

1 **Biogeographical patterns and diversity in the diet of the**
2 **culpeo (*Lycalopex culpaeus*) in South America**

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1 **ABSTRACT**

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3 Here we describe the dietary patterns of the culpeo (or Andean fox) at a biogeographical scale. We
4 also analyze the influence of exotic lagomorphs on its diet and explore differences between culpeo
5 subspecies. We selected 17 mutually comparable diet studies, which include 19 independent diet
6 assessments. Then, we extracted and standardized the values of the different diet components from
7 these studies and calculated the relative frequency of occurrence (RF) of the ten main trophic groups
8 that we found. Further, we calculated the Shannon-Wiener H' trophic diversity index.

9 The results showed that small mammals (41%), lagomorphs (21%), invertebrates (12.4%) and large
10 herbivores (7.3%) were the most consumed groups. A factorial analysis of all trophic groups rendered
11 four orthogonal factors that were used as response variables in relation to a set of environmental
12 predictors. Altitude correlated with most factors (i.e. trophic groups). Exotic lagomorphs were
13 consumed in lowlands, in higher latitudes and in regions showing high values of the human footprint
14 index, replacing in these areas native fauna as the main prey. There were no differences in diet
15 between the two main culpeo subspecies analysed, *L.c. culpaeus* and *L.c. andinus*.

16 Finally, the best explanatory models (GLM) of trophic diversity selected, using the Akaike's
17 information criterion (AIC), showed that the most diverse diets were those composed of large
18 herbivores, edentates, carnivorous species, birds and herptiles (i.e. amphibians and reptiles), in areas
19 of high rainfall located in protected areas. Neither latitude nor altitude seemed to have an effect on
20 the trophic diversity of the culpeos, as they were not retained by the final models.

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28 **Keywords:** Andean fox, canids, carnivores, Neotropical region, top predator, trophic ecology, wolves

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1 Introduction

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3 The functioning and diverse characteristics of ecosystems are determined and conditioned by
4 a multitude of ecological processes and parameters, such as evolutionary history and the dynamics of
5 species interaction, such as parasitic, competitive or predator-prey relationships, the latter being the
6 most important in the configuration of food webs (Ritchie et al., 2012; Soe et al., 2017). In fact, large
7 carnivores and mesopredator predation tend to play a prominent, and often key, role in the functioning
8 of ecosystems (Newsome & Ripple, 2015), affecting prey population cycles (Kausrud et al., 2008)
9 and producing multiple cascading effects (Coulson & Malo 2008; Ripple et al., 2014).

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11 In turn, the ecology of a predatory species is influenced by the conditions of the environment
12 in which it lives. Thus, when the different populations that make up a widely distributed species are
13 considered, there is a wide range of environmental conditions that vary across its range. Faced with
14 different ecological conditions each species presents a certain degree of flexibility in their behavior,
15 which depending on its range and geneflow between subpopulations, can define the species as
16 generalist or specialist. In particular, and in relation to the extent of the trophic niche and prey
17 selection criteria, predators can be considered as generalists or opportunists, strict specialists or as
18 facultative specialists (Glasser, 1984; Jaksic, 2007).

19 In the case of predators that have a wide distribution range, strong spatial variation in diet
20 patterns is observed when studied at a biogeographic scale, as shown for numerous species such as
21 the brown bear (*Ursus arctos*) (Vulla et al., 2009), the Eurasian otter (*Lutra lutra*) (Clavero et al.,
22 2003), the European wildcat (*Felis silvestris*) (Lozano et al., 2006), the European badger (*Meles
23 meles*) (Hounsone & Delahay, 2005), or the red fox (*Vulpes vulpes*) (Soe et al., 2017). For example,
24 it is usual to find clear correlations in diet variation with latitude and climate, also related to the
25 trophic plasticity detected with generalist or facultative specialist strategies (Virgós et al.,1999; Cox
26 & Moore 2005; Lozano et al., 2006). Indeed, diet can have important implications at several levels.
27 On the one hand, there are a multitude of factors associated with the trophic behavior of species,
28 which can have repercussions on other aspects of their ecology. For example, the abundance and
29 distribution of native prey not only affect dietary patterns but also space use, morphological
30 characteristics and mating cycles (Dayan & Simberloff, 1996). On the other hand, the incorporation
31 of exotic or non-native species into the diet and the consumption of anthropogenic food waste can
32 also directly affect the abundance, distribution and behavior of carnivore species (Bino et al., 2010).
33 In addition, processes of competition among predators and their differential vulnerability can modify
34 both resource use patterns, as seen in medium-sized carnivores in North America (Lesmeister et al.,

1 2015), and physical characteristics of the predator, such as body size, through processes of niche
2 segregation (Jimenez et al., 1996).

3 To the factors mentioned above we must add the growing uncertainty on the ability of
4 predators and prey to respond to the effects of global phenomena such as climate change (Bailey &
5 van de Pol, 2016; Keith & Bull, 2016), and other anthropogenic factors (Sandom et al., 2014), which
6 can promote important changes in trophic interactions at a global scale (Grosbois et al., 2008; Merilä,
7 2012) triggering profound changes in the structure of ecosystems (Newsome et al, 2015). For this
8 reason, a better understanding of the trophic ecology of species and their interaction with
9 environmental factors at various scales is necessary to develop species conservation strategies that
10 mitigate the effects of global problems on ecosystems.

11 The way to evaluate the trophic strategy and plasticity of a species is to approach its study at
12 large spatial scales, through the comparison of habitat- and region-specific diet within its range, based
13 on the review and meta-analysis of local data. For many species this biogeographical dietary approach
14 is not yet possible due to the few studies available at a local scale. Fortunately, this is not the case of
15 the culpeo (*Lycalopex culpaeus*), also called Andean fox, a canid that is distributed in various habitats
16 from southern Colombia, through Ecuador, Peru, Bolivia and Chile, to Patagonia and Tierra de Fuego
17 in Argentina (Lucherini, 2016; Guntiñas et al., 2021), for which a number of diet studies have been
18 published. Although on a global scale the International Union for Conservation of Nature (IUCN)
19 classified the culpeo for its entire range as ‘Least Concern’ (Lucherini, 2016), this good conservation
20 status is not mirrored at regional scales. For instance, in Colombia and Ecuador the culpeo is listed
21 as a threatened species (Tirira, 2011; MADT, 2014), emphasizing the need to deepen the knowledge
22 of its ecology.

23 Local studies on the culpeo diet interpret the trophic strategies of the species differently (see
24 Guntiñas et al., 2021), considering it a strict carnivore (Iriarte et al., 1989; Redford & Eisenberg,
25 1992; Jiménez & Novaro, 2004), a practically insectivorous predator (Guzmán-Sandoval, 2007) with
26 tendencies to frugivory (Ebensperger et al., 1991; Cornejo-Farfán & Jiménez-Milón, 2001), or a
27 predator with high level of trophic plasticity that is capable of using a wide combination of resources
28 (Jaksic et al., 1993; Johnson & Franklin 1994b; Castro et al., 1994). Recent studies suggest that culpeo
29 behaves more like a facultative specialist (Guntiñas et al., 2017). However, to date no studies have
30 been carried out that consider the data as a whole at a biogeographical scale so that the global trophic
31 patterns can be detected, as well as their ecological correlates, which would allow a panoramic view
32 of the culpeo trophic ecology to be obtained.

1 The present work reviews culpeo diet studies and data published throughout the species range,
2 with the following aims: 1) to describe the general patterns of the culpeo diet at a biogeographical
3 scale through a meta-analysis and the environmental factors that determine them; 2) to assess the
4 degree of the consumption of exotic lagomorphs by culpeos and, in particular, the influence of this
5 consumption on the use of native fauna as a trophic resource (Crespo & de Carlo, 1963; Jaksic, 1998;
6 Novaro et al., 2000a; Rubio et al., 2013); 3) to evaluate the dietary differences between the two main
7 culpeo subspecies described by Guzmán et al. (2009); and 4) to obtain an explanatory model of the
8 trophic diversity of culpeo in South America.

9

10 **Material and Methods**

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12 We carried out a complete compilation of the published articles and other reports on the diet
13 of the species. For information published prior to 1988 we used the review by Medel & Jaksic (1988).
14 For works published after 1988, we carried out a systematic bibliographic search using the ‘Web of
15 Knowledge’, ‘Google Scholar’ and ‘Scopus’ servers, including terms such as diet, culpeo, Andean
16 fox, *Lycalopex culpaeus*, páramo wolf, and also the specific names that have been used to describe
17 the culpeo previously (i.e. *Dusicyon culpaeus* and *Pseudalopex culpaeus*) (see for more details
18 Guntiñas et al., 2021).

19 Once we selected all the existing studies, a subset was chosen to be used for statistical
20 analyses. These studies met a number of requirements to ensure the representativeness of the data and
21 the statistical power (Guntiñas et al., 2021). Firstly, they had to provide tables of data on the culpeo
22 diet in the form of either frequency of occurrence, relative frequency of occurrence or number of prey
23 items, as well as the sample sizes for the scats or stomachs analyzed. The data had to describe all the
24 resources consumed by the species, so that studies with data focusing only on a particular prey group
25 were excluded. Secondly, the papers had to have a minimum sample size of 30 (Lozano et al., 2006;
26 Soe et al., 2017) per habitat type considered, treating these habitat units as independent samples. And
27 finally, data had to be representative of the annual cycle in each habitat unit (Lozano et al., 2006).

28 With all, 17 (16 articles and one thesis) studies were finally selected meeting the
29 aforementioned criteria, with a total of 19 independent samples (see Figure 1). Altogether the dataset
30 included 4115 scats and/or stomachs with a total of 6220 trophic elements. Due to the variability in
31 data presentation between studies, we standardized the data of the selected studies by calculating the
32 relative frequency of occurrence (RF) for each independent sample. For the analyses, we did not
33 consider whether identified trophic items came from stomachs or scats (Lozano et al., 2006).

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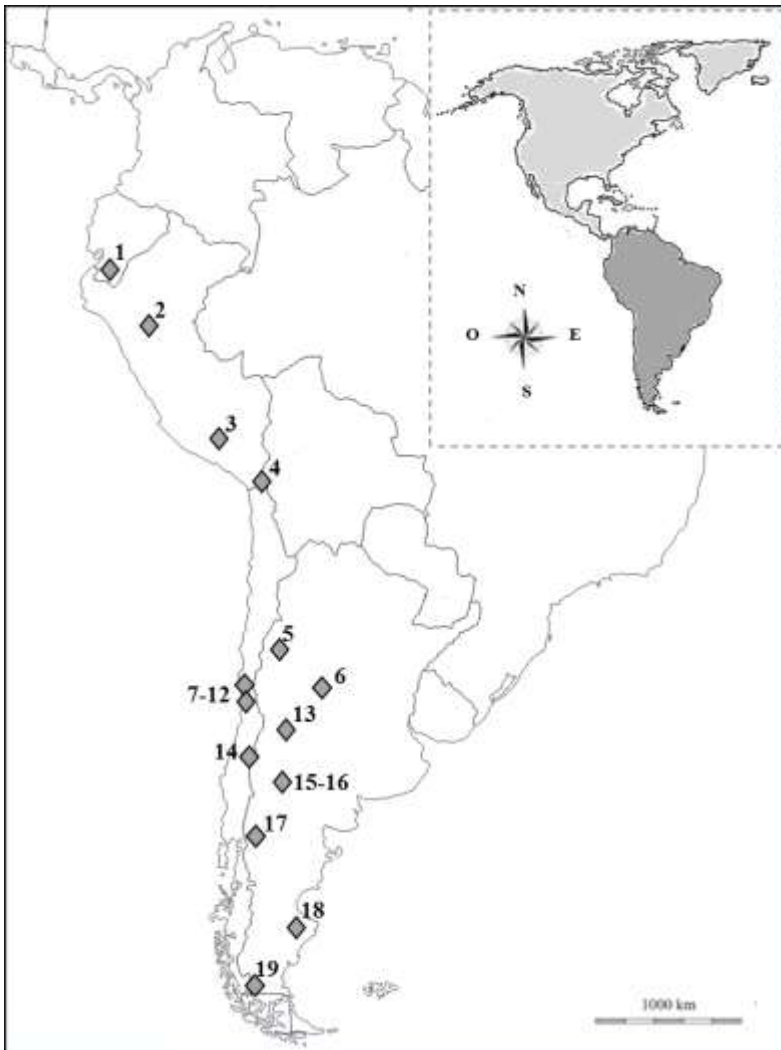


Figure 1.

Location of the different study areas:

1. Guntiñas *et al.*, 2017
2. Romo *et al.*, 1995
3. Cornejo & Jiménez, 2001
4. Marquet *et al.*, 1993
5. Walker *et al.*, 2007
6. Pía *et al.*, 2003
7. Ebensperger *et al.*, 1991
- 8-9. Iriarte *et al.*, 1989
10. Jaksic *et al.*, 1980
- 11-12. Rubio *et al.*, 2013
13. Berg, 2009
14. Achilles, 2007
15. Palacios *et al.*, 2012
16. Novaro *et al.*, 2000
17. Monteverde *et al.*, 2011
18. Zapata *et al.*, 2005
19. Johnson y Franklin, 1994

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7 *Selection of variables*

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9 We categorized the different elements that composed the culpeo diet into ten main trophic
10 groups (Guntiñas *et al.*, 2021): ‘small mammals’ (i.e. mammals weighing less than 300 g, mainly
11 rodents, insectivores and some marsupial species), ‘big rodents’, ‘lagomorphs’, ‘carnivorous’ (i.e.
12 carnivores and carnivorous marsupials), ‘edentates’ (i.e. armadillos); ‘large herbivores’ (i.e. deer,
13 camelids and livestock), ‘birds’, ‘eggs’, ‘herptiles’ (i.e. amphibians and reptiles), and ‘invertebrates’.
14 The relative frequency of occurrence (RF) for each of these trophic groups was recalculated by
15 dividing the number of items in each group by the total number of items. The presence of plant matter
16 in the diet of each study was also recorded.

17

1 We also calculated the trophic diversity of the culpeo in each independent sample as the value
2 of the Shannon-Wiener H' diversity index (Weaver & Shannon, 1949). In order to calculate and
3 compare the value of the index between the different studies, the trophic groups were standardized to
4 the same taxonomic level as the groups in the less detailed publications, leaving the following 19
5 groups: rodents, soriids, procyonids, edentates, mustelids, marsupials, lagomorphs, cattle (sheep),
6 cervids, camelids, felids, carrion, birds, reptiles, fish, amphibians, invertebrates, eggs and rubbish.

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8 We recorded the main habitat type in which the work was carried out using the geographical
9 location of each of the studies where the samples have been taken. Further, we determined whether
10 the site was part of a protected area or not, the average annual rainfall, the altitude and the latitude.
11 We also measured the degree of interference of human activity in the territory by calculating the
12 human footprint index for each independent sample. To do it, we used two of the human footprint
13 index layers which were downloaded (for the years 1993 and 2009) from the Center for International
14 Earth Science Information Network (CIESIN). Based on the sampling year for each study, we
15 attributed the value of the index layer corresponding to the nearest year to each area. On the other
16 hand, we tested whether introduced (i.e. exotic) lagomorph species existed in the different study areas.
17 For this purpose, the layers of presence of the species of interest available on the IUCN server were
18 downloaded and the overlap with the sampling areas of the selected studies was checked. To observe
19 possible differences in diet according to the subspecies, each study was attributed the subspecies *L.c.*
20 *andinus*, *L.c. culpaeus* or *L.c. reissii* based on their geographical distribution (Guzmán et al., 2009;
21 Guntiñas et al., 2021). The subspecies *L.c. reissii* was finally represented by one paper only, so that
22 it was not considered in the analyses.

23 *Statistical analysis*

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26 In order to perform parametric analyses, we first checked both the normality of the considered
27 variables and the homogeneity of variances through the Levene's test, transforming the variables that
28 were not normal (Zar, 2009). Alternatively, we checked whether the kurtosis of these variables was
29 positive, which allows us to assume a low probability of committing type I statistical error
30 (Underwood, 1996).

31 We characterized the different types of culpeo diet by grouping the relative frequencies (RF)
32 of the ten trophic groups into orthogonal factors carrying out a factor analysis and using the principal
33 component analysis (PCA) algorithm. We also tested for spatial autocorrelation in the values of the
34 extracted factors and the trophic diversity values (H') by calculating Moran's index I and their
35 respective correlograms (Dormann et al., 2007; Rangel et al., 2010).

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Pearson's correlation between orthogonal factors and latitude, altitude, human footprint index and trophic diversity was calculated. In addition, we checked whether the latter correlated with each of the RFs of the trophic groups. We also explored whether the degree of protection of the study areas (with or without legal protection) and habitat type (scrub, steppe or mosaic) explained variation in the trophic factors. The influence of the presence of plant matter in the diet on trophic factors and the trophic diversity was also tested by performing a two-way and a one-way MANOVA analyses, respectively. We also assessed whether the presence of exotic lagomorphs, introduced into the study areas, influenced the diet of the species through a MANOVA with the trophic factors (excluding the factor that included the lagomorph group) plus the RF of big rodents and eggs. Furthermore, we analyzed the differences between the diets of the subspecies *L.c. andinus* and *L.c. culpaeus* by means of a MANOVA with the subspecies as a fixed factor and the trophic factors as dependent variables, as well as an ANOVA with the trophic diversity also as a dependent variable.

Finally, general linear models (GLM) were constructed for trophic diversity (H') as a response variable, using 10 predictor variables: the four trophic orthogonal factors, latitude, altitude, protected area, habitat type, precipitation and the human footprint index. Of the total number of models obtained, the most parsimonious were identified through a selection process applying the Akaike's criterion (Burnham & Anderson, 2002). Software for conducting the statistical analyses included SAM v.4.0 (Rangel et al., 2010) and Statistica 10 (StatSoft, 2011).

Results

Relative frequency (RF) values of all the trophic groups calculated for each independent sample, as well as the Shannon-Wiener H' trophic diversity index, are shown in Figure 2. The mean value of the latter was 1.23 (range: 0.36 - 1.88). The mean values of relative frequency (RF), expressed as a percentage, were: 41% small mammals, 21% lagomorphs, 12.4% invertebrates, 7.3% large herbivores, 7.3% birds, 6% big rodents, 2.9% herptiles, 0.9% carnivorous, 0.8% edentates and 0.7% eggs.

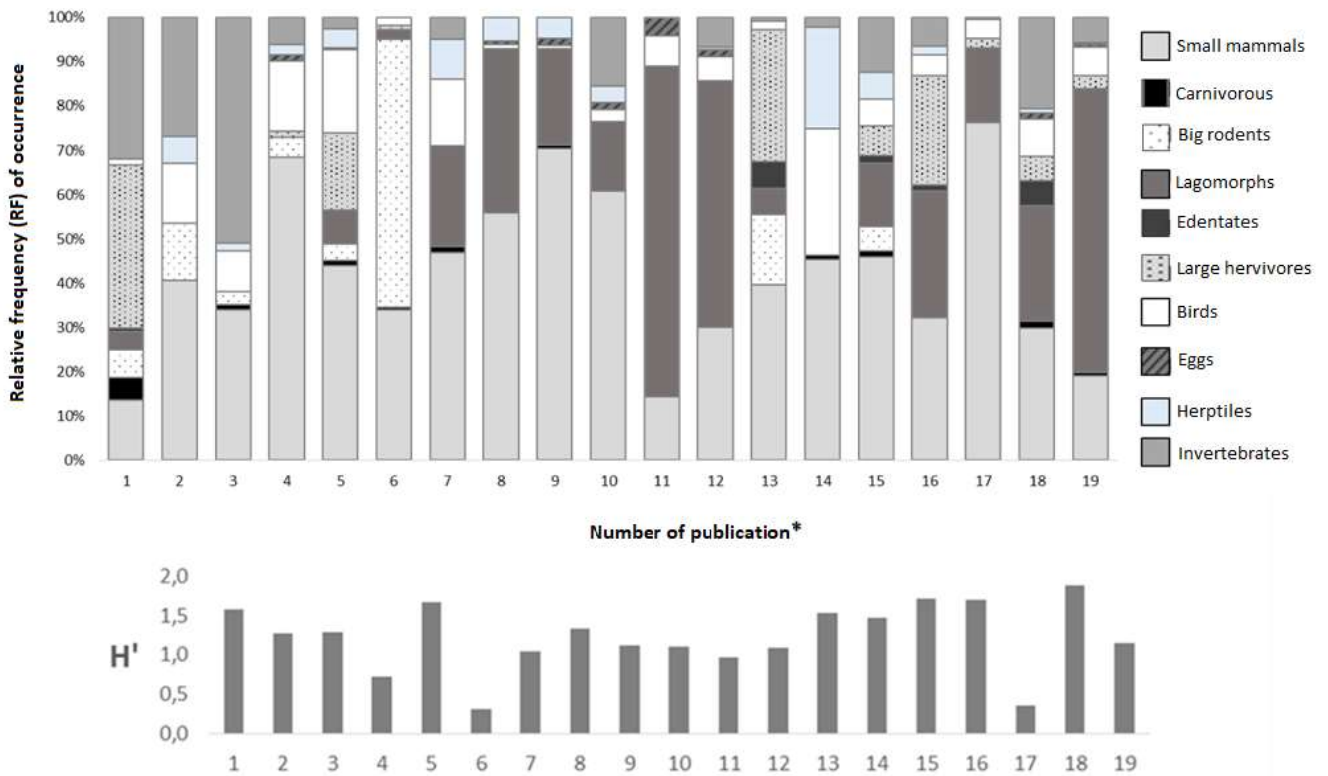
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Figure 2. Relative frequency of occurrence (RF) of the ten trophic groups and values of Shannon-Wiener trophic

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diversity (H') index for each independent sample considered in this study.



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5 * Publication number: 1. Guntiñas et al., 2017; 2. Romo et al., 1995; 3. Cornejo-Farfán & Jiménez-Milón, 2001; 4. Marquet et al.,
6 1993; 5. Walker et al., 2007; 6. Pía et al., 2003; 7. Ebersperger et al., 1991; 8.9. Iriarte et al., 1989; 10. Jaksic et al., 1980; 11.12. Rubio
7 et al., 2013; 13. Berg, 2009; 14. Achilles, 2007; 15. Palacios et al., 2012; 16. Novaro et al., 2000; 17. Monteverde et al., 2011; 18. Zapata
8 et al., 2005; 19. Johnson & Franklin, 1994.

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10 The factor analysis using the RF of the ten trophic groups generated four orthogonal factors
11 (using standardized varimax rotation of axes) that overall explained 73.6% of the variance of the
12 original variables (Table 1). The first factor describes a gradient from culpeo diets with high
13 consumption of carnivorous, large herbivores and edentates (negative scores) towards less rich diets
14 in these groups. The second factor is a gradient from high consumption of lagomorphs and eggs
15 (negative scores) to poorer diets in these trophic groups and richer in big rodents (positive scores).
16 The third factor is a gradient from diets with high consumption of birds and herptiles (negative scores)
17 to low intake of these prey (positive scores). And finally, the fourth factor describes a gradient from
18 diets with high consumption of small mammals (negative scores) to high consumption of
19 invertebrates (positive scores).

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1 **Table 1.** Description of the four orthogonal factors obtained from the factor analysis with the ten trophic groups
2 considered. * indicates significant correlations of the variables.

Variables	Factor 1	Factor 2	Factor 3	Factor 4
Large herbivores	-0.92*	0.16	0.15	-0.01
Big rodents	0.17	0.65*	0.60	-0.04
Birds	0.12	0.08	-0.70*	-0.03
Carnivorous	-0.86*	0.17	0.05	0.01
Edentates	-0.46*	-0.08	0.10	0.16
Eggs	0.21	-0.81*	0.12	-0.20
Invertebrates	0.14	0.32	-0.43	0.74*
Herptiles	0.27	0.25	-0.76*	0.05
Lagomorphs	0.1	-0.9*	0.33	0.13
Small mammals	0.30	0.13	-0.21	-0.85*
Eigenvalue	2.08	2.10	1.82	1.36
% Explained variance	20.82	21.00	18.18	13.57

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4 According to the correlograms of the four trophic orthogonal factors and trophic diversity H' ,
5 which were based on Moran's I index, the diet of the culpeo in South America was not spatially
6 structured, since in general the values that describe its diet in the reviewed studies did not present
7 spatial autocorrelation.

8 Factor 1 was negatively correlated with H' trophic diversity (see Table 2), so the inclusion of
9 carnivorous species, large herbivores and edentates in the diet of the culpeo significantly increased
10 the trophic diversity of the canid, as well as the consumption of birds and herptiles, as factor 3 was
11 also negatively correlated with trophic diversity. Factor 2 correlated positively with altitude, and
12 negatively with the human footprint index and latitude (Figure 3). Therefore, at higher altitudes (and
13 in areas of lower latitudes and human influence) the culpeo consumes more big rodents, while at
14 higher latitudes and when the human footprint is greater in the environment, consumption of
15 lagomorphs and eggs increases. Factor 4 was negatively correlated with altitude (Figure 3), indicating
16 that higher altitudes result in higher consumption of small mammals and that invertebrates are more
17 prevalent in the diet at lower altitudes. Taking each of the ten trophic groups one by one, those that
18 contribute the most to the increase in the diversity of the culpeo diet are large herbivores and birds,
19 while diets including big rodents tend to be less diverse (Table 2).

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Table 2. Pearson's correlations of the four trophic orthogonal factors extracted from the factor analysis with latitude, altitude, human footprint index and trophic diversity H' index. The correlations between the latter and the relative frequency (RF) of the ten trophic groups considered in the review ($n = 19$) are also shown.

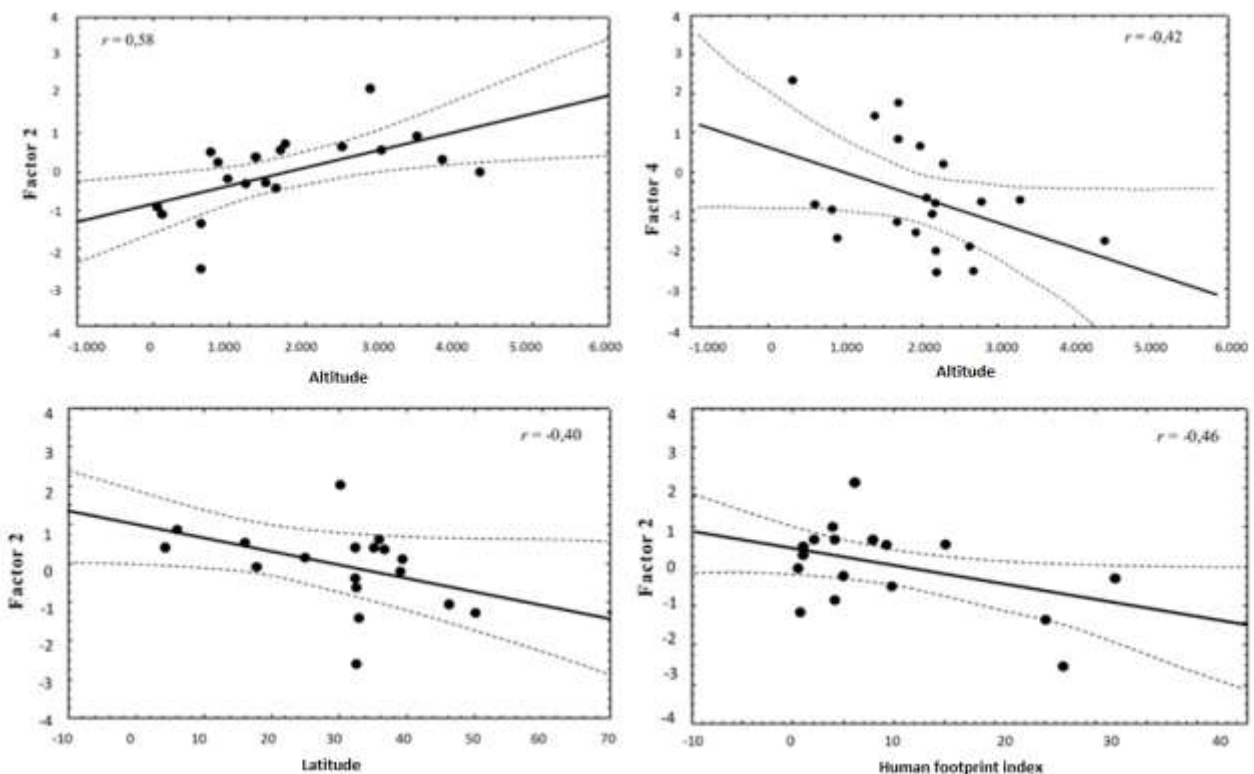
	Latitude	Altitude	Human footprint index	H'
Factor 1	0.26	-0.08	0.22	-0.58 *
Factor 2	-0.40 †	0.58 *	-0.46 *	0.13
Factor 3	0.21	-0.22	0.19	-0.43 *
Factor 4	0.29	-0.43 *	0.02	0.25

	H'
Small mammals	-0.32
Carnivorous	0.33
Big rodents	-0.42 †
Lagomorphs	-0.02
Edentates	0.54
Large herbivores	0.45 *
Birds	0.17 *
Eggs	-0.17
Herptiles	0.29
Invertebrates	0.16

* Significant correlation ($p < 0.05$).

† Marginally non-significant correlation ($p < 0.10$)

Figure 3. Relationships between factors 2 and 4 with altitude, as well as factor 2 with latitude and the human footprint index.



1 The consumption of plant material tended to influence the diet of the culpeo (MANOVA,
2 Wilks' Lambda = 0.59; $F_{4,14} = 2.4$; $p = 0.09$), with significant differences in factor 3 ($F_{1,17} = 4.8$; $p =$
3 0.04). Thus, when there was consumption of plants, there was also a greater consumption of birds
4 and herptiles. However, the consumption of plant matter had no effect on the trophic diversity H'
5 index ($F_{1,17} = 0.01$; $p = 0.98$).

6 Habitat type influenced the diet of the culpeo given that significant differences were found in
7 the trophic orthogonal factors (Table 3), specifically a positive relationship between factor 3 and the
8 mosaic type habitat ($F_{2,13} = 8.13$; $p = 0.005$). Therefore, in mosaic habitats the culpeo consumed less
9 birds and herptiles (Figure 4). No significant differences were detected in the trophic factors
10 depending on whether the studies were carried out in protected or unprotected areas (Table 3).

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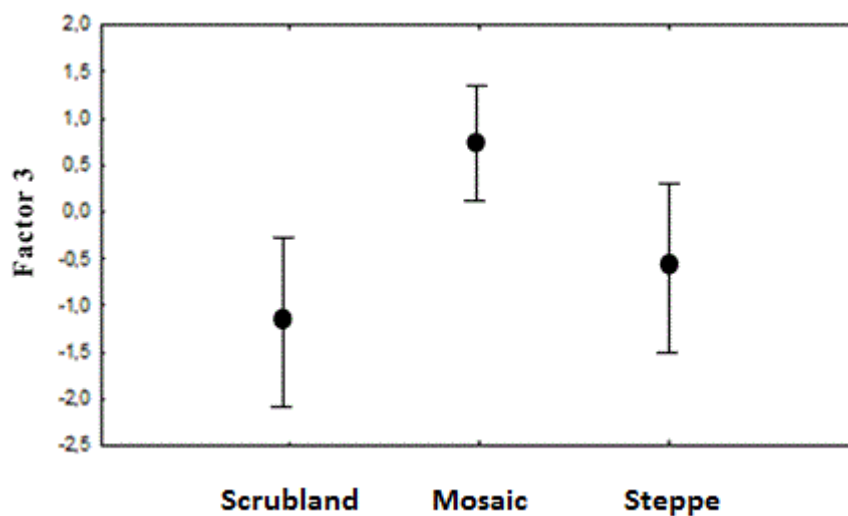
12 **Table 3.** Two-way MANOVA with the four trophic orthogonal factors as dependent variables and two fixed factors
13 (protected area and habitat type).
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	Wilks' Lambda	F	df effect	df error	p
Protected area	0.63	1.49	4	10	0.28
Habitat type	0.25	2.53	8	20	0.04
Interaction	0.5	1.05	8	20	0.43

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17 **Figure 4.** Relationship between factor 3 and habitat type: scrubland, mosaic and steppe (accompanied by standard
18 deviation).



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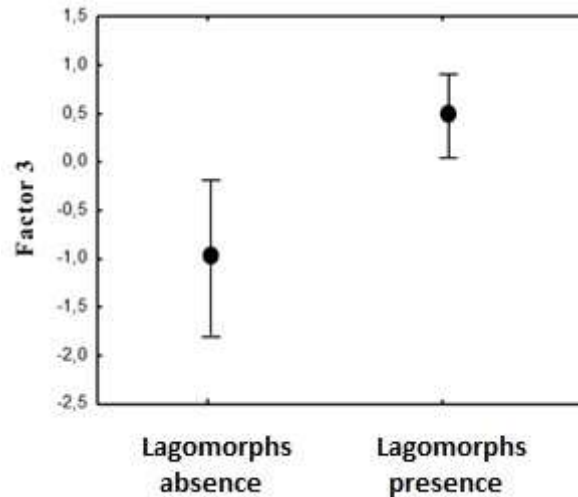
20 The presence of non-native (i.e. exotic) lagomorphs in the environment also influenced the
21 diet of the canid (MANOVA, Wilks' Lambda = 0.37; $F_{5,13} = 4.46$; $p = 0.014$), with a significant

1 relationship with factor 3 ($F_{1,17} = 10.41$; $p = 0.005$). Thus, in areas with the presence of introduced
2 lagomorphs the culpeos consumed fewer birds and herptiles (Figure 5).

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4 **Figure 5.** Relationship between the presence of exotic lagomorphs and factor 3 (accompanied by standard deviation).

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8 Differences between subspecies *L.c. andinus* and *L.c. culpaeus* were not found in their diet,
9 either considering the trophic orthogonal factors (MANOVA, Wilks' Lambda = 0.37; $F_{4,13} = 1.52$; p
10 = 0.25), or their respective H' trophic diversity index (ANOVA, $F_{1,17} = 0.03$; $p = 0.85$).

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12 In total, 1023 GLM models were generated for the trophic diversity (H') as a response variable
13 using the 10 predictors mentioned above. By applying the Akaike's selection criterion only two
14 models were found to be likely (Table 4): the most parsimonious ($r^2 = 0.75$) incorporated factors 1
15 and 3 in addition to precipitation, while the next model ($r^2 = 0.79$) also incorporated the protected
16 area. In both models, the factors and rainfall were negatively correlated with the H' trophic diversity
17 index (Table 5), so that the most diverse culpeo diets were associated with areas of high rainfall and
18 the consumption of carnivorous species, large herbivores, edentates, birds and herptiles (Figure 6).
19 Considering the second most parsimonious model, culpeos that live in protected areas also show a
20 greater diversity in their diet than those living in non-protected areas.

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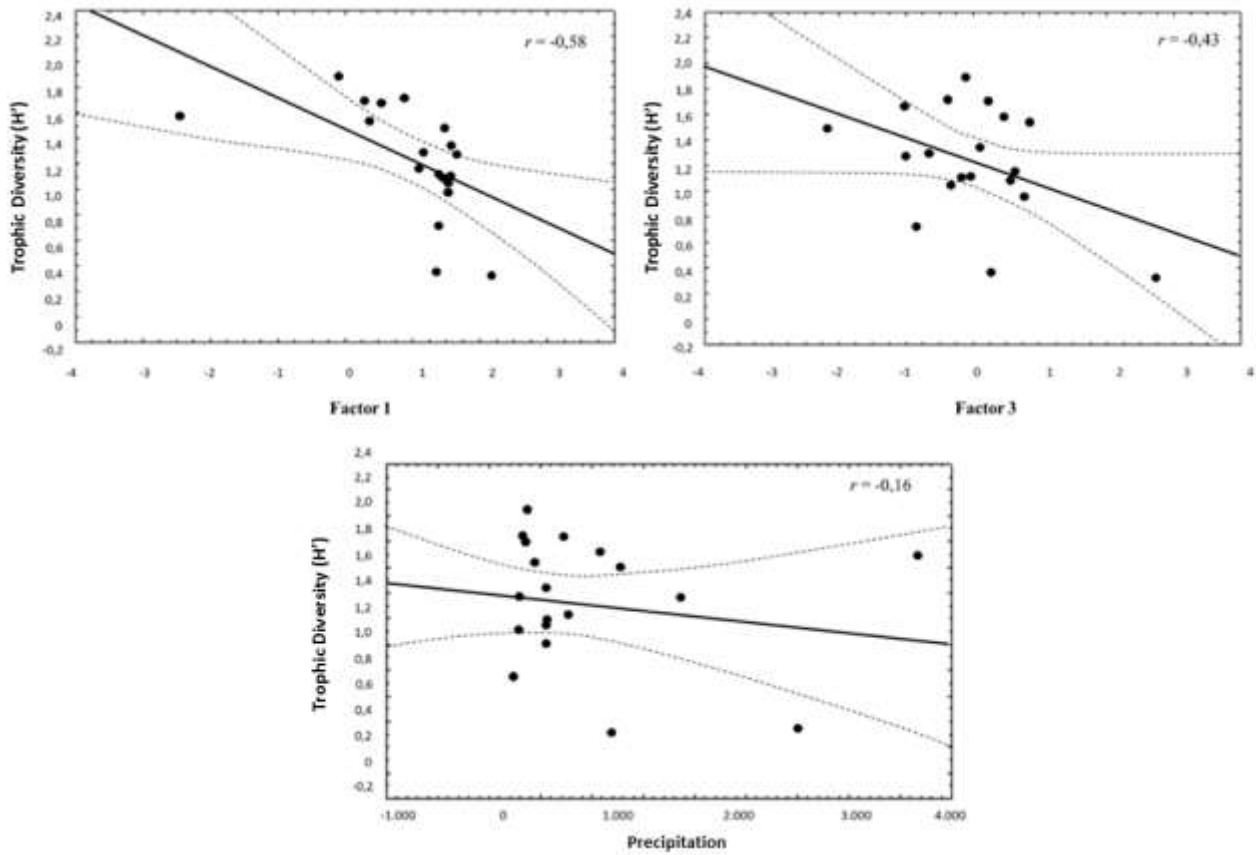
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1 **Figure 6.** Relationship between trophic diversity (H') index and factors 1 and 3, and precipitation, according to the
 2 most parsimonious GLM model obtained.
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Table 4. Explanatory models of culpeo's trophic diversity (H') index. It is shown the two parsimonious models
 obtained with the number of variables used (k), AIC values for small sample sizes (AICc), the difference between each
 selected model and the best model (Δ AIC) and each model weight (AICc wi). According to Burnham & Anderson
 (2002), only models with Δ AIC < 2 are really likely. The models were ordered from the lowest value (best model) to
 the highest value according to the AICc.

Models	k	AICc	Δ AIC	AICc wi
Factor 1 + Factor 3 +Precipitation	3	9.66	0	0.23
Factor 1+Factor 2 +Precipitation + Protected Area	4	11.50	1.8	0.09

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1

2 **Table 5.** Estimates of the most parsimonious GLM model obtained to explain the variation in the trophic diversity (H')
3 index of the culpeo with factor 1, factor 3 and precipitation as predictors.

4

5

	Estimate	Standard error	β	Standard error
Intercept	1.42	0.76		
Factor 1	-0.374	0.07	-0.865	0.152
Factor 3	-0.156	0.07	-0.360	0.131
Precipitation	-0.0003	0.00007	-0.565	0.153

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10 Discussion

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12 The culpeo is a medium-sized, mainly carnivorous canid (Redford & Eisenberg, 1992;
13 Novaro, 1997a; Guntiñas et al., 2017), which can use a wide diversity of prey throughout its
14 distribution range (Guntiñas et al., 2021). It has been described as a polyphagous species (Pía, 2011),
15 as in some regions it uses trophic resources such as fruits and invertebrates (Ebensperger et al., 1991;
16 Cornejo-Farfán & Jiménez-Milón, 2001; Guzmán-Sandoval, 2007). Thus, due to this varied diet
17 between and within trophic groups, the culpeo has generally been considered as an opportunistic
18 species (Crespo & De Carlo, 1963; Jacksic et al., 1980; Johnson & Franklin, 1994; Castro et al.,
19 1994). To date, no dietary patterns have been described based on geographical variation, except for
20 the exotic lagomorph consumption in the new areas the culpeo has expanded into, where native prey
21 species seem to have been replaced by exotic ones (Lucherini, 2016; Guntiñas et al., 2021).

22

23 Our results show that small mammals are an important prey item across the culpeo's range,
24 as reflected in numerous studies (Iriarte et al., 1989; Ebensperger et al., 1991; Johnson & Franklin,
25 1994; Meserve et al., 1996; Novaro et al., 2000a; Pía et al., 2003; Zapata et al., 2005; Walker et al.,
26 2007). In studies that quantified prey availability in the environment, a clear dietary selectivity has
27 been repeatedly shown, i.e. in the face of a decline in small mammals (especially rodents), the diet
28 did not change as might be expected in a truly opportunistic species (Jaksic et al., 1992; Martínez et
29 al., 1993). In most of the studies reviewed small mammals have a high relative frequency of
30 occurrence, although presenting a greater consumption at high altitudes. Therefore, the culpeo shows
31 a certain degree of specialization, and could have a strong effect on small mammal populations and
32 be a key predator regulating and/or limiting their populations (Krebs, 2002; Guntiñas et al., 2021).

1

2 Species are located at different levels within the food web, where top predators would be at
3 the highest positions, potentially consuming the rest of the species, and with few or no other species
4 that predate them (Essington & Hansson 2004; Essington et al., 2005). In this context, the pattern of
5 diets rich in carnivorous species, large herbivores and edentates obtained in this review (associated
6 with factor 1), clearly corresponds to those of an apical predator. In Andean systems, the only natural
7 species that can prey on culpeos is the puma (*Puma concolor*) (see Guntiñas et al., 2021). Aside from
8 the puma, the culpeo, also by preying on other carnivores, would act as an important regulator of
9 mammal populations of species of equal or greater size (such as ungulates). This corresponds more
10 to the role of a large carnivore than to those of small or medium-sized carnivores that the culpeo is
11 classified into (Carbone et al., 2007), and indicates the key role of culpeos in high-Andean ecosystems
12 (Guntiñas et al., 2021).

13

14 Regarding whether the presence of exotic lagomorphs introduced into the environment cause
15 a change in the diet of the culpeo, the results of this review at the global scale indicate that where
16 lagomorphs are present, there is a lower consumption of birds and herptiles. This pattern could be
17 due to the reduced availability of these groups in environments where hares and rabbits are present,
18 or because birds and herptiles are ignored in such areas (actually, these taxa appear to be secondary
19 for the culpeo throughout its range). But beyond birds and herptiles, no widespread substitution of
20 native prey (especially small rodents) has been detected by the dietary dominance of lagomorphs, as
21 suggested in studies at the local scale (Crespo & De Carlo, 1963; Jaksic, 1998; Novaro et al., 2000a;
22 Rubio et al., 2013), although in other studies this pattern was not observed (Meserve et al., 1987).

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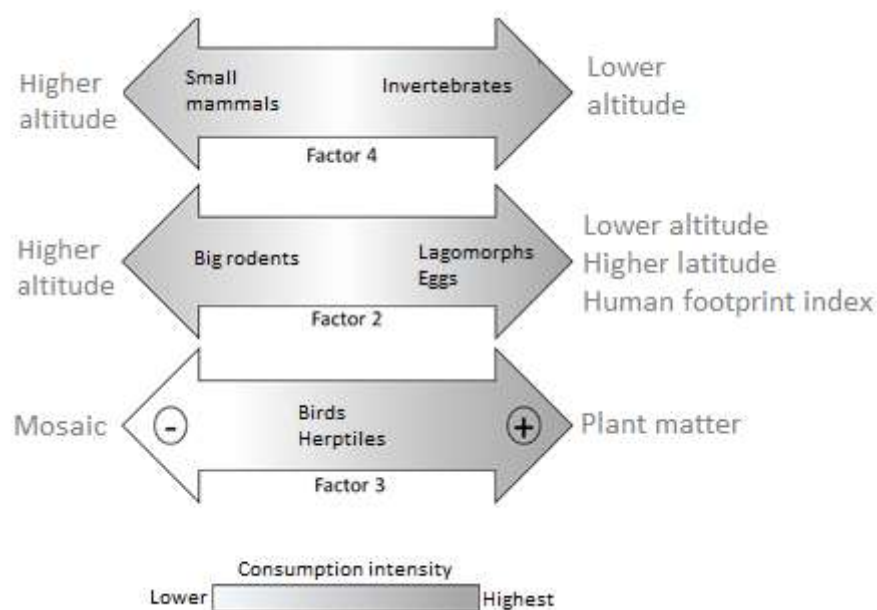
24 Considering the data globally, in the regions where lagomorphs are consumed, small
25 mammals and other prey groups are still consumed, which were also important in terms of relative
26 frequency of occurrence. It should be noted that the lagomorph prey group is the second most
27 important trophic group in terms of RF intake. As the majority of these are exotic species (European
28 hare *Lepus europeaus*, as well as the European rabbit *Oryctolagus cuniculus*), with only one study
29 representing a native lagomorph, it is likely that the culpeo has taken advantage of this new
30 environmental resource there where it has appeared, similarly to how it takes advantage of the
31 availability of big rodents elsewhere. Furthermore, diets rich in lagomorphs and eggs as well as poorer
32 in big rodents (according to factor 2), occur at low altitudes, low latitudes and in regions with an
33 important human influence on the territory. Therefore, the consumption of lagomorphs, especially
34 European hares (taking into account that they are also found at the highest latitudes), can be associated
35 with lowlands and impacted populations of culpeos, such as agricultural and livestock areas, which

1 may coincide with the works describing some substitution in the diet of native prey by exotic
2 lagomorphs (Crespo & De Carlo, 1963; Jaksic, 1998; Novaro et al., 2000a; Rubio et al., 2013).

3
4 Depending on the altitude there is a clear pattern of trophic groups consumed, so that in higher
5 altitude areas there is a greater consumption of small mammals and big rodents, while in lower lands
6 there is a greater consumption of lagomorphs, eggs and invertebrates (Figure 7). In regions of low
7 altitude, the high consumption of invertebrates appears to be consistent with some authors' views on
8 the importance of this group in highly seasonal Mediterranean ecosystems (Ebensperger et al., 1991;
9 Correa & Roa, 2005). On the other hand, at high altitudes, the higher consumption of small mammals
10 and big rodents could perhaps be due to their greater availability, a particular prey selection by
11 culpeos, or also because of the lower availability of other trophic resources.

12
13 It seems that the culpeo makes use of the resources available in each study area, determined
14 by a series of environmental factors. Culpeos can specialize in them and so not behave merely as a
15 generalist or opportunist. The aforementioned evidence that culpeos can maintain their consumption
16 of small mammals even when their abundance decreases, or the high degree of consumption of large
17 herbivores in certain regions as is the case with ungulates in the high Andes of Ecuador (Gutiñas et
18 al., 2017), indicates that the culpeo behaves more like a facultative specialist than a strict generalist
19 (Glasser, 1984; Gutiñas et al., 2017).

20
21 **Figure 7.** Conceptual model that describes the variation in consumption of trophic groups by the culpeo, grouped in
22 orthogonal factors, in relation to some environmental variables according to the results obtained in this review.



1 When culpeos consume plant material they often include other alternative or secondary food
2 resources, such as birds and herptiles (Figure 7), perhaps also in response to the low abundance or
3 availability of preferred prey (such as rodents) and therefore due to the need to supplement the diet.
4 In addition, the consumption of birds and herptiles was lower in mosaic-type habitats, indicating a
5 possible reduced availability for the culpeo of this prey in scrubland and steppe areas.

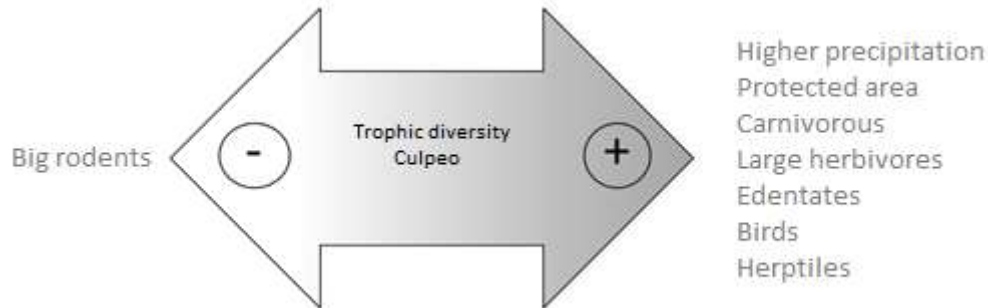
6
7 No differences have been found in the diet between the subspecies *L.c. andinus* and *L.c.*
8 *culpaeus*, neither in the trophic groups consumed nor in the trophic diversity, suggesting that both
9 subspecies display a similar trophic behavior. However, as more diet publications emerge in regions
10 where the ecology of culpeo is poorly known, this picture could change. So, it would be interesting
11 to review the trophic data again in the future, including also the subspecies *L.c. reissii* and increasing
12 the number of case studies of *L.c. andinus*.

13
14 On the other hand, one of the best-known biogeographical patterns of dietary variation in a
15 number of species is that it is a function of the latitudinal gradient, increasing from the poles towards
16 the tropics (Rosenzweig, 1995). Altitude is also an important driver of species diversity in the diet,
17 as mountains are sites of high diversity and endemism, although under particular conditions this
18 pattern is not always met (Gentry, 1995). In the case of generalist predators with a wide range of
19 distribution, whose diets reflect the availability of prey in the environment, changes would be
20 expected according to these biogeographical patterns (e.g. Clavero et al., 2003; Lozano et al., 2006).
21 In the case of the culpeo, with populations distributed in a marked latitudinal (from 3° to 50° south
22 latitude) and altitudinal (from sea level to 3,800 m) gradient, no differences in trophic diversity were
23 found based on these geographical variables. This result could be explained because the culpeo does
24 not behave like a generalist predator, as mentioned above, so its role as a facultative specialist
25 carnivore (Guntiñas et al., 2017, 2021) could mask latitudinal and altitudinal effects by specializing
26 locally in particular trophic resources. According to the most parsimonious model obtained, the most
27 diverse culpeo diets are those associated with high precipitation rates, as well as the consumption of
28 carnivorous species, large herbivores, edentates (i.e. armadillos), birds and herptiles (Figure 8). In
29 addition, it is also possible that in areas with some type of government protection the canid's diet may
30 be more diverse. Well-conserved areas, which host populations of species such as large herbivores,
31 carnivores and edentates, would presumably have a greater diversity of species, and therefore of
32 potential prey types, that culpeos could incorporate into their diet.

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Figure 8. Conceptual model describing the variation in trophic diversity (H') of the culpeo diet according to the results obtained in this review.



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8 Acknowledgments

9

10 This research was carried out partly with the economic support of the Universidad Técnica
11 Particular de Loja (UTPL), Ecuador. JL was supported by a Prometeo Fellowship from SENESCYT,
12 the National Agency for Education and Science of Ecuador, between 2014 and 2015. He was also
13 supported by Department of Biodiversity, Ecology and Evolution in Complutense University of
14 Madrid (Spain) during the editing of this article. AFM was supported by a Ramón y Cajal research
15 contract from the MINECO (RYC-2016-21114).

16

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18 References

19

20 Achilles NT (2007). Dieta estival del culpeo (*Pseudalopex culpaeus*, Molina 1782) en Nevados de
21 Chillán, centro-sur de Chile. M.Sc. Thesis, Facultad de Ciencias Veterinarias. Universidad Austral
22 de Chile, Chile.

23 Bailey LD y Pol M (2016). Tackling extremes: challenges for ecological and evolutionary research on
24 extreme climatic events. *Journal of Animal Ecology*, 85(1): 85-9.

25 Ballari SA y Barrios- García MN (2014). A review of wild boar *Sus scrofa* diet and factors affecting
26 food selection in native and introduced ranges. *Mammal Review*, 44(2): 124-134.

- 1 Berg JE (2007). The carnivore assemblage of La Payunia Reserve, Patagonia, Argentina: Dietary niche,
2 prey availability, and selection (Doctoral dissertation, University of Montana).
- 3 Bino G, Dolev A, Yosha D, Guter A, King R, Saltz D, Kark S (2010). Abrupt spatial and numerical
4 responses of overabundant foxes to a reduction in anthropogenic resources. *Journal of Applied*
5 *Ecology*, 47: 1262–1271.
- 6 Burnham K, Anderson D (2002). *Model Selection and Multimodel Inference: a practical information-*
7 *theoretic approach*. Springer-Verlag, New York.
- 8 Carbone C, Teacher A y Rowcliffe JM (2007). The Costs of Carnivory. *PLoS Biology*,5(2): 1-6.
- 9 Castro SA, Silva SI, Meserve PL, Gutierrez JR, Contreras LC, Jaksic FM (1994). Frugivoría y dispersión
10 de semillas de pimiento (*Schinus molle*) por el zorro culpeo (*Pseudalopex culpaeus*) en el Parque
11 Nacional Fray Jorge (IV Región, Chile). *Revista Chilena de Historia Natural*, 67(2): 169-176.
- 12 Clavero M, Prenda J, Delibes M (2003). Trophic diversity of the otter (*Lutra lutra* L.) in temperate and
13 Mediterranean freshwater habitats. *Journal of Biogeography*, 30(5): 761-769.
- 14 Cornejo A y Jiménez P (2001). Dieta del zorro andino *Pseudalopex culpaeus* (Canidae) en el matorral
15 desértico del sur del Perú. *Revista de Ecología Latino Americana*, 8: 01-09.
- 16 Correa P, Roa A (2005). Relaciones tróficas entre *Oncifelis guigna*, *Lycalopex culpaeus*, *Lycalopex*
17 *griseus* y *Tyto alba* en un ambiente fragmentado de la zona central de Chile. *Mastozoología*
18 *neotropical*, 12(1): 57-60.
- 19 Coulson T, Malo A (2008). Case of the absent lemmings. *Nature* 456, 43–44.
- 20 Cox CB y Moore PD (2005). *Biogeography: an ecological and evolutionary approach*. Blackwell
21 Publishing, Oxford
- 22 Crespo JA y de Carlo J (1963). Estudio ecológico de una población de zorros colorados *Dusicyon*
23 *culpaeus* (Molina) en el oeste de la provincia de Neuquen. *Revista del Museo Argentino de*
24 *Ciencias Naturales Bernardina Rivadavia e Instituto Nacional De Investigacion de Ciancias*
25 *Naturales-ecologia*, 1(1): 56.
- 26 Dayan T y Simberloff D (1996). Patterns of size separation in carnivore communities. *Carnivore*
27 *behavior, ecology, and evolution*, 2: 243-266.
- 28 Dormann CF, McPherson JM, Araujo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W,
29 Kissling D, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schroder B, Schurr FM, Wilson
30 R (2007). Methods to account for spatial autocorrelation in the analysis of species distributional
31 data: a review. *Ecography*, 30: 609-628.

- 1 Ebensperger LA, Mella JE, Simonetti JA (1991). Trophic-niche relationships among *Galictis cuja*,
2 *Dusicyon culpaeus*, and *Tyto alba* in central Chile. *Journal of Mammalogy*, 72(4): 820-823.
- 3 Eisenberg JF y Redford KH (1992). *Mammals of the Neotropics, Volume 2: The Southern Cone: Chile,*
4 *Argentina, Uruguay, Paraguay (Vol. 2).* University of Chicago Press.
- 5 Essington E y Hansson S (2004). Predator-dependent functional responses and interaction strengths in a
6 natural food web. *Can. J. Fish. Aquat. Sci.*, 61: 2215–2226.
- 7 Essington TE, Beaudreau AH, Wiedenmann J (2005). «Fishing through marine food webs» (PDF).
8 *Proceedings of the National Academy of Sciences*, 103 (9): 3171-3175.
- 9 Gentry AH (1995). Patterns of diversity and floristic composition in Neotropical montane forests. En:
10 Churchill *et al.* (eds.) *Biodiversity and conservation of Neotropical montane forests.*
11 *Proceedings.* Nueva York. The New York Botanical Garden, p. 103-126.
- 12 Glasser JW (1982). A theory of trophic strategies: the evolution of facultative specialists. *Ecology*, 63:
13 250-262.
- 14 Glasser JW (1984). Evolution of efficiencies and strategies of resource exploitation. *Ecology*, 65: 1570-
15 1578.
- 16 Guzmán JA, D'Elia G, Ortiz JC (2009). Variación geográfica del zorro *Lycalopex culpaeus* (Mammalia,
17 Canidae) en Chile: implicaciones taxonómicas. *Revista de biología tropical*, 57(1-2): 421-432.
- 18 Guzmán-Sandoval J, Sielfeld W, Ferrú M (2007). Dieta de *Lycalopex culpaeus* (Mammalia: Canidae) en
19 el extremo norte de Chile (Región de Tarapacá). *Gayana*, 71(1): 1-7.
- 20 Grosbois V, Gimenez O, Gaillard JM, Pradel R, Barbraud C, Clobert J, Weimerskirch H (2008).
21 Assessing the impact of climate variation on survival in vertebrate populations. *Biological*
22 *Reviews*, 83(3): 357-399.
- 23 Guntiñas, M., Lozano, J., Cisneros, R., Llorente, E, Malo, A.F. (2021). Ecology of the culpeo (*Lycalopex*
24 *culpaeus*): a synthesis of existing knowledge. *Hystrix, the Italian Journal of Mammalogy*, 32(1):
25 5-17.
- 26 Guntiñas M, Lozano J, Cisneros R, Narváez C, Armijos J (2017). Feeding ecology of the Andean fox in
27 southern Ecuador: wild ungulates being the main prey. *Contributions to Zoology*, 86 (2): 169-
28 180.
- 29 Guzmán JA, D'Elia G, Ortiz JC (2009). Variación geográfica del zorro *Lycalopex culpaeus* (Mammalia,
30 Canidae) en Chile: implicaciones taxonómicas. *Revista de biología tropical*, 57(1-2): 421-432.
- 31 Hounscome T y Delahay R (2005). Birds in the diet of the Eurasian badger *Meles meles*: a review and
32 meta- analysis. *Mammal Review*, 35(2): 199-209.

- 1 Iriarte JA, Jimenez JE, Contreras LC, Jaksic FM (1989). Small-mammal availability and consumption by
2 the fox, *Dusicyon culpaeus*, in central Chilean scrublands. *Journal of Mammalogy*, 70(3): 641-
3 645.
- 4 ITIS: Integrated Taxonomic Information System on-line database (2016). Results for *Lycalopex*
5 *culpaeus*, En: <http://www.itis.gov>. Descargado el 13 de Dic 2016.
- 6 Jaksic FM, Schlatter RP, Yáñez JL (1980). Feeding ecology of central Chilean foxes, *Dusicyon culpaeus*
7 and *Dusicyon griseus*. *Journal of Mammalogy*, 61(2): 254-260.
- 8 Jaksic FM, Jiménez JE, Castro SA, Feinsinger P (1992). Numerical and functional response of predators
9 to a long-term decline in mammalian prey at a semi-arid Neotropical site. *Oecologia*, 89(1): 90-
10 101.
- 11 Jaksic FM, Meserve PL, Gutiérrez JR, Tabilo EL (1993). The components of predation on small mammals
12 in semiarid Chile: preliminary results. *Revista Chilena de Historia Natural*, 66: 305-321.
- 13 Jaksic FM (1998). Vertebrate invaders and their ecological impacts in Chile. *Biodiversity and*
14 *Conservation*, 7(11): 1427-1445.
- 15 Jaksic F (2007). *Ecología de comunidades*. Ediciones UC.
- 16 Jiménez JE, Yáñez JL, Tabilo EL, Jaksic FM (1996). Niche-complementarity of South American foxes:
17 reanalysis and test of a hypothesis. *Revista Chilena de Historia Natural*, 69: 113-123.
- 18 Jiménez JE y Novaro AJ (2004). Culpeo (*Pseudalopex culpaeus*), In: Sillero-Zubiri C, Hoffmann M,
19 Macdonald DW. (eds) *Canids: Foxes, Wolves, Jackals and Dogs*. Status Survey and Conservation
20 Action Plan, 44–49. IUCN/SCC Canid Specialist Group, Gland and Cambridge, UK.
- 21 Johnson WE y Franklin WL (1994). Role of body size in the diets of sympatric gray and culpeo foxes.
22 *Journal of Mammalogy*, 75(1): 163-174.
- 23 Kausrud KL, Mysterud A, Steen H, Vik JO, Østbye E, Cazelles B et al. (2008). Linking climate change
24 to lemming cycles. *Nature*, 456: 93–97.
- 25 Keith SA y Bull JW (2017). Animal culture impacts species' capacity to realise climate- driven range
26 shifts. *Ecography*, 40(2).
- 27 Krebs CJ (2002). Beyond population regulation and limitation. *Wildlife Research*, 29(1): 1-10.
- 28 Lesmeister DB, Nielsen CK, Schauber EM, Hellgren EC (2015). Spatial and temporal structure of a
29 mesocarnivore guild in Midwestern North America. *Wildlife Monographs*, 191(1): 1-61.
- 30 Lozano J, Moleón M, Virgós, E (2006). Biogeographical patterns in the diet of the wildcat, *Felis silvestris*
31 Schreber, in Eurasia: factors affecting the trophic diversity. *Journal of biogeography*, 33(6): 1076-
32 1085.

- 1 Lucherini M (2016). *Lycalopex culpaeus*. In: The IUCN Red List of Threatened Species 2016. [Cited 2
2 Dec 2016.] En: <http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T6929A85324366.en>.
3 Descargado el 2 de Oct 2017
- 4 Marquet PA, Contreras LC, Torresmura J, Silva SI, Jaksic FM (1993). Food habits of *Pseudalopex* foxes
5 in the Atacama Desert, pre-Andean ranges, and the high-Andean plateau of northernmost Chile.
6 *Mammalia*, 57(1): 131-135.
- 7 Martínez DR, Rau JR, Jaksic FM (1993). Respuesta numérica y selectividad dietaria de zorros
8 (*Pseudalopex spp.*) ante una reducción de sus presas en el norte de Chile. *Revista Chilena de*
9 *Historia Natural*, 66: 195-202.
- 10 Medel R y Jaksic FM (1988). Ecología de los cánidos sudamericanos: una revisión. *Revista Chilena de*
11 *Historia Natural*, 61(1): 67-79.
- 12 Merilä J (2012). Evolution in response to climate change: in pursuit of the missing evidence. *BioEssays*,
13 34(9): 811-818.
- 14 Meserve PL, Shadrack EJ, Kelt DA (1987). Diets and selectivity of two Chilean predators in the northern
15 semi-arid zone. *Revista Chilena de Historia Natural*, 60(1): 93-99.
- 16 Monteverde MJ, Piudo L (2011). Activity patterns of the culpeo fox (*Lycalopex culpaeus magellanica*)
17 in a non-hunting area of northwestern Patagonia, Argentina. *Mammal study*, 36(3): 119-125.
- 18 Newsome TM y Ripple WJ (2015). A continental scale trophic cascade from wolves through coyotes to
19 foxes. *Journal of Animal Ecology*, 84: 49–59.
- 20 Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, Dickman CR (2015). The
21 ecological effects of providing resource subsidies to predators. *Global Ecology and*
22 *Biogeography*, 24(1): 1-11.
- 23 Novaro AJ (1997a). *Pseudalopex culpaeus*. Published by the American Society of Mammalogists.
24 *Mammalian species*, 558: 1-8.
- 25 Novaro AJ, Funes MC, Walker RS (2000a). Ecological extinction of native prey of a carnivore
26 assemblage in Argentine Patagonia. *Biological Conservation*, 92(1): 25-33.
- 27 Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA,
28 Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF,
29 Wettengel WW, Hedao P, Kassem KR (2001). Terrestrial ecoregions of the world: a new map of
30 life on Earth. *Bioscience*, 51(11): 933-938.
- 31 Palacios R, Walker RS, Novaro AJ (2012). Differences in diet and trophic interactions of Patagonian
32 carnivores between areas with mostly native or exotic prey. *Mammalian Biology-Zeitschrift für*
33 *Säugetierkunde*, 77(3): 183-189.

- 1 Pía MV, López MS, Novaro AJ (2003). Efectos del ganado sobre la ecología trófica del zorro culpeo
2 (*Pseudalopex culpaeus smithersi*) (Carnivora: Canidae) endémico del centro de Argentina.
3 Revista Chilena de Historia Natural, 76(2): 313-321.
- 4 Pía MV (2011). Influencia conjunta de la vegetación, asentamientos humanos, caminos y actividades
5 ganaderas sobre la ocurrencia y dieta de los carnívoros tope de Achala (Córdoba, Argentina)
6 (Doctoral dissertation, PhD Thesis, Universidad Nacional de Córdoba, Argentina).
- 7 Ritchie EG, Elmhagen B, Glen AS, Letnic M, Ludwig G, McDonald RA (2012). Ecosystem restoration
8 with teeth: what role for predators? Trends in Ecology and Evolution, 27: 265–2.
- 9 Rangel TF, Diniz-Filho JAF, Bini LM (2010). SAM: a comprehensive application for Spatial Analysis
10 in Macroecology. Ecography, 33: 46-50.
- 11 Redford KH y Eisenberg JF (1992). Mammals of the Neotropics, Vol. 2. University of Chicago Press,
12 430 pp.
- 13 Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M. et al. (2014). Status and
14 ecological effects of the world's largest carnivores. Science, 343: 1241484.
- 15 Romo MC (1995). Food habits of the Andean fox (*Pseudalopex culpaeus*) and notes on the mountain cat
16 (*Felis colocolo*) and puma (*Felis concolor*) in the Rio Abiseo National Park, Peru. Mammalia,
17 59(3): 335-344.
- 18 Rosenzweig ML (1995). Species diversity in space and time. Cambridge University Press.
- 19 Rubio AV, Alvarado R, Bonacic C (2013). Introduced European rabbit as main prey of the native
20 carnivore culpeo fox (*Lycalopex culpaeus*) in disturbed ecosystems of central Chile. Studies on
21 Neotropical Fauna and Environment, 48(2): 89-94.
- 22 Sandom C, Faurby S, Sandel B, Svenning JC (2014). Global late Quaternary megafauna extinctions
23 linked to humans, not climate change. In Proc. R. Soc. B (Vol. 281, No. 1787, p. 20133254). The
24 Royal Society.
- 25 Soe E, Davison J, Süld K, Valdmann H, Laurimaa L, Saarma U (2017). Europe- wide biogeographical
26 patterns in the diet of an ecologically and epidemiologically important mesopredator, the red fox
27 *Vulpes vulpes*: a quantitative review. Mammal Review.
- 28 StatSoft Inc (2011). STATISTICA (data analysis software system), version 10: <https://www.statsoft.com>.
- 29 Stephens DW y Krebs JR (1986). Foraging theory. Princeton University Press, Princeton, NJ.
- 30 Tirira D (2011). Lobo de Páramo (*Pseudalopex culpaeus*). In: Tirira D (ed) Libro Rojo de los mamíferos
31 del Ecuador 2th ed. Fundación Mamíferos y Conservación, Pontificia Universidad Católica del
32 Ecuador y Ministerio del Ambiente del Ecuador. Quito.

- 1 Underwood AJ (1996). Experiments in ecology. Cambridge University Press, Cambridge.
- 2 Virgós E y Casanovas JG. (1999). Environmental constraints at the edge of a species distribution, the
3 Eurasian badger (*Meles meles* L.): a biogeographic approach. Journal of biogeography, 26(3):
4 559-564.
- 5 Vulla E, Hobson KA, Korsten M., Leht M., Martin AJ, Lind, A, Saarma U (2009). Carnivory is positively
6 correlated with latitude among omnivorous mammals: evidence from brown bears, badgers and
7 pine martens. In Annales Zoologici Fennici (Vol. 46, No. 6, pp. 395-415). Finnish Zoological and
8 Botanical Publishing.
- 9 Walker RS, Novaro AJ, Perovic P, Palacios R, Donadio E, Lucherini M, López MS (2007). Diets of three
10 species of Andean carnivores in high-altitude deserts of Argentina. Journal of Mammalogy, 88(2):
11 519-525.
- 12 Weaver W y Shannon CE (1949). The mathematical theory of communication. Illinois University Press,
13 Urbana, IL.
- 14 Zapata SC, Travaini A, Delibes M, Martínez-Peck R (2005). Food habits and resource partitioning
15 between grey and culpeo foxes in southeastern Argentine Patagonia. Studies on Neotropical Fauna
16 and Environment, 40(2): 97-103.
- 17 Zar JH (2009). Biostatistical Analysis. Prentice Hall. Englewood Cliffs, New Jersey.
- 18