, and it is found in many of the ecosystems of South America. Behavioral patterns are modeled by a multitude of factors, with prey availability being one of the most important, as well as interaction with other carnivores. Nevertheless, it is evident that at a local scale there is a marked tendency towards 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.

The assessment of the conservation status of the species differs among regions, depending on the actual status of the species and the degree of knowledge about its populations in each country. In general, there is no sufficient information to draw clear conclusions on the culpeo's conservation status or population trends. In relation to potential threats, it seems that direct persecution and habitat alteration (such as that caused by mining or grazing) are the most obvious risk factors faced by the species, although transmission of pathogens and widespread changes in the landscape due to ecological drivers (such as the effects of climate change) are factors that could also affect the species at a global level. The existence of a network of protected natural areas, such as national parks, nature parks, life reserves, etc, has a beneficial effect on the conservation of culpeos. However, these areas must have an extension that guarantees the long-term viability of canid populations.

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, or on the dynamics of contagion and prevalence of pathogens in Chile. However, more works are 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.

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Fig.1. Map of the proposed distribution of culpeo subspecies based on studies by Guzman et al. (2009), and distribution area for the species defined by Lucherini (2016) (top right map). The number of studies published on the species between 1987 and 2020 for each region as well as the general themes, are also shown in the large map (left).

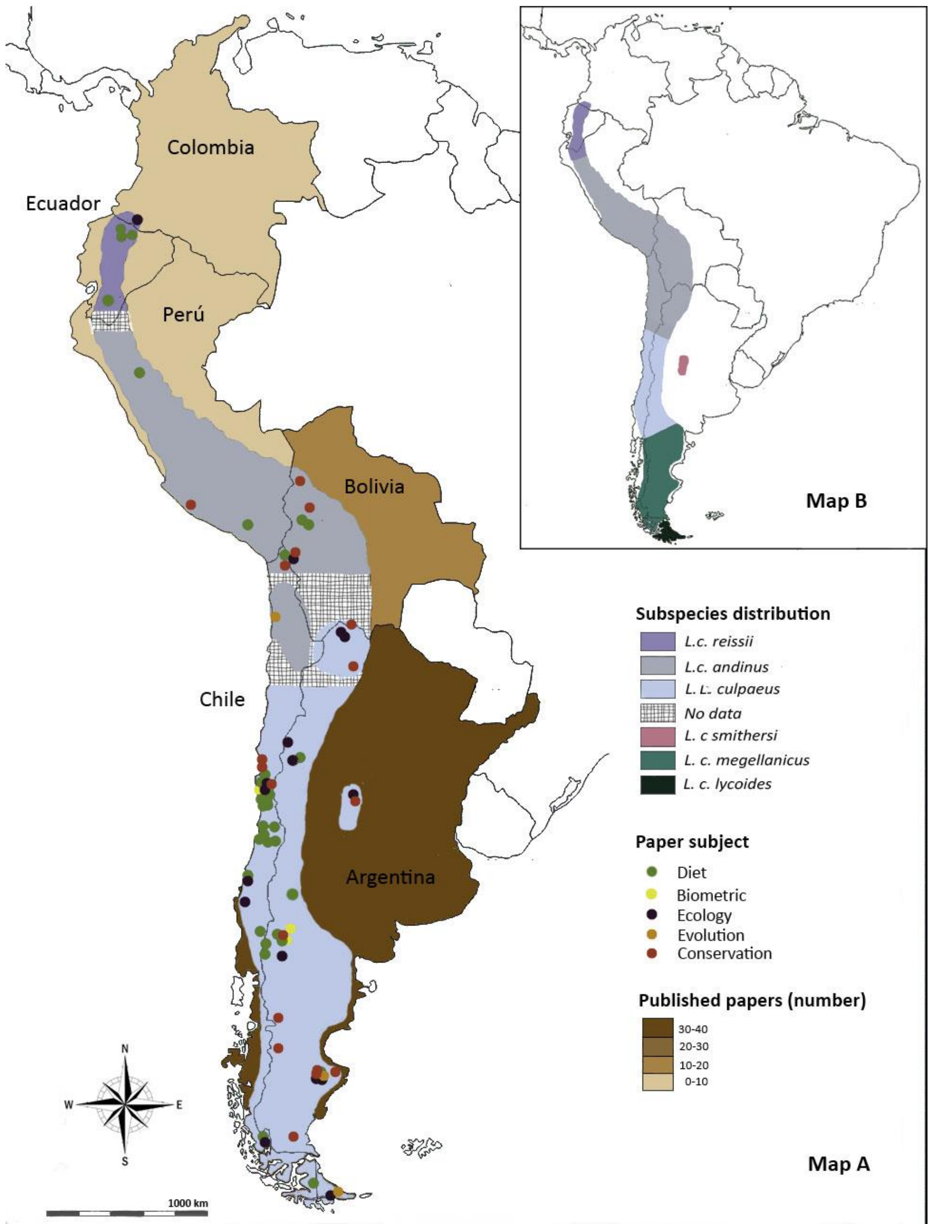

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Table 1. Culpeo densities reported in different studies, as well as the methods employed, study areas and countries.

(culpeos/km² + SE)	(Scats/km)	Method	Study area	Country	Source
0.7		Intensive trapping	North-west Patagonia	Argentina	Crespo and De Carlo 1963 (In Bellati and Thurgen 1990)
1.9		_	North-west Patagonia	Argentina	Rabinovich et al. 1987 (In Bellati and Thurgen 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 In1994: 0.82 ± 0.64					In non-hunting area
In 1993: 1.31 ± 0.76 In 1994: 1.07 ± 0.72					In hunting area
0.2 ± 1.3					In the total area
1.3		Based on sightings	Torres del Paine	Chile	J. Rau pers.comn (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	Pia et al. 2003
	1.01		Quebrada del Condorio National Park		In National Park
	0.87		Sierras Grandes of Córdoba		In a ranch

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Table 2. 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 1997 (In Pacheco et al. 2004)
3.5 ± 0.6			100% MCP	Jonhson and Franklin 1994
7.7 ± 1.4			95% HME	Jonhson and Franklin 1994
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