Feeding ecology of the culpeo in southern Ecuador: wild ungulates being the main prey

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Abstract

This study details for the first time the food habits of the culpeo or Andean fox (*Lycalopex culpaeus*) in high areas of the Ecuadorian Andes during a complete annual cycle. Our objective was to identify prey species, calculate their contribution to diet and test for temporal variation. In total, 304 Andean fox scats were collected within the Podocarpus National Park (Loja province, southern Ecuador). By analysing the content of scats 413 prey items were identified and classified into eight prey groups. Subsequently, the frequency of occurrence (FO) for each prey group was calculated per month together with the relative contribution of estimated consumed biomass (CB). In addition, the Shannon-Wiener's index was calculated as a measurement of monthly diet diversity. The results show a diet dominated by cervids belonging to the *Mazama* and *Pudu* genus (70% FO), followed by small mammals (30% FO), large rodents (12% FO), carnivorous species (10% FO) and lagomorphs (8% FO). There was temporal variation in the consumption of both deer and small mammals. Cervids also provided the major part of the consumed biomass (70% CB), the remaining prey categories each accounted for less than 11% CB. Negative correlations in consumption were observed between cervids and two other groups, rabbits and small mammals. Trophic diversity values fluctuated throughout the year showing a mean of 1.7. The results obtained show a diets very different from those previously reported; deer being the bulk of the diet instead of rodents or other mammals. The consumption of carnivorous species in the area was also high in comparison with other regions. Overall, this study clearly demonstrates that the culpeo is an important top predator in the high-Andean ecosystem.

Contents

Introduction

The culpeo or Andean fox (*Lycalopex culpaeus,* Molina 1782) is the second largest canid (4-13.8 kg) in South America (Jiménez *et al.,* 1995; Jiménez and Novaro, 2004). It is distributed along the Andes Mountain range, from southern Colombia to Tierra del Fuego, Argentina (Jiménez *et al.,* 1995). It is present at low altitudes in the Pacific and Atlantic coasts (Jaksic *et al.,* 1980; Meserve *et al.,* 1987; Medel and Jaksic, 1988; Marquet *et al.,* 1993), and reaches the 4800 meters above sea level (m.a.s.l) in the Andes Mountains (Jiménez *et al.,* 2008). Andean foxes occupy a large variety of habitats and environmental gradients: ranging from arid steppes (Meserve *et al.,* 1987; Martínez *et al.,* 1993; Arim and Jaksic, 2005), high steppes (Marquet *et al.,* 1993; Johnson and Franklin, 1994; Walker *et al.,* 2007; Palacios *et al.,* 2012), dense shrubs (Iriarte *et al.,* 1989), to altered ecosystems (Novaro *et al.,* 2000; Pia *et al.,* 2003) and pine reforested areas (Acosta-Jamett and Simonetti, 2004), or even rainforest (Jiménez *et al.,* 2008).

This species is considered to be a trophic generalist (e.g. Walker *et al.,* 2007). Indeed, culpeos exploit a wide variety of vertebrate, invertebrate and plant species according to their availability (Acosta-Jamett and Simonetti, 2004), although a degree of selectivity has been also reported (Meserve *et al.,* 1987; Iriarte *et al.,* 1989; Martínez *et al.,* 1993; Corley *et al.,* 1995). The culpeo is the most carnivorous of the Neotropical canids (Jiménez and Novaro, 2004), with a diet generally dominated by small mammals , especially rodents (Iriarte *et al.,*
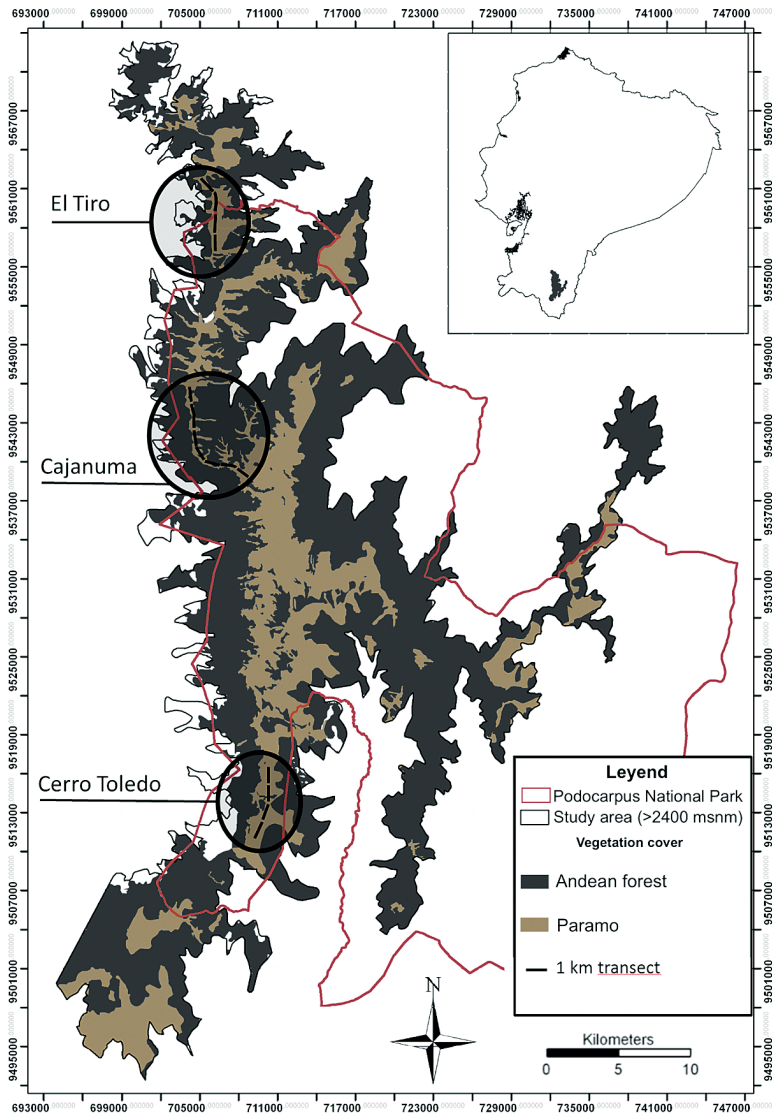
Fig. 1. Location of the study area in Podocarpus National Park (PNP), southern Ecuador. The three main places where the 16 fixed 1-km transects were concentrated are also shown (El Tiro, 4 km; Cajanuma, 8 km and Cerro Toledo, 4 km). Transects are not scaled.

1989; Ebensperger *et al.,* 1991; Jaksic *et al.,* 1992, 1993; Castro *et al.,* 1994; Pia *et al.,* 2003; Correa and Roa, 2005; Achilles, 2007; Pia, 2013). Exotic lagomorphs (i.e. the European hare *Lepus europaeus* and the wild rabbit *Oryctolagus cuniculus*) can become important food sources for culpeos (Johnson and Franklin, 1994; Novaro *et al.,* 2000; Pia *et al.,* 2003; Walker *et al.,* 2007; Pia, 2013; Rubio *et al.,* 2013), and arthropods often appear in the culpeo's diet (e.g. Corley *et al.,* 1995; Correa and Roa, 2005; Guzmán-Sandoval *et al.,* 2007; Walter *et al.,* 2007). In addition, birds and reptiles can be considered prey, although studies show

their contribution to the diet be variable (Achilles, 2007; Silva *et al.,* 2005; Walker *et al.,* 2007).
The culpeo is a brave predator able to attack large prey such as alpaca calves (*Vicugna pacos*), vicunas (*Vicugna vicugna*) and llamas (*Lama glama*), as observed in Bolivia (Franklin, 1982, in Donadio *et al.,* 2012; Zacari and Pacheco, 2005). In Argentina Andean foxes also prey on lambs (Novaro *et al.,* 2000, 2005), the species being persecuted due to damages produced on livestock (Jiménez and Novaro, 2004). Furthermore, and like other canid species, culpeos can consume different amounts of carrion (Novaro *et*

al., 2000; Walker *et al.*, 2007; Stucchi and Figueroa, 2010).

Plants also usually form an important part of the Andean fox's diet (Jaksic *et al.*, 1980; Ebensperger *et al.*, 1991; Cornejo and Jiménez, 2001; Zapata *et al.*, 2005). Plant consumption probably depends on the existing availability of prey (Castro *et al.*, 1994; Silva *et al.*, 2005). Andean foxes are known to be important seed dispersers of mesquite species (*Prosopis flexuosa* and *P. pallida*) (Cornejo and Jiménez, 2001; Maldonado *et al.*, 2014) and pepper (*Schinus molle*) (Castro *et al.*, 1994), although its role as an effective dispersant for other species is unclear (León-Lobos and Kalin-Arroyo, 1994; Silva *et al.*, 2005).

Nevertheless, most studies dealing with the culpeo's diet are from Chile and Argentina, so there are vast regions of South America where the feeding ecology of the species has been poorly studied, including entire countries (with their associated habitats and particular ecological conditions) where the diet is completely unknown. This is the case of Ecuador, where the species has recently been listed as Vulnerable (Tirira, 2011). The culpeo is distributed throughout the country, but it is generally considered to be a canid habiting highlands and cold areas (cloud forests and 'paramos'), between 2600 and 4500 m.a.s.l., along the Andes range (Tirira, 2007). In this important region of the world no systematic and representative study examining the diet of the Andean fox has been published to date.

The aim of this study is to describe the trophic patterns of the Andean fox in the high Andes of southern Ecuador over a complete annual cycle, thus obtaining the first systematic outcome on the species feeding ecology in the country. In particular, it is intended: 1) to identify the culpeo's prey species in the Podocarpus National Park and to describe the annual pattern of frequency in the diet of different prey groups; and 2) to evaluate the temporal variation during the year both in the consumption of prey groups and trophic diversity.

Methods

Study area

The study was conducted in the high areas of the Podocarpus National Park (PNP), this being the most important protected area in southern Ecuador (*Fig.* 1). It is located within the so-called 'Huancabamba depression', which is considered a transition zone between the Northern and Southern Andes mountains because their maximum elevations (3800 m.a.s.l) are the lowest in the Andean range. The PNP occupies 145000 ha of this region, in the provinces of Loja and Zamora-Chinchipe (MAE, 2015). The PNP has a humid-subhumid ombrotype and the temperature varies between 2 and 22 °C. The vegetation consists of tropical rainforest at low altitude, followed by different types of Sub-Andean, Andean and High-Andean forest (i.e. cloud forests) at higher altitudes. Between 2600 (m.a.s.l) and the high peaks (3600 m.a.s.l.) a moorland type habitat (known as 'paramo') appears, occupying a narrow strip along the ridge in a north-south gradient (Rivera, 2007; MAE, 2015). These paramos are characterised by the abundance of rosette and pad plant species: *Bambu* and *Chusquea* are the dominant plant genus, alongside *Polylepis*, *Escallonia* and *Clusia* shrub species (see Sierra, 1999). These mountain ecosystems in the PNP are the most humid in Ecuador, with rainfall exceeding 6000 mm/year, low temperatures and strong winds (Richter, 2003; Rivera, 2007).

Collection of culpeo scats

This study is based on analysing scat contents to determine the culpeo's diet. It is a non-invasive method that shows what the species real consumes (Putman, 1984; Corbett, 1989) and is widely used for studying the feeding habits of carnivores (e.g. Halter, 1967; Reynolds and Aebischer, 1991; Juarez and Marinho-Filho, 2002; Malo *et al.*, 2004). In Particular, this method has already been used to study the culpeo's diet (e.g. Iriarte *et al.*, 1989; Ebensperger *et al.*, 1991). All accessible areas of paramo in the PNP were sampled for culpeo scat collection. These areas were concentrated in three zones of the PNP known locally as Cajanuma, El Tiro and Cerro Toledo. A different number of fixed 1-km transects (16 in total) were established in each area on existing paths (see *Fig.* 1). During 2009 each 1-km transect was sampled in search of fresh scats once a month (thus resulting in a total of 192 km of overall sampling effort), at 30 day intervals and starting in the middle of each month (so that any scat found was assigned to the corresponding sampled month). Previously, a survey to remove old scats was undertaken in all transects. Samplings were always conducted by the same observers, who were well trained prior to starting the fieldwork (Lozano *et al.*, 2013).

Collected scats were stored at -80 °C when clearly identified as belonging to Andean foxes. Scats were first identified based on a set of context-based diagnostic characteristics (Romo, 1995; Cornejo and Jiménez,

2001; Achilles, 2007; Palacios *et al.*, 2012; Pia, 2013), which included location (scats directly on the path or close by), general morphology (canid-like scats, different from those of cats, bears, etc), and diameter (2-3 cm). In addition, genetic analyses were performed in the lab to confirm scat identification. 89 scats were randomly selected from the total sample, and DNA was extracted by applying the QIAGEN QIAamp DNA Stool Mini Kit (QIAGEN, CA.USA). The protocol described by De Barba *et al.*, (2014) was used for mitochondrial DNA amplification. Amplification was successful for 81.2% of the total sample (i.e. 70 scats), the genetic material being positively identified as belonging to culpeo in all cases. Therefore, observers in the field had a 100% success rate in the identification of these 70 scats, demonstrating that with good previous training correct identification of culpeo scats based on external features is possible in the area (see Lozano *et al.*, 2013). Hence, no relevant confusion with the scats of other animals inhabiting the same environment, such as pumas (*Puma concolor*), Andean bears (*Tremarctos ornatus*) or domestic dogs (*Canis familiaris*), was assumed.

Diet analysis

We collected a total of 304 culpeo faeces. Each scat was air dried, soaked in soapy water, and washed through 1-mm and 3-mm sieves, thus disaggregating the content (hair, feathers, bones, hooves, invertebrate and plant remains) for the identification of prey groups (e.g. Ackerman *et al.*, 1984). Determination of mammalian species was performed according to the patterns of cuticle and medulla in the structure of guard hairs (see Arita and Aranda, 1987; Chehébar and Martín, 1989). Hairs present in the scats were compared with those of a reference collection, which accounted for 46 previously collected potential prey species. Likewise, bone remains were compared when necessary with the reference collection located at San Francisco de Quito University. To estimate biomass consumption by culpeos, the mean body mass for the Ecuadorian species identified as prey was obtained from the literature (e.g. Tirira, 2007), and a maximum consumption of 800 g was assumed considering the culpeo's size (Sillero-Zubiri *et al.*, 2004). For small food items, such as invertebrates and fruits, representative values of biomass were used (e.g. Malo *et al.*, 2004; see *Tab*. 1).

Food items were classified into eight prey groups (*Tab. 1*): small mammals, big rodents, armadillos, rabbits, carnivorous (i.e. including marsupial carnivores), cervids, fruits and others (including birds and invertebrates, which were only consumed in small quantities). The relative contribution of each prey item and group to the diet was measured by calculating their frequency of occurrence (FO), i.e. the number of scats in which a given prey item or group was found divided by the total number of scats, expressed as a percentage. Furthermore, the consumed biomass (CB) of each prey group was estimated, and also expressed as a percentage, multiplying the number of each item by its assigned weight and then dividing the result by the total sum of biomass.

Data from the three sampling sites (*Fig. 1*) were pooled for statistical analyses because sites cannot really be considered as independent areas. Indeed, based on the genetic individualisation of scats, several individuals used more than one site (Authors, unpublished data), so any comparison among sites is rendered meaningless. Then, for the PNP as a whole, G-tests (Sokal and Rohlf, 1981) were performed to search for statistically significant differences in the FO of the eight prey groups in different months. Spearman's correlation coefficients (Moran, 1948) were calculated to test for the existence of relationships between prey groups over time. The Kruskal-Wallis test was conducted to test for differences in the biomass contribution between prey groups. Moreover, the Shannon-Wiener's index (Shannon and Weaver, 1949) was used to measure trophic diversity. Data from November and December were combined to get a representative sample size. All statistical analyses were performed using the software Statistica 10 (StatSoft 2011).

Results

We identified a total of 413 prey items in 304 scats (*Tab. 1*), collected during a year of sampling. A total of 16 mammalian species were identified, which were by far the most consumed prey. Indeed, mammals were present in 100% of the scats analysed. Cervids were the most consumed prey group, with a frequency of occurrence (FO) of 71%. The next most significant group in terms of FO was small mammals (26%), followed by big rodents (12%), carnivorous (10%) and rabbits (8%) (*Tab*. 1). Birds and fruits were poorly represented, both being found in only 3% of the scats analysed. Contributions of consumed biomass in terms of percentage were similar, except for small mammals (0.95% CB), others (0.11% CB) and fruits (0.02% CB), with values much lower than those provided by FO.

Prey items		n	Weight (g)	FO %	CB %
SMALL MAMMALS		**80**		**26.32**	**0.95**
Caenolestidae	*Caenolestes caniventer*	23	0.037	7.57	0.34
	Caenolestes fuliginosus	32	0.028	10.53	0.36
	Caenolestes spp.	1	0.030		0.01
Soricidae	*Cryptotis montivaga*	14	0.012	4.61	0.07
Cricetidae	*Cricetidae spp*.	10	0.040	3.29	0.16
BIG RODENTS		**37**		**12.17**	**10.22**
Cuniculidae	*Cuniculus paca*	18	9000	5.92	5.80
Dasyproctidae	*Dasyprocta punctata*	9	4000	2.96	2.90
Sciuridae	*Sciurus spp*	10	0.375	3.29	1.51
CARNIVOROUS		**30**		**9.87**	**9.38**
Mephitidae	*Conepatus semistriatus*	1	2400	0.33	0.32
Didelphidae	*Didelphis marsupialis/pernigra*	10	1500	3.29	3.22
	Marmosa robinsoni	1	0.076	0.33	0.03
Felidae	*Puma concolor*	3	75000	0.99	0.97
Procyonidae	*Nasuella olivacea*	15	1300	4.93	4.84
ARMADILLOS	*Dasypus novemcinctus*	**4**	**5200**	**1.32**	**1.29**
CERVIDS	*Mazama rufina*	171	11000	56.25	54.82
	Pudu mephistophiles	46	7000	15.13	15.16
RABBITS	*Sylvilagus brasiliensis*	**25**	**0.95**	**8.22**	**8.06**
OTHERS		**11**		**3.62**	**0.11**
Insecta	Coleopterans	1	1	0.33	0.00
	Myriapods	1	1	0.33	0.00
Birds	*Psittacidae*	1	40	0.33	0.02
	Other birds	8	10	2.63	0.08
FRUITS		**9**	**5**	**2.96**	**0.02**
Total number of scats		*304*			
Total prey items		*413*			

Table 1. Culpeo diet in the Podocarpus National Park (Andean highlands of southern Ecuador). The number of each prey items found in scats (n), the weight (biomass) assigned to each prey item (in grams), the frequency of occurrence (FO, in percentage), and the estimated consumed biomass (CB, in percentage) for each prey item, are reported. To estimate CB a maximum of 800 g was established for the culpeo.

Considering prey species, the little red brocket deer (*M. rufina*) showed the highest FO, followed by the northern pudu (*Pudu mephistophiles*). The most consumed small mammals were marsupials: the gray-bellied shrew opossum (*Caenolestes caniventer*) and the silky shrew opossum (*C. fuliginosus*). Big rodents were also important for the Andean fox's diet, especially the spotted paca (*Cuniculus paca*) and the central american agouti (*Dasyprocta punctata*). The tapeti or forest rabbit (*Sylvilagus brasiliensis*) is the only lagomorph present in the region and it also preyed upon (8.2% FO). The nine-banded armadillo (*Dasypus novemcinctus*) also appeared in the diet (1.32% FO). A focal point of the culpeo's diet was the relatively high consumption of carnivores and similar (i.e. Didelphidae), such as the western mountain coati (*Nasuella olivaceae*), the striped

hog-nosed skunk (*Conepatus semistriatus*), and opossums (*Didelphis marsupialis* and/or *D. pernigra*), accounting for 9.8% FO. Interestingly, remains of puma (*Puma concolor*) were also found in three scats (*Tab. 1*).

Temporal variation was found in the most consumed group (i.e. cervids) (n = 217, G = 19.7, d.f = 10, p = 0.03), where the highest consumption occurred during April, May and June (*Fig. 2*). Likewise, in the second most consumed group, small mammals, temporal variation was also found (n = 80, G = 27.92, d.f. = 10, p = 0.002), with an intense consumption in August (*Fig. 2*). For the forest rabbit a higher consumption during April and June was recorded, showing a marginally non-significant difference (n = 25, G = 17.46, d.f. = 10, p = 0.06). For the rest of the prey groups no temporal variations in consumption were found: big rodents (n = 37, G = 10.10,
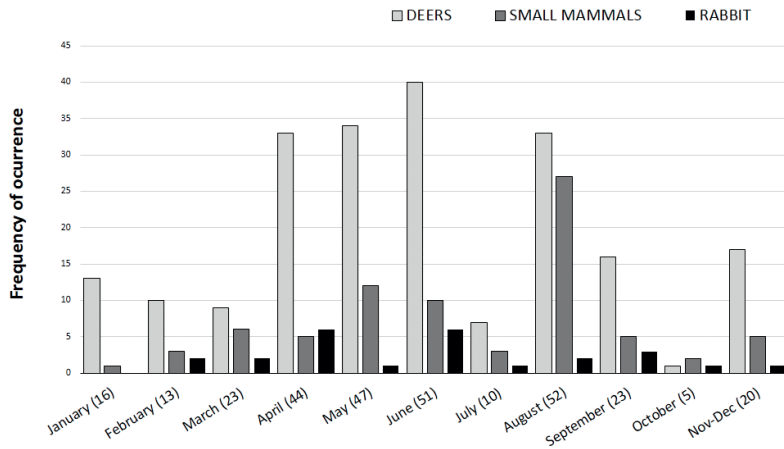
Figure 2. Frequency of occurrence (FO) across months of the culpeo's prey groups showing temporal variation in the high areas of the Podocarpus National Park (PNP): cervids, small mammals and rabbits. In brackets the number of scats found per month is shown.
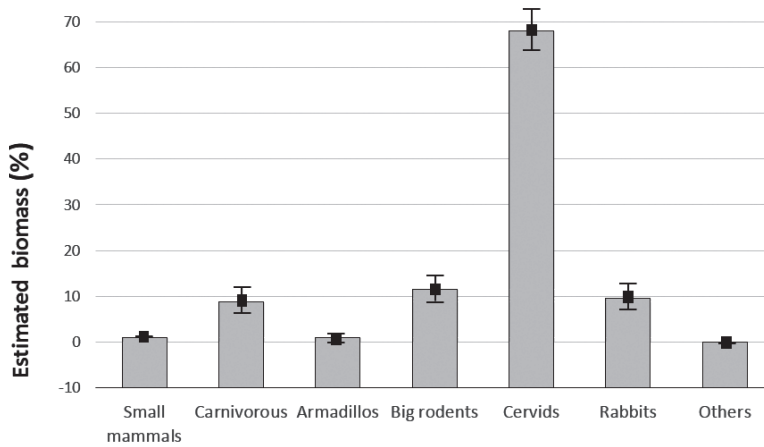

Figure 3. Annual average of prey group contributions in estimated consumed biomass (CB, expressed as percentage) to the culpeo's diet in the high areas of the Podocarpus National Park (PNP, southern Ecuador).
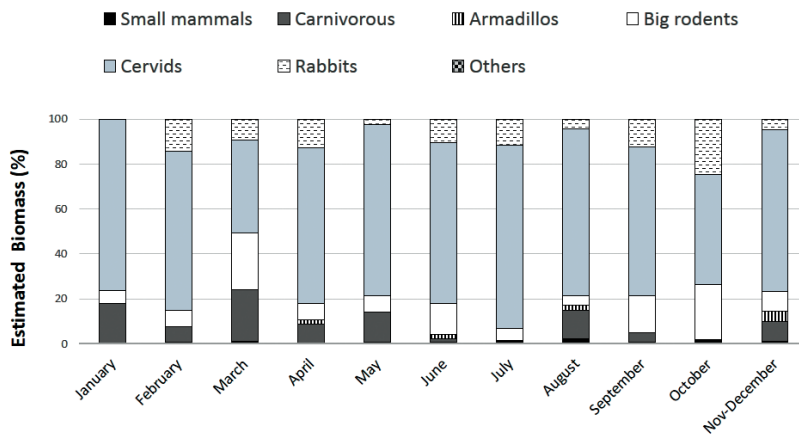

Figure 4. Contribution in estimated consumed biomass (CB, expressed as percentage) across months of the culpeo's prey groups in the high areas of the Podocarpus National Park (PNP, southern Ecuador).

d.f = 10, *p* = 0.43), carnivorous (n = 30, G = 14.1, d.f = 10, *p* = 0.17), armadillos (n = 4, G = 5.48, d.f = 10, *p* = 0.86), fruits (n = 9, G = 14.12, d.f = 10, *p* = 0.16) and others (n = 11, G = 7.00, d.f = 10, *p* = 0.72). Over time significant negative Spearman correlations were found between the consumption of deer and small mammals (January = -0.54, p < 0.05; March = -0.52, p < 0.05: August = -0.55, p < 0.05; September = -0.67, p < 0.05), as well as between the consumption of deer and rabbits (February = -0.79, p < 0.05; April = -0.54, p < 0.05).
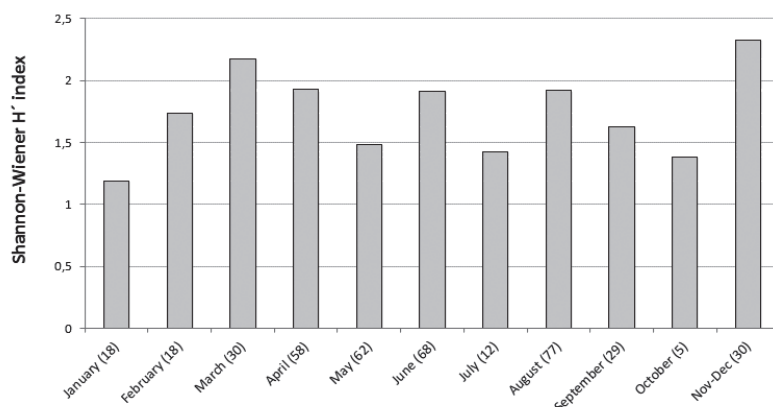
Figure 5. Trophic diversity of culpeos across months in the high areas of the *Podocarpus* National Park (PNP, southern Ecuador), according to the Shannon-Wiener's index. In brackets the number of prey items per month is shown.

In relation to the annual average contribution of biomass there was a significant difference between prey groups ($H(6, N = 77) = 55.46$; $p < 0.001$), given that a high cervid contribution was found (*Fig. 3*). Big rodents, rabbits and carnivorous were the next most significant groups, showing similar contributions (around 10% CB). Finally, contribution to consumed biomass by the resting groups was minimal. Throughout the year a clear predominance of deer consumed biomass is observed, which decreases in March just when the biomass contribution of big rodents and carnivorous increases (see *Fig. 4*). Although in variable values, rabbits, carnivorous, and big rodents provided biomass in considerable amounts during all months, whereas the contribution of small mammals and other food items was always very low (*Fig. 4*).

In addition, values given by the Shannon-Wiener's index as a measurement of the culpeo's trophic diversity fluctuated throughout the year, showing an average of 1.7. January presented the lowest diversity value (1.2), whereas it doubled in March (2.2) (*Fig. 5*).

Discussion

The culpeo has been described as a generalist species, able to harness a diversity of food resources (Jiménez *et al.*, 2008). In the high areas of the PNP the species has a predominantly carnivorous diet (98% of items are of animal origin). In this sense, the results match those reported in the pioneering studies of Crespo and Carlo (1963) in Argentina (prey animals with 96.9% FO), and Fugger (1979) in Chile (with 95% and 97% FO in Ayacucho and Cuzco, respectively). However, the trophic pattern found in southern Ecuador, regarding the type of prey and its frequency in the diet, is completely different from those reported to date.

Indeed, in contrast to studies carried out in other areas of Latin America, the culpeo in southern Ecuador seems to prey mainly on wild ungulates (*Mazama* and *Pudu* genus), which were the bulk of the diet in terms of both frequency of occurrence and biomass contribution. Therefore, the high representation of their remains in the scats (i.e. 70% FO) supports the idea that the culpeo actively hunts deer, being able to be an important predator of these species in the region. This pattern differs from all published studies, where cervids have little or even no representation. For example, in a study of the culpeo's diet in the paramos of Peru (Romo, 1995), where deer were present, no deer remains were found in the culpeo scats. In the PNP cervids belonging to the *Mazama* and *Pudu* genus were the most consumed prey throughout the year, with a peak frequency in June, and high values for FO during April, May and August. Perhaps this pattern relates to a higher temporal availability of pregnant females, cubs and juveniles during these months. In Ecuador it is thought that deer can breed throughout the year, but unfortunately data on deer phenology in the different Ecuadorian regions is lacking. Months showing high consumption of deer could also coincide with a period of low availability of other potential prey. Small mammals were the second most consumed prey group in terms of FO (although its contribution to consumed biomass was apparently irrelevant) and consumption levels were particularly high during August, perhaps indicating a significant temporal variation in their abundance, population age structure or mean body weight throughout the year (Malo *et al.*, 2013). Moreover, it has been observed that the higher the consumption of deer the lower the consumption of small mammals (precisely during January, February, March and September). Taking all the above into account, this variation could indicate temporary changes in the availability of these prey groups (Malo *et al.*, 2013).

It is likely that the high consumption of deer (and of other animals such as carnivorous) in the PNP is in part due to the culpeo's scavenging activity. Although scavenging on deer was not detected in Peru (Romo, 1995), general scavenging activity by culpeos has been reported on many occasions (Walker *et al*., 2007). However, PNP rangers have observed direct predation of culpeos on deer (PNP staff, pers. comm.), which is not strange when considering that consumed deer were medium-small species, mainly *Mazama rufina* (8-14 kg) and *Pudu mephistophiles* (5-10 kg) (see Tirira, 2007). Indeed, predation and attacks on animals of equal or even greater size, such as offspring and subadults of alpacas, vicuñas, llamas and guanacos, as well as sheep and goats, have been reported in Argentina and Chile (Novaro *et al*., 2000; Pia, 2003, 2004; Zacari and Pacheco, 2005). For example, Novaro *et al*. (2009) photographed and verified an episode of direct attack on young guanacos (33 kg), also observing continuous reactions of defense by guanaco family groups as soon as culpeos were sighted. Apparently, any animal weighing less than 35 kg can be potential prey for culpeos, given that this predator is able to kill individuals 6.6 times heavier than itself (see Jiménez and Novaro, 2004). Therefore, although culpeos could take deer meat from carcasses (left behind by the scarce numbers of pumas living in the area, for instance), it seems certain that in the PNP they often actively hunt deer.

The forest rabbit was the fourth most consumed species (showing a similar significance in biomass contribution) by the Andean fox. It is known that lagomorphs are important prey for this carnivore, with numerous studies highlighting the consumption of the European hare (Johnson and Franklin, 1994; Corley *et al*., 2005; Walker *et al*., 2007) and the European or wild rabbit (Iriarte *et al*., 1989; Rubio *et al*., 2013). It is interesting to note that only in Ecuador and northern Peru do the culpeo and the forest rabbit overlap in their respective ranges of distribution, the latter being the only lagomorph present in Ecuador. The consumption of forest rabbits tends to present temporal variation, showing FO peaks in the months of April and June (as with deer, although FO values for rabbits are much smaller). In fact, a negative correlation appears between the consumption of cervids and that of rabbits during April and February, which seems to be a trend for the remaining months. As previously commented in relation to deer, it is possible that the consumption pattern mimics the variation in rabbit availability in the environment (for example, due to potential seasonal breeding patterns of rabbits, although unfortunately no data is available concerning rabbit reproduction in the area).

This study also reports a new pattern found in relation to the consumption of carnivorous species (Palomares and Caro, 1999), which show a FO of around 10% (and a biomass contribution of 9%). In a few previous studies examining culpeo's diet, carnivorous species are described as prey in less than 3% FO in the culpeo diet: for example, in Argentina Johnson and Franklin (1994) recorded the consumption of patagonian hog-nosed skunk (*Conepatus humboldti*) with an 0.8% FO; Walker *et al*. (2007) used the carnivorous taxon as a consumed group with an appearance in faeces of 2.5%; while in Zapata *et al*. (2005) this prey group represents 1.8% of the FO. Thus, the present work reports the highest value of consumption of carnivorous species, including those of medium size such as the Andean coati, the skunk, and also species of the genus *Didelphis*. In addition, hair remains of puma were found in scats collected during different samplings and times, thus belonging to three different individuals. In fact, puma remains were also found in the culpeo's diet elsewhere (see Pia, 2013). There are two possible explanations for this finding: one, pumas were consumed as carrion (the most probable if these individuals were adults); and two, there was active predation on young pumas. In support of the latter it is known that coyotes kill adult bobcats (see Palomares and Caro, 1999), whose sizes could be similar in some cases to those of adult culpeos (especially males) and young pumas (especially females). Because these felids can kill culpeos (Pacheco *et al*., 2004; De Oliveira and Pereira, 2014), young pumas could be killed in turn by adult culpeos if given the opportunity, as a culpeo's strategy for reducing the risk of intra-guild predation (e.g. Palomares and Caro, 1999). However, having only the evidence of hair remains in scats we were unable to differentiate between the two possibilities.

Interestingly, we have not found remains of livestock in scats, despite the presence of livestock in the PNP (cattle, horses, poultry, etc). It is possible that due to the high density and availability of wild prey in the PNP, attacks from Andean foxes to livestock do not occur, as often happens with large predators and other canid species (e.g. Imbert *et al*., 2016). Considering other prey groups, it is also notable that in the PNP bird consumption seems minimal (2.6% FO). Again, this pattern significantly differs from those found during other research, where birds attain a FO of almost 12% (Marquet *et al*., 1993; Romo, 1995; Walker *et al*., 2007). In the case of the nine-banded armadillo the FO found (1.3%) was similar to that described for other species of

the same family (see Novaro *et al.*, 2000; Zapata *et al.*, 2005). The consumption of invertebrates was also low (0.7% FO). The importance of this group for the culpeo differs greatly among studies, as it is present in some (Ebensperger *et al.*, 1991; Correa and Roa, 2005; Achilles, 2007; Guzmán-Sandoval *et al.*, 2007) but not in others (Leon-Cobos 1994; Pia, 2013). Finally, the estimated biomass provided by birds, armadillos and invertebrates was almost irrelevant.

Fruit consumption showed low values (3% FO) compared to those observed in other studies, where the FO reaches values of almost 70% (Romo, 1995). Although this is not the only study where a low consumption is described (see Marquez *et al.*, 1993), the culpeo in the PNP did not use this resource significantly at any particular time of the year, showing instead a markedly carnivorous diet. Some studies have observed a negative correlation between consumption of fruits and abundance of rodent (Castro *et al.*, 1994; Silva *et al.*, 2005) and invertebrate (Cornejo and Jiménez, 2001) prey availability. In the desert of Peru, Romo (1995) found a 70% FO of *Vaccinium* berries in the culpeo's diet. This source of food is also abundant in the PNP, but consumption levels remain low. Thus, this could indicate a continuous supply of their most consumed prey throughout the year. Indeed, deer have long life cycles and their populations fluctuate less than those of smaller species such as rodents or rabbits. However, fruits might be more relevant in the diet if longer time series are considered, given that it has been observed that its importance can vary between years (Arim and Jaksic, 2005; Silva *et al.*, 2005). Therefore, more studies are needed to assess the role of the Andean fox as a seed disperser in the high-Andean ecosystem.

In the study area the trophic diversity of Andean foxes fluctuated across time. During most of the year Shannon-Wiener's index values remain below the average (i.e. H' = 1.7), showing a relatively low dietary diversity. In fact, diversity values are higher than, or close to, the mean value during only four months. March was the month showing the highest value of trophic diversity, while January presented the lowest one, when the diet was clearly dominated by cervids. Lower trophic diversity values (H' = 1.2 and H' = 1.3) were described in Central Chile (see Rubio *et al.*, 2013), whereas a high diversity value (H' = 3) was found in the south of Peru (Cornejo and Jiménez 2001).

The results of this work, which is the first systematic approach to the feeding ecology of the Andean fox in Ecuador, show that the species could behave as a facultative specialist rather than a generalist (see Glasser

1982, 1984). This hypothesis seems more likely when studies from other countries are also taken into account. Thus, as described for other carnivores such as the European wildcat (*Felis silvestris*) (Malo *et al.*, 2004; Lozano *et al.*, 2006), the red fox (*Vulpes vulpes*) (Delibes-Mateos *et al.*, 2008) and the pine marten (*Martes martes*) (Rosellini *et al.*, 2008), the culpeo could specialise on different prey groups or mammal species according to their availability. In contrast to other regions, in the PNP the culpeo has specialised in consuming cervids (probably including carrion), although small mammals or alternative food types could become the bulk of the diet if deer availability decreases. Consequently more studies on feeding ecology, in particular accounting for prey availability, are needed to test this hypothesis. Furthermore, the important consumption of carnivorous species in the PNP seems to demonstrate that the culpeo is a top predator in the high Andes. If so, we can speculate that the culpeo, along with the puma, could regulate the populations of meso-predators, having a strong influence on both carnivore community structure and the functioning of the ecosystem functioning (see Ripple *et al.*, 2014).This hypothesis has important consequences for conservation purposes. Nevertheless, more studies on population dynamics and the effects upon food-webs will be needed to gain a better understanding of the ecological role played by the culpeo, or Andean fox, in the high mountains of Ecuador.

Acknowledgements

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