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Latitudinal patterns in the diet of Andean condor (*Vultur gryphus*) in Chile: Contrasting environments influencing feeding behavior

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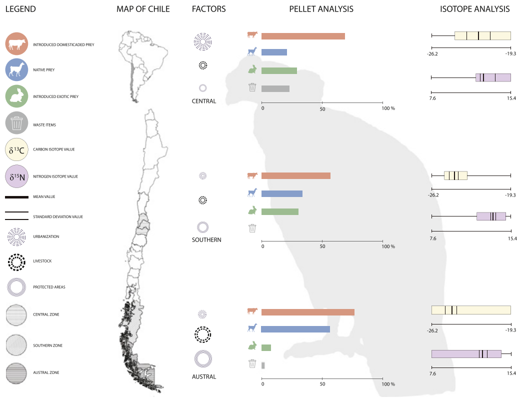
HIGHLIGHTS

- Anthropized environments alter availability of resources for Andean condors.
- Little evidence as to how condor's diet vary along their large latitudinal range
- Introduced domestic and exotic species are common Andean condor prey across Chile.
- Condors in anthropized areas use C_4-based food from landfills/corn-fed livestock.
- Anthropic subsidies may help stabilize populations, also enhance mortality risks.

GRAPHICAL ABSTRACT



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ABSTRACT

Human-dominated environments alter the availability and quality of resources for many species, especially for scavengers that have large home ranges and plastic foraging behaviors that enable them to exploit novel resources. Along the western slope of the Andes, the modification of natural landscapes have resulted in significant declines in native prey, the introduction of non-native species, and an increase in the availability of anthropogenic resources. These factors have likely influenced the resources available to Andean condors (*Vultur gryphus*), however, data are lacking as to how condor's diet vary along their large latitudinal range. We evaluated differences in Andean condor diet along a ~2500 km latitudinal gradient in Chile from the heavily modified Central zone (32–34°S) to the more pristine Austral zone (44–56°S). We assessed diet composition through the identification of prey remains in condor pellets, and carbon and nitrogen isotope analysis of condor feathers and their primary prey identified from pellet analysis. Our results identified medium- and large-bodied domesticated mammals (ungulates) and introduced exotic species (lagomorphs) as common prey across the study area. Condors from the Central zone had the largest isotopic niche width, probably related to consumption of anthropogenic resources with distinctly high carbon isotope values indicative of C_4-based foods likely acquired from landfills or corn-fed livestock. Isotopic niches for condors from the Southern and Austral zones almost completely

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overlapped. Andean condor diet is strongly influenced by local conditions determining differential access to prey sources. The high dependence of Andean condors on livestock across a large geographical area, and landfills in more (sub)urban areas, may help stabilize their populations via anthropogenic resources subsidies. Long-term dependence on such resources, however, may have health costs including contaminant exposure and greater mortality risk. These data will help identify potential threats related to resource availability and use, and better inform management and conservation decisions.

1. Introduction

Land-use activities have transformed >50% of the Earth's surface to provide humans access to critical natural resources and ecosystem services. The clearing of natural forest and grassland ecosystems for forestry, agricultural, and livestock production, and more recently for (sub)urban and industrial expansion (Ellis et al., 2010), has influenced the availability and quality of resources on which many species rely (Barbar et al., 2015). In particular, predators (Newsome et al., 2015) and scavengers (Cortés-Avizanda et al., 2016) have been disproportionately impacted by both direct (e.g., overhunting) and indirect (e.g., habitat loss) anthropogenic influences. Vulture populations in particular have been severely affected as a result of negative interactions with humans (Ogada et al., 2012) and currently 52% of vulture species are threatened with extinction worldwide (IUCN, 2020).

Large-bodied soaring scavengers such as vultures have extensive home ranges and can efficiently search large areas to locate patchily distributed prey (Barbar et al., 2015). In natural environments, seasonal variation in mortality and movement of potential prey strongly influences the territory and movement of scavengers (Kendall et al., 2014; Newsome et al., 2015; Lambertucci et al., 2018; García-Jiménez et al., 2018). In anthropized environments, domestic herbivores as well as introduced wild herbivores change the species composition and abundance of prey for scavengers (Jaksic et al., 2002; Vázquez, 2002), which results in close and in some cases obligatory ecological relationships between introduced herbivores and scavengers (Barbar et al., 2016). Population declines of natural prey, the presence of veterinary drugs in carcasses, sanitary regulations, and livestock management strategies can alter prey availability, and may have contributed to large-scale declines in Old World vultures (Donázar et al., 2009; Margalida et al., 2014, 2017; Buechley and Şekercioğlu, 2016; Arrondo et al., 2018). While livestock may benefit scavengers by providing resource subsidies (Jaksic et al., 2002; Vázquez, 2002), these sources of prey have also been identified as high-risk resources that may impact scavenger health and by extension lead to increased mortality risk (Blanco et al., 2017). Although livestock carcass dumps, landfills, and even fisheries bycatch have become a novel and relatively predictable food source for scavengers (Cortés-Avizanda et al., 2016; Tauler-Ametller et al., 2017), the use of these resources may be associated with either beneficial and detrimental health effects (Plaza and Lambertucci, 2017).

The Andean condor (*Vultur gryphus*) is the largest avian scavenger in South America and occurs along the Andes mountain range from ~5°N to 55°S latitude (Del Hoyo et al., 1994). In most areas in this distribution, condor populations have declined due to poisoning, hunting, and decreases in resource availability. Only in the southernmost margin of its range does condor population size appear to be more dense (Lambertucci, 2010; Pavez, 2012) and stable (Jaksic et al., 2001). Like other scavengers, the Andean condor has had to adapt to a changing environment and to modify its foraging behavior and diet (Lambertucci et al., 2009, 2018). Historically, Andean condors consumed a combination of marine resources sourced from the productive Humboldt Current (Lambertucci et al., 2018) and native terrestrial resources such as guanacos (*Lama guanicoe*) and lesser rheas (*Rhea pennata*) (Lambertucci et al., 2009). In addition to dramatic declines in native fauna (Ceballos, 2002), a suite of terrestrial mammals (e.g., red and fallow deer, wild boar) were introduced to Chile and Argentina more than a century ago (Jaksic et al., 2002) and are considered to be an ecological plague that have negative impacts on agriculture, livestock, and native vegetation and fauna (Vázquez, 2002). Some introduced species such as the lagomorphs like European hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) may also provide an indirect ecological benefit by serving as an alternate source of prey to large native predators and by extension decreasing predation pressure on native herbivores (Jaksic et al., 2002). These two lagomorph species, along with the introduced red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*) are important dietary components of Andean condors inhabiting some regions of Chile and Argentina (Lambertucci et al., 2009; Perrig et al., 2016; Ballejo et al., 2017; Pavez et al., 2019). At present, Andean condors feed primarily on introduced terrestrial mammals (e.g., ungulates and lagomorphs) that are the most abundant sources of carrion in rural environments (Lambertucci et al., 2009; Ballejo et al., 2017; Pavez et al., 2019). Nevertheless, livestock production over the past 50 years in Chile has declined up to 40%, and along with the intensification and technological advances of livestock production strategies has led to a decrease in the availability of carrion to Andean condor populations, especially in the central area of the country (INE, 2018). While Andean condors have historically avoided habitats extensively modified by human activities (Wallace and Temple, 1988), the recent decline in ranching activities and the scarcity of native prey in central Chile (Pavez, 2012) have changed their feeding behavior to include more reliable sources of anthropogenic foods in landfills and (sub)urban areas (Pavez et al., 2019).

Although the diet of Andean condors has been studied previously (Wallace and Temple, 1987; Lambertucci et al., 2009; Perrig et al., 2016; Pavez et al., 2019), all of these efforts focused on a single population in a relatively small area of the species large latitudinal range. The objective of our study was to characterize Andean condor diet across a wide latitudinal range of >2500 km (from ~32 to 56°S) along the western slope of the Andes to assess spatial variation in prey composition that may relate to varying levels of anthropogenic influence. We use faunal analysis of condor pellets collected from 20 roosting sites coupled with carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis of condor feathers and potential prey sources. This work provides a better understanding of the role that different sources of prey are playing in maintaining condor populations across Chile, which currently hosts ~70% of the global populations of this iconic species. These data may also help identify potential threats related to local resource availability and used to guide management decisions for Andean condor conservation strategies.

2. Materials & methods

2.1. Study area

Our study was conducted in continental Chile from 32°10′ S to 56°30′ S covering a latitudinal range of ~2500 km and altitudes between ~50 and ~2100 m above sea level, conditions that determine a wide variety of climates and landscapes and contrasting situations in relation to anthropogenic activities (Sánchez and Morales, 2002), availability and diversity of food resources for the Andean condor. We defined a priori three zones within the study area considering two main criteria. First, each zone were separated at least by 400 km of distance along a north-south axis based on the minimal adult/territorial home ranges described in Pavez (2014) and Lambertucci et al. (2014) (Fig. 1a). Second, the selected zones where Andean condors occur at the highest densities in Chile, which combined host 91% (central zone: 21%, southern zone: 70%) of the total population in the country (Pavez, 2012), overlaps with intensive livestock (INE, 2018). The Central zone is characterized by Mediterranean climate and high human intervention, while the Southern and Austral zones are characterized by extreme and cold climates and low levels of human intervention (see Supplementary material).

2.2. Sample collection

Between winter of 2016 and 2017, we sampled 20 Andean condor communal roosts (Fig. 1), eight of which were from the Central zone, six from the Southern zone, and six from the Austral zone. We non-invasively collected a total of 2520 pellets and 1390 molted feathers from the base of these roosts by visiting them between 12:00 and 17:00 when condors are away on foraging flights (Pavez, 2014). Additionally, we collected feather and hair samples from potential prey sources for condors within each zone (Table S1).

2.3. Pellet analysis

Pellets were dried at room temperature for one week. Only whole pellets from the three main communal roost of each zone were used (Fig. 1), selecting randomly 343 pellets. Then, pellets were mechanically disaggregated to separate the main diagnostic elements and identify prey items microscopically (Nikon Model Eclipse E200) following techniques and keys described by Chehébar and Martin (1989) and Wolfe and Long (1997) for hair items, and Day (1966) and Peterson (2010) for feather items. In addition, we developed a key identification reference from all potential Andean condor preys. We differentiate between digested and undigested plants to identify whether its presence was from digestive system of herbivores and thus incidental, or plants obtained from the substrate respectively. Waste and debris were macroscopically analyzed (elements >5 mm) and classified according to their composition as described in Pavez et al. (2019).

We grouped prey items into five categories that varied in taxonomic resolution: (i) mammals (species), (ii) birds (orders), (iii) anthropogenic waste and debris, (iv) digested and undigested plants, and (v) other (e.g., rock fragments). We did not include feathers identified as order Falconiformes in our diet analysis because they could be condor feathers ingested during grooming. Because it is impossible to assess whether prey are completely consumed, we did not attempt to measure prey biomass, relative digestibility of prey items, or the minimum number of individual prey in a given pellet (Marti et al., 2007). Consequently, results are presented as percent frequency of occurrence (FO%) relative to the total number of pellets examined in a given region or across the entire study area. We test the efficiency of the number of samples analyzed by performing a sample-based rarefaction curve ($Chao_2$ and S_{Mean}) richness estimator derived from 100 bootstrap randomizations using Estimates Version 9.1.0© (Colwell et al., 2012). The sampling efficiency for the total study area was 75.2%, being higher for the Central (84.5%) and Southern (84.3%), than the Austral zone (72.2%).

In addition, we developed a prey proportion and a geographical distances matrix between each roost through a Mantel permutation test with 10,000 randomizations (Bonnet and Van de Peer, 2002) using GenAlEx 6.5 package (Peakall and Smouse, 2012) to evaluate whether similarities in condor's diet composition was not related to distance between roosts (Mantel test, $r = 0.21$, $P = 0.15$).

Condor prey diversity was determined based on specific richness and relative frequency calculated via Shannon's index: $H' = \text{Sum}\ p_i \ln p_i$ where p_i represents the proportion of each species in the sample (Shannon, 1948). *t*-Tests for independent samples were performed in IBM SPSS Version 22.0© (Armonk, NY: IBM Corp.) to further examine differences among zones.

Correspondence analyses (CA) (Hill, 1974) were performed in Past Version 3.20© to examine the main source of diet variation in each zone in relation to four prey categorizations: (i) taxon and others (birds, mammals, plants and rock fragments), (ii) trophic level (carnivores, herbivores, omnivores), (iii) prey size (small-sized <10 kg, medium-sized >10 < 100 kg, and large-sized >100 kg), and (iv) origin (relative to native species – living within its natural range; introduced species – free ranging species living outside its native range; domestic species – depending on and providing services to humans; and anthropic material – human waste) (Occhipinti-Ambrogi and Galil, 2004). We conducted four different CAs to isolate the amount of variation in Andean condor diet explained by each set of explanatory variables based on a Chi^2 distance. Univariate general linear models (GLM) and a posteriori Least Significant Distance (LSD) post hoc test for multiple comparisons were performed in IBM SPSS Version 22.0© (Armonk, NY: IBM Corp.) to further examine trends identified by each CA.

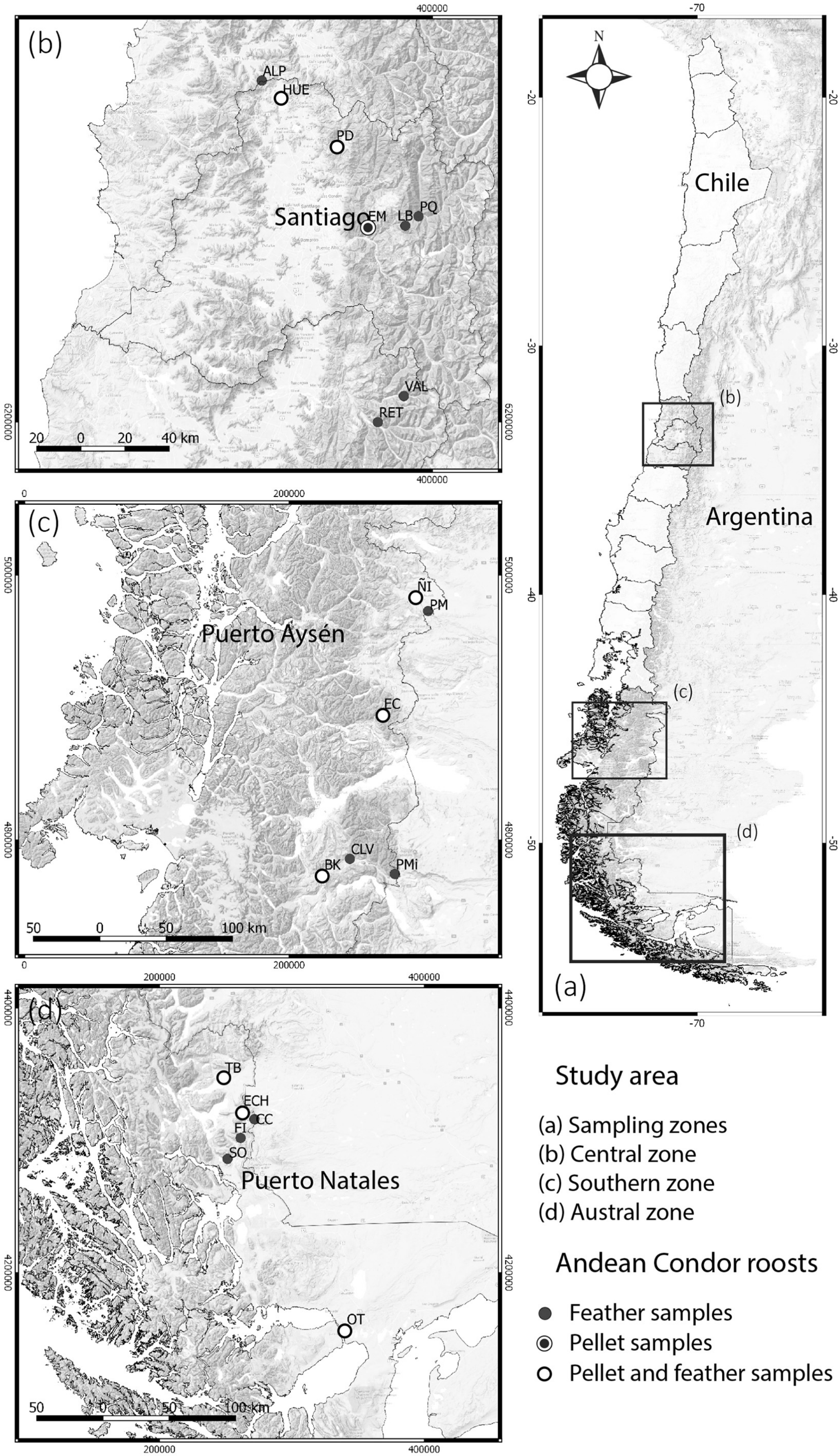
2.4. Stable isotope analysis

Feathers from a total of 205 condors were obtained from 20 selected communal roosts along the study gradient (Fig. 1, see Supplementary information for details). Feathers were washed with distilled water, during which barbs were separated to eliminate surface contaminants, and thoroughly dried. We relied on allometric estimations (Rohwer et al., 2009) and molting patterns of California condors (*Gygmogyps californianus*) to estimate that each secondary feather represented ~2-–3 months. We cut 20 segments from the base to the tip of the vane on both sides of the rachis and cut these segments into small (1 × 1 mm) pieces until further stable isotope analysis. We also analyzed hair and feather samples of 12 main preys that occurred at least in one of the selected zones (Table S1). We treated prey individually, because after performing a K nearest neighbor randomization test (all pairwise Ps < 0.05), we could not find biologically meaningful prey groups.

We used feather $\delta^{13}C$ and $\delta^{15}N$ trophic discrimination factors estimated during a controlled feeding experiment on captive Californian condors of 0.4 ± 0.4‰ and 3.1 ± 0.1‰ respectively (Kurle et al., 2013). Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values were measured on a Costech 4010 elemental analyzer coupled to a Thermo Scientific Delta V isotope ratio mass spectrometer. All isotope measurements were conducted at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM) and expressed in the common delta ("δ") notation (see Newsome et al., 2007 for more details).

For each zone, we evaluated stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ in feathers of Andean condor and feathers and hairs of their main food sources detected by pellet analysis in a biplot space qualitatively (Fig. 2A, B, C, D) using package Stable Isotope Bayesian Ellipses in R (SIBER, Jackson et al., 2011). Models were built over three Markov chains with 100,000 steps per chain with a burn of 50,000 iterations. Then, for each zone and age classes we calculated: (i) Andean condor δ^{13} C and $\delta^{15}N$ mean values (±SD) (ii) Niche width estimated through Standard Ellipse Area corrected by sample size (SEAc) (Jackson et al., 2011 –Table S2). The Analyses for graphical representations were developed in RStudio using the SIAR package (Parnell et al., 2010).The statistical differences between means for each zone and age class were analyzed by means of a repeated measurements-MANOVA test and a posteriori LSD test for multiple comparisons in IBM SPSS Version 22.0© (Armonk, NY: IBM Corp.). Significance was assumed at $P < 0.05$.

To avoid bias in the interpretation of the results, we also examined the following patterns. Since terrestrial ecosystems in Chile are dominated by plants that use the C3 photosynthetic pathway (Sanhueza and Falabella, 2010), we assumed that condors with $\delta^{13}C$ values that were higher than the potential prey sources we analyzed were consuming anthropogenic resources such as corn-based feed livestock, who are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Study area
(a) Sampling zones
(b) Central zone
(c) Southern zone
(d) Austral zone
Andean Condor roosts
● Feather samples
◉ Pellet samples
○ Pellet and feather samples

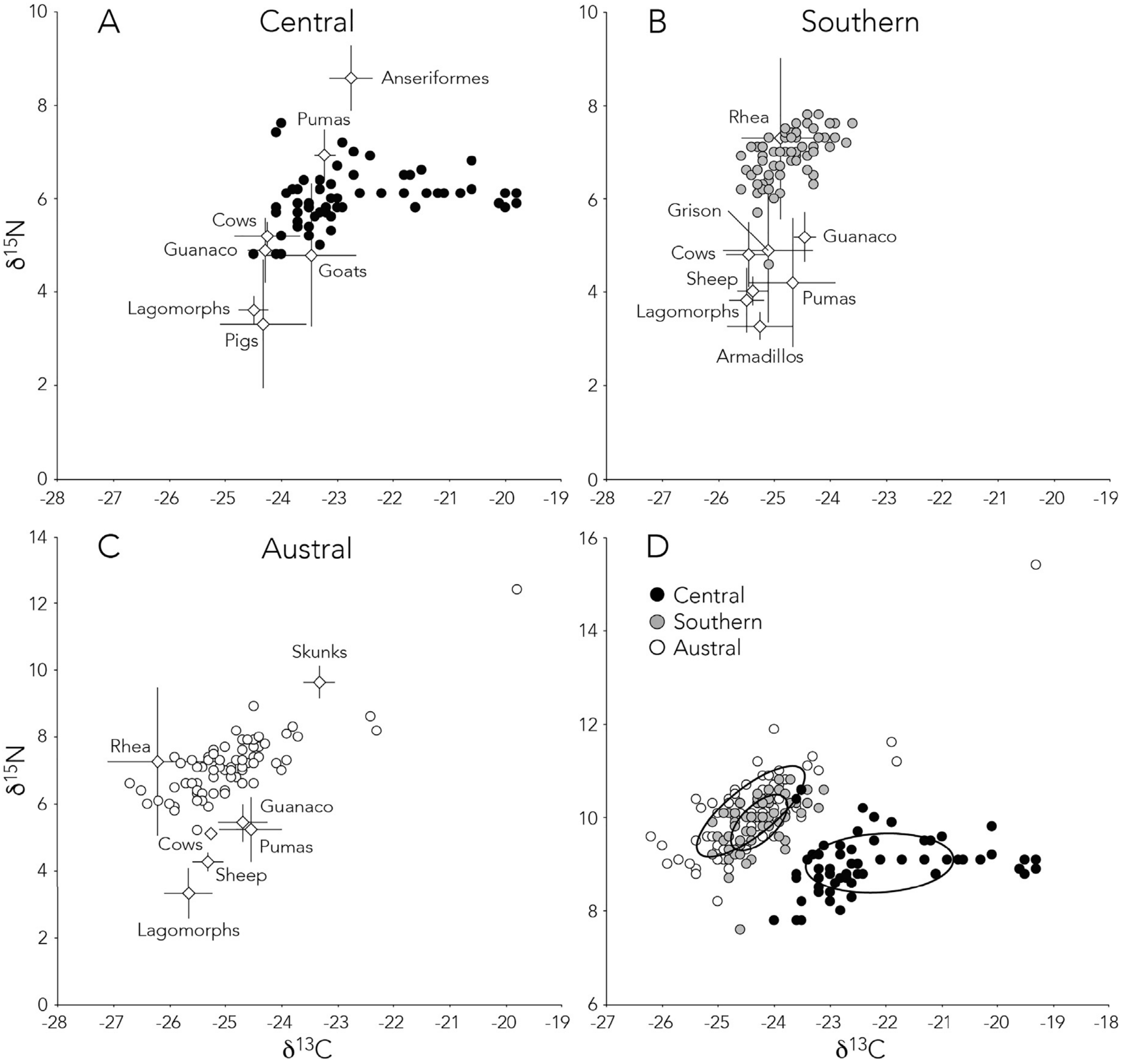

Fig. 2. δ^{13}C and δ^{15}N values of Andean condor (*Vultur gryphus*) feathers (circles) and hair and feathers (diamonds) of their primary food sources as indicated with pellet analysis at (A) Central, (B) Southern, (C) Austral zones of Chile, and (D) the whole study area; error bars for prey represent standard deviation. Condor feathers are corrected for trophic discrimination by subtracting 0.4 ± 0.4‰ and 3.1 ± 0.1‰ per mil from measured feather δ^{13}C and δ^{15}N values respectively. Ellipses represent standard ellipses areas (SEAc) estimated for each zone. Note that scales for δ^{13}C and δ^{15}N values vary among panels.

more enriched in ^{13}C because of C_4 plant intake (Jahren and Kraft, 2008). To confirm these assumptions, we compared the δ^{13}C and δ^{15}N composition of the two main prey species (guanaco - native, and cow - domestic) consumed by condors across the entire study area via a one-way ANOVA and a posteriori LSD test for multiple comparisons in IBM SPSS Version 22.0© (Armonk, NY: IBM Corp.). Only cattle δ^{13}C values showed significant differences among regions ($F_{2,5} = 8.23$, $P = 0.03$), with individuals from the Central zone having slightly higher δ^{13}C values (mean: -24.3 ± 0.5) than the Southern (mean: -25.3 ± 0.4; LSD: $P = 0.05$) and the Austral zone (mean: -25.3 ± 0.01; LSD: $P = 0.04$).

3. Results

3.1. Pellet analysis

We identified 39 different items in 343 pellets collected from nine selected communal roosts (three roosts per zone). Twenty-nine items were animal remains (mammals, birds, and insects), seven anthropogenic waste items, two plant types (digested and undigested) and one rock fragment (Table 1). Pellets collected from the Central and Southern zones had lower prey species richness (15 species) than those from the Austral zone (26 species). Likewise, the highest Shannon's diversity values for pellets from the Austral zone ($H' = 2.43 \pm 0.007$) were significantly higher than from the Southern ($H' = 2.13 \pm 0.007$, $t_{318.96} = -2.601$, $P < 0.01$) and Central ($H' = 2.06 \pm 0.007$, $t_{328.87} = -3.16$, $P < 0.01$) zones. Across the entire study area, the most frequent items consumed by condors were mammals (>90% FO).

The correspondence analysis revealed a variety of prey consumption patterns through the study area (Fig. 3). The first and second axes explained 100% of the cumulative variance: Axis 1 between 77% and 81% and Axis 2 between 19% and 23% depending on the prey category criterion. Axis 1 separated the Central and Austral zones, where the Austral zone was strongly and positively related to native mammals, carnivores, and small-sized prey species. Axis 2 separate the Southern zone from

Fig. 1. (A) Map of study area showing the three zones: (B) Central, (C), Southern, and (D) Austral. Condor roosts (n = 20 total) are shown by circles feathers, pellets, and a combination of feathers and pellets were sampled.

Table 1
Results of prey identification from condor pellets expressed as frequency of occurrence of total pellet (FO%), for all zones and for each zone separately.

Items	Species	All zones	Central	Southern	Austral
Mammals	**DOMESTICATED**				
	Bos taurus	36.2	41.7	27.5	40.0
	Ovis orientalis	23.0	1.0	18.3	46.7
	Equine (*Equus*)	8.7	11.7	6.7	8.3
	Capra hircus	2.6	8.7		
	Canis lupus familiaris	1.2	3.9		
	Felis silvestris catus	0.9		0.8	1.7
	Sus scrofa domesticus	0.6	1.9		
	Subtotal of domesticated mammals	**67.7**	**68.6**	**56.6**	**76.5**
	INTRODUCED				
	Oryctolagus cuniculus	16.6	23.3	22.5	5.0
	Lepus europaeus	1.7	1.9	2.5	0.8
	Lagomorph	2.3	1.9	3.3	1.7
	Sus scrofa	0.3			0.8
	Subtotal of introduced mammals	**21.3**	**29.1**	**30.3**	**7.8**
	NATIVE				
	Lama guanicoe	13.1	10.7	10.8	17.5
	Puma concolor	3.5	1.0	2.5	6.7
	Chaetophractus villosus	2.6		4.2	3.3
	Galictis cuja	2.6		1.7	5.8
	Conepatus humboldtii	1.7		0.8	4.2
	Lycalopex culpaeus	0.9			2.5
	Dolichotis patagonum	0.3			0.8
	Lagidium wolffsohni	0.3			0.8
	Lontra provocax	0.3			0.8
	Pudu puda	0.3	1.0		
	Zaedyus pichiy	0.3			0.8
	Irenomys tarsalis	0.3		0.8	
	Unidentified rodent	0.6		0.8	0.8
	Subtotal of native mammals	**38.7**	**20.9**	**33.3**	**56.5**
	Unidentified mammal	24.2	22.3	34.2	15.8
	Subtotal of all mammals	**93.6**	**94.2**	**92.5**	**94.2**
Birds	*Anseriformes*	6.1	3.9	5.0	9.2
	Rheiformes	5.0		2.5	11.7
	Sphenisciformes	0.9			2.5
	Phoenicopteriforme	0.9			2.5
	Galliforme	0.6	1.0		0.8
	Passeriforme	0.3			0.8
	Unidentified birds	10.2	5.8	10.0	14.2
	Subtotal of birds	**23.6**	**11.7**	**18.3**	**39.2**
Waste	Low density polyethylene (LDPE)	2.3	6.8		0.8
	Glass	1.2	3.9		
	Polypropylene (PP)	1.2	3.9		
	Paper	0.6	1.9		
	Polyamides (PAs)	0.6	1.9		
	Polyethylene Terephthalate (PET)	0.3	1.0		
	Textile	0.3	1.0		
	Unidentified plastic	3.8	10.7		1.7
	Subtotal of waste	**6.7**	**19.4**	**0.0**	**2.5**
Plants	Digested	49.3	47.6	57.5	42.5
	Undigested	32.7	34.0	25.8	38.3
	Subtotal of plants	**69.1**	**73.8**	**68.3**	**65.8**
Insects	Insects	0.3			0.8
Others	Rock fragments	9.9	27.2	3.3	1.7
No. items		971	327	291	353
No. pellets		343	103	120	120

the Central and Austral zones and was strongly and positively related to medium-sized and domesticated mammals. Large-sized mammal herbivores ($F_{2,6} = 0.19$, $P = 0.83$; $F_{2,51} = 0.29$, $P = 0.75$, respectively), plants ($F_{2,3} = 0.002$, $P = 0.99$), and introduced small-bodied prey items ($F_{2,8} = 0.49$, $P = 0.63$) were common to all zones (these items are located near the origin of the axes, Fig. 3). The Austral zone showed a positive relation with small and medium-bodied native prey species and waste items of anthropogenic origin, and a significant effect with carnivores ($F_{2,21} = 5.35$, $P = 0.01$) in comparison to Central and Southern zones ($P < 0.01$), and with birds ($P = 0.05$) in comparison to the Central zone ($P = 0.05$). The Southern zone showed a positive relationship with medium and large-sized domestic herbivores, but we found no significant effects with specific prey types. The Central zone showed a positive relationship with medium and large-bodied domestic prey species (Fig. 3) and had a significant effect with anthropogenic waste ($F_{2,15} = 3.97$, $P = 0.04$) in comparison to the Southern ($P = 0.02$) and Austral zones ($P = 0.04$).

3.2. Stable isotope analysis

Our results revealed that isotopic values and isotopic niche metrics differed both among geographic zones and age classes. Specifically, $\delta^{13}C$ and $\delta^{15}N$ values of condor feathers differed significantly among zones ($F_{2,196} = 14.62$, $P < 0.01$). Post hoc tests revealed that feathers from the Central zone had significantly higher $\delta^{13}C$ ($F_{2,196} = 114.82$, $P < 0.01$) but lower $\delta^{15}N$ values ($F_{2,196} = 42.53$, $P < 0.01$) than those from the Southern and Austral zones ($P < 0.01$); in the latter two zones, $\delta^{13}C$ and $\delta^{15}N$ values were indistinguishable ($P > 0.05$). Condor individuals from the Central zone also had a larger isotopic niche width (see SEAc - Table S2, Fig. 2D), while condors from the Southern zone showed the smallest. Overlap among isotopic niches was greatest between condors from the Southern (72%) and Austral zones (31%), while there was no isotopic overlap between these two zones and condor feathers from the Central zone (Fig. 2D).

Individuals from different age classes showed marginally significant differences in mean (±SD) $\delta^{13}C$ values ($F_{2,196} = 2.74$, $P = 0.06$), which were higher in subadult individuals ($-23.6 \pm 1.5‰$) than in juvenile (-23.8 ± 1.4, LSD, $P = 0.09$) and adult (-23.7 ± 1.3, LSD, $P = 0.02$). Subadults from the Southern and Austral zones had a larger isotopic niche width (Table S2) and the lowest degree of overlap with adults (Southern: 56%, Austral: 38%) and juveniles (Southern: 62%, Austral: 58%), while the latter two age classes had a higher degree of overlap (Southern: 92%, Austral: 90%). In contrast, juveniles from the Central zone, had the largest isotopic niche width (Table S2), and the lowest degree of overlap with subadults (51%) and adults (54%) in this zone.

Estimates of diet composition via Bayesian mixing models for condors collected across the entire study area showed that livestock contributed between 40 and 60% to the diet, with the greatest contribution to condor's diet in Central zone. Native prey contributed between 16 and 44% to condor's diet among zones and was highest in the Austral zone. Introduced lagomorphs contributed ~25% to condor's diet in Central and Southern zones, which decreased to only 5% in the Austral zone (Table S3). Across the entire study area, cows represented the largest component of diet (24–49%), followed by sheep (16–26%), and lagomorphs (5–26%). The relative contribution of prey changed within each zone (Table S3). In the Central zone, cows represented the largest component of diet (36 ± 49%), followed by lagomorphs (24 ± 30%), and then goats (12 ± 23%). In the Southern zone, the primary prey consumed were lagomorphs (26 ± 31%) and cows (24 ± 30%) followed by lesser rheas (19 ± 27%) and sheep (16 ± 26%). In the Austral zone, sheep (26 ± 31%) and cows (24 ± 30%) had similar contributions to condor's diet, followed by lesser rheas (19 ± 27%) and guanacos (12 ± 23%).

4. Discussion

Our results identified medium and large-sized domesticated mammals (cows and sheep) and introduced exotic species (lagomorphs) as common prey for condors across Chile (Fig. 3). We also found differences in diet among the three latitudinal zones considered in our study. Condors in the Central zone consumed a higher proportion of C_4-based anthropogenic resources in comparison to those from the Southern or Austral zones, while extensive use of marine resources was limited to a few individuals in the Austral zone. Below we discuss

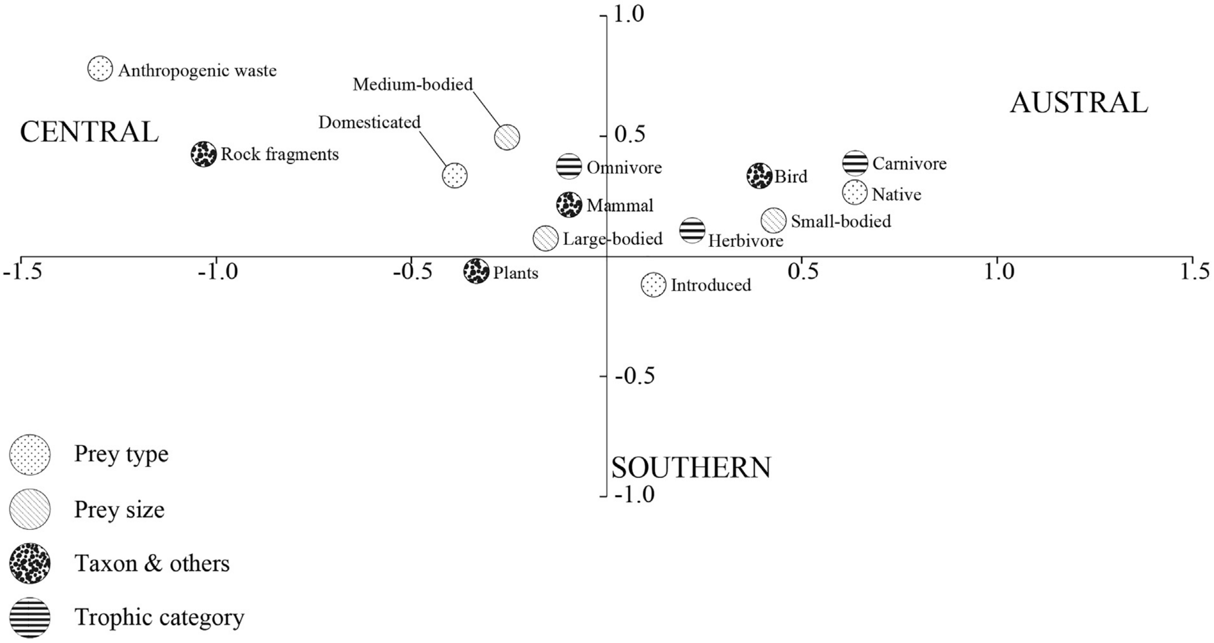

Fig. 3. Canonical correspondence analysis (CCA) of condor diets based on pellet analysis in Central, Southern, and Austral zones of Chile. The biplot ordination diagram summarizes the four analyses performed for each grouping variable: Items categorization are represented by dotted circles for Prey type; circles with diagonal dashed lines represent Prey size; circles with dots represent Taxonomic categories; circles with horizontal lines represent trophic categories. Zones are shown in bold font.

how these patterns in condor's diet may relate to regional prey availability, ontogeny, and place our results in the context of previous work on the diet and behavior of this species. Finally, we offer a brief discussion of how our results may inform the conservation and management of this threatened species.

4.1. Prey composition: identify, diversity, and size

Our study is the first to examine Andean condor diet over a large latitudinal range (~2500 km) containing a wide variety of environmental conditions that influence resource availability. The richness of prey species (29 species) documented here (Table 1) has not been previously reported to our knowledge (Lambertucci et al., 2009; Perrig et al., 2016; Ballejo et al., 2017; Pavez et al., 2019). In regard to non-native prey species, cattle are the most abundant livestock produced in Chile (INE, 2018), and our results from pellet analysis show that this food source is the most important source of prey for condor populations across the country, especially in the Central zone (Table 1, S3). Domesticated mammals account for 69%, 57% and 77% of identifiable fragments in condor pellets collected from the Central, Southern, and Austral zones respectively. In contrast, native prey dominated condor's diet in the Austral zone, accounting for 57% of identifiable fragments, whereas this group of resources contributed 33% and 21% in the Southern and Central zones respectively. Even though 79% of sheep and cattle production in Chile occurs in the Austral zone (INE, 2018), native prey (e.g., guanacos and lesser rheas) showed the highest contribution to condor's diet (57%) in this zone based on pellet analysis. As such, we infer that domestic livestock (Tables 1, S3) are likely a less important source of prey for sustaining condor populations in the relatively pristine Austral zone compared to the highly modified Central zone where livestock appears to be the primary source of prey. By comparison, guanaco populations in the Southern and especially Central zones are small and fragmented (González et al., 2013), and unsurprisingly our analysis shows that this prey source contributes minimally to condor's diet in these areas. The Austral zone also supports the most dense population of pumas in the country, which are the primary predator of guanacos (Franklin et al., 1999). Trophic facilitation by this apex carnivore (Perrig et al., 2016) may have a stronger influence than the availability of anthropogenic resources on condor's diet in the Austral zone in comparison to the Central and Southern zones.

Although large mammals are available to condors across Chile and may be a preferred resource representing 60% of diet according to pellet and isotope analysis, our results also show that a variety of small-bodied native and non-native prey species contributed to condor's diet (Fig. 3, Table 1). Even native birds (e.g., Anseriformes) were identified from pellet samples (Table 1), which were not found in previous studies of condor's diet composition (Lambertucci et al., 2009; Perrig et al., 2016; Ballejo et al., 2017). The most abundant small-bodied prey found in condor pellets was non-native lagomorphs, which are likely the most abundant small-bodied prey in South America (Barbar et al., 2016). European hares (*Lepus europaeus*) are an important component of condor's diet in northern (Perrig et al., 2016) and southern (Lambertucci et al., 2009) Argentina, as well as in Central and Southern Chile (Tables 1, S3; Pavez et al., 2019). Consumption of small-bodied prey like lagomorphs may be driven by a variety of ecological and anthropogenic processes that influence their availability (Vázquez, 2002; Barbar et al., 2015). For example, other raptors (e.g., caracaras) and avian scavengers (e.g., turkey vultures) may enhance the detection and thus accessibility of small-bodied prey to condors, which outcompete these smaller species for carcasses (Wallace and Temple, 1987). Likewise, a series of lagomorph mass mortality events have been occurring because of myxomatosis outbreaks in the Central and Southern zones over the last decade. For example, an extensive outbreak in 2017 and the consequent unpredictable increase in the density of rabbit carcasses in (sub) urban areas surrounding Santiago (SAG comm., 2014, 2018), along with the availability of predictable and available food resources in landfills, are likely the reasons for why condors are now permanent year-round residents in the metropolitan area. These examples are a testament to the high dietary plasticity of Andean condors and their ability to quickly adapt to novel resources and occupy human-modified habitats, which has been previously documented for this (Lambertucci et al., 2018) and other vulture species (Newsome et al., 2015). But the presence of

Andean condors in (sub)urban areas with high human population densities has not been previously described as they are believed to be misanthropes that tend to avoid such habitats (Donázar et al., 1999).

4.2. Regional differences in condor's diet composition

Both pellet and isotope analysis show that condor's diet differ across Chile. Several individual condors from the Central zone have relatively high δ^{13}C values (>−21‰) indicative of consuming anthropogenic resources that are ^{13}C-enriched relative to native prey (Fig. 2A; Tauler-Ametller et al., 2018). The Mediterranean climate of central Chile characterized by cold and wet winters but dry and warm summers produces ecosystems in which C_3 plants (δ^{13}C values: −24‰ to −30‰) dominate primary production (Sanhueza and Falabella, 2010). Native C_4 vegetation is practically non-existent in terrestrial environments from central and southern Chile at any elevation (Falabella et al., 2008). Anthropogenic foods have characteristically high δ^{13}C values due to the use of corn-based products (e.g., corn syrup and cornmeal) as a stable carbohydrate and/or the consumption of corn-based feed by livestock (Jahren and Kraft, 2008). Thus, the relatively high δ^{13}C values (>−21‰) of some condor individuals from the Central zone (Fig. 2A, D) is likely the result of consumption of anthropogenic resources, most of which are likely obtained from landfills (Tauler-Ametller et al., 2018; Pavez et al., 2019). These assumptions are supported by dietary data derived from pellet analysis (Pavez et al., 2019, Table 1), in which a high frequency of anthropogenic waste were found in pellets from the Central zone (19%) relative to its occurrence in more pristine environments (Southern: 0%; Austral: 3%). It is important to note that many types of anthropogenic resources are completely digestible and may not be easily identifiable in pellet or scat analysis. Thus, the combination of stable isotope analysis with traditional approaches on prey identification in guts or feces is perhaps that best approach to quantify the contribution of anthropogenic resources in animal diets (Newsome et al., 2010, 2015).

Unsurprisingly, the cow samples we collected in the Central zone have low δ^{13}C values indicative C_3-based ecosystems because they were collected from animals feeding in open pastures at relatively high elevations (>1000 m). We assume that livestock raised in more confined conditions at lower elevations (400–1000 m) have higher δ^{13}C values resulting from being raised on corn-based feed. Although, to our knowledge, there are no records of δ^{13}C values in cattle or any other livestock species in Chile, 75% of the corn grown in the country is destined for cattle feed, which is used extensively in the more arid Central zone relative to regions further south (ODEPA, 2017).

We found no evidence of a large marine component in condor's diet; however, a few individuals from the Austral zone had relatively high δ^{13}C and δ^{15}N values consistent with consumption of marine-derived resources (Table 1; Fig. 2C). These isotopic patterns are corroborated by pellet analysis, which identified penguins (Sphenisciformes), Chilean flamingos (*Phoenicopterus chilensis*) and Kelp geese (Anseriformes) in samples collected from the Austral zone (Table S3). These findings agree with previous historical isotope-based studies in northern Patagonia (Lambertucci et al., 2018) and observational studies in northern Perú (Temple and Wallace, 1989) and southern Argentina (Lambertucci et al., 2018).

While the Southern and Austral zones contain similar environments and support similar types and abundances of terrestrial and marine food resources, the lower prey diversity in pellets (Table S3) and smaller isotopic niche width (Table S2) of condors in the Southern (15 species, 0.7‰^{2}) versus Austral (26 species, 1.7‰^{2}) zone is noteworthy. This pattern may be a consequence of contrasting landscape characteristics of the western versus eastern slopes of the Andes. Condors in the Southern zone may primarily breed and forage on the eastern slope where topographic characteristics like the presence of slopes and cliffs enhance flight conditions (Péron et al., 2017) and provide better roosts and nesting sites. These conditions along with a more moderate climate and extensive meadows (Pérez-García et al., 2017) may enhance terrestrial prey availability on the eastern versus densely forested western slope of the Andes in this region.

4.3. Age-related variation in condor's diet

Isotopic patterns among age classes within zones (Table S2) suggest that hierarchical behavior may play a role in allowing access to foraging areas and resources of different quality (Wallace and Temple, 1987; Donázar et al., 1999). Hierarchy in Andean condors is sex- and age-based, with males dominating over females and adults over immatures (Donázar et al., 1999). Lower degrees of isotopic niche overlap, larger isotopic niches, and higher δ^{13}C values in subadults versus adults collected from both the Southern and Austral zones suggest that these age classes partition resources, where subadults have a more diverse prey base to avoid intraspecific resource competition with adults (Duriez et al., 2012; Moreno-Opo et al., 2016). Subadults generally have larger home ranges than adults (Donázar et al., 1999), which may allow them access to less competitive resources obtained from interspecific interactions with other avian scavengers and raptors in which condors dominate by size (Wallace and Temple, 1987; Moreno-Opo et al., 2020), and from habitats of lower quality in human-dominated habitats like agricultural lowlands where anthropogenic resources are associated with higher risk of indirect mortality (Donázar et al., 1999; Blanco et al., 2017). In the Central zone, juveniles had larger isotopic niches than the other age classes, with a distribution that overlapped extensively with subadults (97%) and adults (94%). Overall, the lower degree of isotopic variation among age classes in the Central zone may results from lower availability and depletion of prey associated with extensive human modification of the environment (Jaksic et al., 2001; Pavez, 2012), forcing to exploit ^{13}C-enriched anthropogenic resources (Table S2, Fig. 2D). Observed differences in foraging behavior among age classes could be driven by several factors. First, subordinate younger age classes feed after dominant adults and on portions of carcasses that are less nutritious (e.g., tendons and skin) (Wallace and Temple, 1987) and likely have higher δ^{13}C values than lipid-rich internal organs (Tieszen et al., 1983) that are preferred and first consumed by dominant adults. Second, dominant and territorial adults would foraging in higher quality areas characterized by better flight and roosting conditions, higher and more consistent prey availability, and lower human disturbance (Wallace and Temple, 1987; Donázar et al., 1999). Larger isotopic niche widths observed in juveniles and subadults likely reflects exploitation of larger and suboptimal areas (Donázar et al., 1999) where the competence with adults for better conditions or prey tissues decreases.

The lack of significant differences in δ^{13}C and δ^{15}N values and the high degree of isotopic niche overlap between juvenile and adults, however, suggests that other social behavioral traits such as collaborative behavior and kin associations (Padró et al., 2018) may be an important factor in condor foraging ecology. Andean condors possess one of the longest post-fledging dependence periods among birds (up to one year) (Del Hoyo et al., 1994), and recently Padró et al. (2019) described close familiar aggregations over small geographic distances. So, it is possible that kinship and associations in communal roosting sites lead to a cooperative strategy to enhanced fitness gains between genetic relatives when resources are not limited such as in Southern and Austral zone observed patterns, while differed when are scarce as we described in Central zone (Table S2) (Deygout et al., 2010).

The two methodologies we used to study diet provided complementary and integrative information on the diversity and relative contribution of prey to Andean condor diets along a broad latitudinal range across Chile. Pellet analysis tends to overestimate the contribution of large mammals while underestimating small prey (Stephen et al., 2001), and it generally does not provide accurate estimates of the percent biomass of prey types consumed by scavengers (Perrig et al., 2016). Complementary methods (e.g., direct observation) to minimize these biases are recommended, however, they can be time- and cost-intensive (Simmons et al., 1991; Stephen et al., 2001; Marti et al., 2007). In our study, pellet analysis was useful to identify variation in prey diversity and predict the relative proportion of prey types in condor diets within and among latitudinal zones.

5. Conclusions

Our results show that condor's diet varies across along a latitudinal gradient along the western slope of Andes and are strongly influenced by the availability of native versus anthropogenic resources. We also observed a high degree of dietary plasticity among individuals within a single region that appears to be related to age-based hierarchies and access to relatively predictable anthropogenic resources found in lowland agricultural areas (livestock) and/or landfills (refuse), especially in the Central zone. Currently, domesticated (non-native) mammals (cows and sheep) are a major source of food for Andean condors across the large geographical area studied here. These dependable resources may help stabilize condor populations as their primary sources of native prey (e.g., guanacos and rheas) continue to decline in some areas, however, the long-term implications of this subsidization are poorly understood and may ultimately be costly given that the spatial and temporal abundance of anthropogenic resources (e.g., livestock) vary with socio-economic factors and are associated with greater mortality risks (Pavez, 2001; Lambertucci, 2007; Carrete et al., 2007; Lambertucci et al., 2011). To better understand the potential benefits and costs for Andean condor populations, additional studies are needed to better integrate both ecological and anthropogenic factors associated with the increasingly close relationship between condors and humans. We anticipate that this information will inform future decisions regarding Andean condor conservation and management.

Credit authorship contribution statement

Melanie Duclos: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration. **Pablo Sabat:** Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization, Supervision. **Seth D. Newsome:** Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization, Supervision. **Eduardo F. Pavez:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft. **Cristóbal Galbán-Malagón:** Conceptualization, Investigation, Writing - review & editing, Visualization. **Fabian M. Jaksic:** Investigation, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration. **Verónica Quirici:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.140220.

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