

# Functional Ecology

## More than just meat: Carcass decomposition shapes trophic identities in a terrestrial vertebrate

Gonzalo Barceló<sup>1\*</sup>, Paula L. Perrig<sup>1,2</sup>, Prarthana Dharampal<sup>3</sup>, Emiliano Donadio<sup>4</sup>, Shawn A. Steffan<sup>3,5</sup> and Jonathan N. Pauli<sup>1</sup>

(1) Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Dr., Madison, Wisconsin 53706, USA.

(2) Grupo de Investigaciones en Biología de la Conservación, INIBIOMA (Universidad Nacional del Comahue - CONICET), Quintral 1250, Bariloche, Rio Negro 8400, Argentina.

(3) Department of Entomology, University of Wisconsin-Madison, Madison, Wisconsin 53706, USA.

(4) Fundación Rewilding Argentina, Scalabrini Ortiz 3355 4J, CP 1425, Buenos Aires, Argentina.

(5) USDA-ARS, Vegetable Crop Research Unit, Madison, WI 53706, USA

\* Corresponding author: Gonzalo Barceló. Address: 1630 Linden Dr., Madison, Wisconsin 53706, USA. Email: [barcelocarva@wisc.edu](mailto:barcelocarva@wisc.edu)

### Acknowledgements

This work was supported by the National Agency for Research and Development (ANID/DOCTORADO BECAS CHILE/2017–72180367, GB) and with a grant from University of Wisconsin-Madison Graduate School (JNP). We thank personnel of San Guillermo National Park for providing logistical support and to many volunteers for their assistance during field and laboratory work, especially José A. Gallo and Bruno D. Varela. We thank Burcu Laçin Alas and Matt Smith for their assistance in the laboratory and Bill Karasov and two anonymous reviewers for their constructive comments.

### Conflicts of interest

The authors declare that they have no conflict of interest.

### Author Contributions

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/1365-2435.14041](https://doi.org/10.1111/1365-2435.14041)

This article is protected by copyright. All rights reserved

GB, JNP and SAS designed the study. PLP and ED collected field data. GB and PD analyzed the data. GB and JNP lead the writing and all authors contributed critically and approved the final manuscript.

**Data availability statement**

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.vhhmgqnrj> (Barceló et al., 2022).

MR GONZALO BARCELÓ (Orcid ID : 0000-0002-9391-9571)

MISS PAULA LETICIA PERRIG (Orcid ID : 0000-0002-4269-9468)

DR PRARTHANA DHARAMPAL (Orcid ID : 0000-0002-7635-7079)

DR SHAWN ALAN STEFFAN (Orcid ID : 0000-0002-2219-6409)

Article type : Research Article

### Abstract

1. Most food web models fail to account for the full complexity of interactions within a community, particularly where microbes are involved. Carcasses are microbe-rich resources and may represent a common nexus for the macro- and microbiome, effectively uniting autotrophs, consumers, predators, and microbiota.
2. We evaluated the role of carcasses as multitrophic resources and explored dietary partitioning for a sexually dimorphic obligate scavenger known for its hierarchical social system. This study was set in a well-studied community of camelids (*Vicugna vicugna*, *Lama guanicoe*), pumas (*Puma concolor*), and Andean condors (*Vultur gryphus*) in the Andes. We hypothesized that condors, by feeding on trophically distinct dietary substrates within any given carcass, would have highly variable trophic position (TP) values. Further, we expected that the microbial consumers within the carcass would inflate TP values in both, the carrion and the condors. Thus, we expected that the trophic heterogeneity within a carcass could facilitate sex-based dietary partitioning in condors.
3. We used a multifaceted approach to assess the foraging of Andean condors, using regurgitated pellet and bulk isotopic analyses, and also quantified the TP of the entire community of graminoids, camelids, camelid carrion, pumas, and female and male condors employing compound-specific stable isotopes analysis of amino-acids.

4. Our analysis of condor pellets and bulk isotopes revealed non-trivial plant consumption, close to 10% of condor diet. Isotope analysis of amino-acids revealed that condors had highly variable TPs ( $2.9 \pm 0.3$ ) compared to pumas ( $3.0 \pm 0.0$ ) and camelids ( $2.0 \pm 0.1$ ), likely representing “trophic omnivory”, wherein the condors consume plants (TP= $1.0 \pm 0.1$ ) and microbe-colonized carrion ( $2.3 \pm 0.1$ ). Female condors exhibited a TP ( $2.8 \pm 0.2$ ) lower than strict carnivory, suggesting that they consume more plant biomass in a carcass, while males (TP= $3.1 \pm 0.3$ ) are likely consuming more of the microbe-rich animal tissue.
5. Our study highlights that carcasses represent a trophically heterogeneous resource and that vertebrate scavengers can feed across trophic groups within the carcass, from autotrophs to secondary consumers, and from both the macro- and microbiome. Thus, integration of microbes in macroecological contexts can help to resolve trophic identity, and better characterize the importance of microbes in detritivorous and omnivorous species.

## Resumen

1. La mayoría de los modelos de redes tróficas fallan en capturar la completa complejidad de las interacciones dentro de una comunidad, especialmente cuando hay microbios involucrados. Los cadáveres son un recurso rico en microbios que representa un nexo entre los macro- y microbiomas, uniendo efectivamente a autótrofos, consumidores, depredadores y microbios.
2. Evaluamos el rol de los cadáveres como un recurso multitrófico y exploramos la partición dietaria para un carroñero obligado con dimorfismo sexual conocido por su sistema social jerárquico. Este estudio se realizó en una comunidad bien estudiada de camélidos (*Vicugna vicugna*, *Lama guanicoe*), pumas (*Puma concolor*), y cóndores (*Vultur gryphus*) en los Andes. Hipotetizamos que los cóndores al alimentarse de distintos sustratos tróficos dentro de un cadáver debiesen tener un valor de posición trófica (PT) altamente variable. Además, esperamos que los consumidores microbianos dentro del cadáver aumenten los valores de PT tanto en la carroña como en los cóndores. Por ende, esperamos que la heterogeneidad trófica dentro del cadáver facilite la partición dietaria entre sexos en cóndores.

- Accepted Article
3. Usamos una aproximación multifacética para evaluar la dieta de los cóndores, usando egagrópilas y análisis de isótopos estables, y también cuantificamos las PT de la comunidad de graminoideas, camélidos, carroña de camélidos, pumas y cóndores macho y hembra empleando análisis de isótopos estables compuesto-específicos de aminoácidos.
  4. Nuestros análisis de egagrópilas e isótopos revelaron consumo no trivial de plantas, cercano al 10% de la dieta del cóndor. Los análisis de isótopos de aminoácidos revelaron que los cóndores tenían una PT altamente variable ( $2.9 \pm 0.3$ ) comparada con pumas ( $3.0 \pm 0.0$ ) y camélidos ( $2.0 \pm 0.1$ ), posiblemente representando “omnivoría trófica”, donde los cóndores consumen plantas ( $TP=1.0 \pm 0.1$ ) y carroña de camélidos colonizada por microbios ( $2.3 \pm 0.1$ ). Cóndores hembra mostraron una PT ( $2.8 \pm 0.2$ ) menor a la carnivoría estricta, sugiriendo que consumen más biomasa vegetal del cadáver, mientras que los machos ( $TP=3.1 \pm 0.3$ ) están probablemente consumiendo más de los tejidos animales colonizados por microbios.
  5. Nuestro estudio destaca que los cadáveres representan un recurso tróficamente heterogéneo, desde autótrofos a consumidores secundarios, y desde el macro y microbioma. Así, la integración de microbios en contextos macroecológicos puede ayudar a resolver las identidades tróficas y caracterizar de mejor manera la importancia de los microbios en especies detritívoras y omnívoras.

### Keywords

carrion – detritivory – food webs – guanaco – microbe – necrobiome – omnivore – vulture.

## Introduction

Predation is one of the most studied and captivating trophic interactions (Sergio et al., 2006; Wilson & Wolkovich, 2011). Apex carnivores exert disproportionate effects on prey both directly (“consumptive”) and indirectly (“non-consumptive”), sometimes with cascading consequences for lower trophic levels (Estes et al., 2011). Consequently, the regulation of food webs by apex carnivore has been widely explored not only in an ecological context, but also in terms of animal conservation and ecosystem restoration (Ritchie et al., 2012; Wallach et al., 2015). There has been, however, a growing interest in actors beyond the classic “green food web” (i.e., living primary producers-consumers-predators) to include those in the “brown food web” (i.e., detritus-microbiota-scavengers). It is becoming increasingly recognized that this traditional view of neatly compartmentalized green or brown food webs is not broadly representative of most food webs—indeed green and brown food-chains are usually so intertwined that it becomes trivial to characterize a higher-order consumer as either ‘green’ or ‘brown’ (Steffan & Dharampal, 2019; Wilson & Wolkovich, 2011).

Carcasses are one example blurring the lines between green and brown food webs and uniting the macro- and micro-biome (Barry et al., 2019; Burkepile et al., 2006; Shukla et al., 2018). Although vertebrate carcasses comprise a small fraction of total detritus in an ecosystem, they have a disproportionate local impact in nutrient deposition and cycling, especially of nitrogen, phosphorous and calcium, and represent nutritionally rich, yet ephemeral, resources (Carter et al., 2007; Parmenter & Macmahon, 2009). Consequently, carcasses are crucial for a diversity of scavengers and decomposers that compete for access to them (Burkepile et al., 2006). Although generally considered as a discrete and homogeneous dietary item, carcasses are a composite of organisms: animal tissue, plant matter and digesta held in the digestive tract, invertebrate scavengers and microbes that are consuming necrotic tissue. A single carcass can hold a diversity of organisms that span multiple trophic levels, from autotrophic biomass to secondary and tertiary consumers, including both macro- and microbiota. This so-called “necrobiome” provides a framework to explore cross-kingdom interactions, where microbes can impact entire ecosystems (Benbow et al., 2019). Scavengers are likely consuming all components of a carcass (Pechal et al., 2019; Steffan & Dharampal, 2019) – not only the carrion (i.e. tissue of the dead animal) but also the innumerable microscopic consumers embedded within the carrion (Steffan et al. 2017, Steffan & Dharampal 2019).

Obligate scavengers have evolved a suite of behavioral, physiological, and anatomical adaptations to exploit ephemeral carrion resources (Ruxton & Houston, 2004).

Predators, by hunting prey regularly and often in a spatially predictable fashion, can provide some spatiotemporal consistency in carcass availability (Wilmers et al., 2003). Vultures occupy an important place in the food web by recycling nutrients (Moleón & Sánchez-Zapata, 2015), regulating disease outbreaks (Wilson & Wolkovich, 2011) and modulating predation rates due to competition-facilitation interactions with predators (Elbroch & Wittmer, 2013; Moleón et al., 2014). In the last century, the global abundance and distribution of vultures have declined in part due to decreased availability of safe carrion (Buechley & Şekercioğlu, 2016; Pauli et al., 2018). These declines are likely disrupting important community interactions involving carcasses and the necrobiome (Benbow et al., 2019).

The Andean condor (*Vultur gryphus*) – the largest vulture (1.3 m height and 3 m wingspan) and one of the heaviest flying birds (13 kg body mass, Ferguson-Lees & Christie, 2001) – is considered carnivorous. Condors primarily consume carrion of large herbivores, generally provisioned by pumas (*Puma concolor*) in areas where native communities have been preserved, but they also can consume smaller-bodied vertebrates including exotic lagomorphs (Ballejo et al., 2018; Duclos et al., 2020; Perrig et al., 2017). Researchers have observed plant matter in the pellets of condors previously (Duclos et al., 2020; Pavez et al., 2019), although it is often considered to be incidental ingestion. Plant consumption among condors is a potential mechanism by which condors acquire pigments, notably carotenoids, which are associated with social dominance (Blanco et al., 2013; Marinero et al., 2018). Although male condors are up to 50% larger than females (Alarcón et al., 2017) and assume priority at carcasses (Alarcón et al., 2017; Donazar et al., 1999; Wallace & Temple, 1987), xanthophyll carotenoid concentrations in blood are highest in immature and female condors (Blanco et al., 2013). Possibly, then, dominant males are consuming the protein-rich components of the carcass and relegating subordinate individuals to plant material.

Research to-date has found little evidence of sex-based partitioning of diet (Perrig et al., 2021), although this could be overlooking fine-scale diet partitioning that happens within the carcass. Microbial or detrital impact on large vertebrate systems has been documented extensively (Hyodo et al., 2015; Stevens & Hume, 1998); however, the quantification of such microbivory has only recently been documented through trophic inflation of detrital complexes

in invertebrates and fish (Dharampal et al., 2019; Steffan et al., 2017). Given that carcasses are a heterogeneous pool of resources, it is possible that sexes partition dietary resource at a carcass, possibly resulting in different trophic positions (TP). To-date, the relative importance of carcass components to Andean condors has not been quantified.

To explore resource allocation from the carcass and to examine trophic identities of scavengers, we studied a camelid-puma-condor community in San Guillermo National Park (hereafter, San Guillermo NP; Fig. 1). Located in northwestern Argentina, San Guillermo NP is one of the few places that maintained trophic interactions among native camelids (vicuñas [*Vicugna vicugna*] and guanacos [*Lama guanicoe*]), pumas and Andean condors (Donadio et al., 2010; Donadio, Buskirk, & Novaro, 2012; Perrig et al., 2017). Previous work in San Guillermo NP identified that puma predation is the primary cause of adult camelid mortality (accounting for >90% of carcasses; Donadio et al., 2012). Given that pumas are solitary hunters and leave large quantities of carcass materials behind (Elbroch et al., 2014), the majority (88%) of the condor diet in San Guillermo NP consists of camelids, 85% of which resulted from puma provisioning (Perrig et al., 2017).

We hypothesized that the trophic identity of a carcass would be an assemblage of multiple trophic positions – plant digesta (TP ~ 1), camelid biomass (TP = 2) and microbes (TP ~ 3) – and that obligate scavengers, by consuming them all, would have intermediate non-integer ( $2.5 < x < 3.5$ ) trophic positions. Specifically, we predicted that camelids and pumas would have integer TPs corresponding to strict herbivory and carnivory (TP = 2 and TP = 3, respectively), and exhibit little variance. However, we predicted that camelid necrotic tissue, i.e., carrion, would be trophically inflated due to microbial colonization (Steffan et al., 2017). Consequently, the Andean condors consuming the microbe-colonized carrion would develop a trophic position above pumas consuming only the camelid meat. In effect, microbes within a carcass are trophically analogous to pumas, thus when a condor consumes both the camelid and the embedded microbes, the condor feeds at a higher trophic position. We also predicted that condors were consuming non-trivial amounts of plant material and hence, the condor population would exhibit higher intra-population variation in TP. Finally, we predicted that condors would exhibit sex-based dietary partitioning, in which dominant males would consume more carcass meat and females would consume more plant material. To test our hypothesis, we quantified the TP of the entire community using compound-specific stable isotopes analysis of amino acids



(CSIA-AA). Additionally, we documented the relative contribution of individual food sources to scavengers via regurgitated pellets and the analysis of bulk isotopes ( $^{13}\text{C}$  and  $^{15}\text{N}$ ).

## Methods

San Guillermo NP (29°12'S – 69°20'W) extends over 1660 km<sup>2</sup> in the Andean plateau in the province of San Juan, Argentina. This high-altitude region is characterized by a semiarid climate (100 – 500 mm/year) with temperatures ranging between 27 °C and -23 °C (Salvioli, 2007), where vegetation is dominated by grass and shrub steppes. We reanalyzed 177 regurgitated pellets from active Andean condors roosting sites collected by Perrig et al. (2017) in summer 2013 in the park to estimate the amount of plants consumed (as plants were not accounted for in the original analysis). Pellets were oven-dried (55°C for 48 h) and then microscopically identified dietary items to estimate, 1) occurrence, as the percentage of times an item occurred in the total number of pellets, and 2) the relative volumetric content, in relation to the total volume of pellets, for each category of dietary items, grouped as camelids (vicuña and guanaco), plants, livestock (cow [*Bos taurus*], horse [*Equus ferus*], goat [*Capra aegagrus*] and sheep [*Ovis aries*] and others (hares [*Lepus europeus*] and southern mountain viscachas [*Lagidium viscacia*]).

We also used samples collected in summer 2013 for a complementary analysis of  $^{13}\text{C}$  and  $^{15}\text{N}$  bulk isotopes (Perrig et al. 2017), which estimate assimilated diet components avoiding biases associated with differential digestibility, as well as  $^{15}\text{N}$  CSIA-AA, to estimate the trophic position of all members of the food web. Past analyses have shown that the enrichment in  $^{15}\text{N}$  between the diet and the consumer is uneven across AAs but is highly consistent for particular AAs (Chikaraishi et al., 2009). Thus, by quantifying the ratio of  $^{15}\text{N}$  between an AA that reflects the source (e.g., phenylalanine), and one that reflects the fractionation by the consumer (e.g., glutamic acid), one can robustly predict the TP of a consumer (Steffan et al., 2015).

For the  $^{13}\text{C}$  and  $^{15}\text{N}$  stable isotope analysis of bulk tissue we used samples of condor feathers ( $n = 47$ , adult males = 14, adult females = 23, immature males = 2, immature females = 8) from feeding and roosting sites, hair from camelids (vicuña  $n = 7$ , guanaco  $n = 7$ ) found on carcasses and hair from cows ( $n = 10$ ) and goats ( $n = 6$ ) (Perrig et al., 2017). We additionally collected the dominant autotrophs and main dietary items of vicuñas (Cajal, 1989) in the park from living plants: rushes (*Juncus* sp.;  $n = 3$ ) and fescues (*Festuca* spp.;  $n = 3$ ). We molecularly identified the sex and individual for each condor feather and evaluated age class based on their

Accepted Article  
color (Perrig et al., 2019). We prepared hair and feather samples for bulk isotope analysis by washing and rinsing 3 times with a solution 2:1 trichloromethane-methanol to remove dirt and surface oil, then all samples were homogenized in small parts (< 1mm) with surgical scissors and dried for 72 hours at 60°C. Values for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in bulk tissue were calculated by weighing the samples ( $0.6 \text{ mg} \pm 0.005$ ) and placing them in tin capsules, then measured with a Costech 4010 elemental analyzer attached to a Thermo Finnigan DeltaPLUS XP or V Flow Isotope Ratio Mass Spectrometer (University of Wyoming, Laramie, USA). Results are provided in per mil (‰) notation relative to the international standards of Peedee Belemnite (PDB) and atmospheric nitrogen (AIR) for carbon and nitrogen, respectively calibrated against internal laboratory standards.

We estimated the proportional assimilation of isotopically distinct food sources by Andean condors using a Bayesian-based mixing model in MixSIAR (Stock & Semmens, 2016) with Markov chain Monte Carlo (MCMC; chain length = 300,000; burn = 200,000; thin = 100; chains = 3). Based on the pellet analysis, we identified five isotopically distinct and biologically meaningful dietary sources: large livestock (cows), small livestock (goats), camelids (vicuña and guanaco), fescues and rushes. We used raw isotopic compositions values of the dietary source and average and standard deviation for their concentration dependence (i.e. relative weight of N and C; Table S1). We used trophic discrimination factors of  $3.1\text{‰} \pm 0.1$  and  $0.4\text{‰} \pm 0.4\text{‰}$  for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively, previously observed for Californian condors on a controlled feeding trial (Kurlle et al., 2013). We ran four MixSIAR model sets with age-sex class as a fixed effect, using either informed priors based on pellet content or a uniform prior and using both the whole condor data set ( $n = 47$ , adult males = 14, adult females = 23 and immatures = 10) and the subset utilized in CSIA-AA (adults only,  $n = 15$ , males = 7, females = 8). To make diet estimates from pellets and bulk stable isotopes comparable, we merged a posteriori large and small livestock into “livestock” and fescues and rushes into “plants”; for each category, we added individual estimations from MCMC chains and derived the mean and Bayesian credible interval from the aggregated chain (Phillips et al., 2014; Stock et al., 2018).

We examined the values of  $\delta^{15}\text{N}$  in glutamic acid and phenylalanine for all community members in San Guillermo NP. We used a subset of samples mentioned above, rushes ( $n = 2$ ), fescues ( $n = 2$ ), vicuñas ( $n = 3$ ), guanacos ( $n = 3$ ), adult female ( $n = 3$ ) and male condors ( $n = 2$ ), and we added puma hair ( $n = 4$ ) from individuals captured using foot snares (Smith et al., 2019),

and decomposing subcutaneous muscle intermingled with skin from camelid carrion ( $n = 4$ ). Camelid carrion was collected after condors abandoned the carcasses (>3 days after death) from the hind limbs simultaneously with camelid hair. The carrion was analyzed to account for the microbial activity in the necrotic tissue as a contrast to camelid hair that does not change their isotopic signature after growth. Previous work has shown that skin, muscle and keratin are reliable proxies for whole body glutamic acid and phenylalanine  $\delta^{15}\text{N}$  measurements (Dharampal et al. unpublished data). All these samples were analyzed following Chikaraishi et al. (2007; 2009). Our sample sizes exceed those of previous work addressing trophic ecology with CSIA which have repeatedly demonstrated sufficient precision to identify trophic position (Blanke et al., 2017; Pauli et al., 2019; Steffan et al., 2015; Takizawa et al., 2020). This is because of the lower variance of the intra-trophic  $\delta^{15}\text{N}$  difference value between glutamic acid and phenylalanine and the greater magnitude of effect in glutamic acid fractionation compared to bulk isotopes. We nevertheless increased our sample size with additional adult female ( $n = 5$ ) and male condor ( $n = 5$ ) samples using the N-acetyl methyl esters (NACME) derivatization technique (Corr et al., 2007; Yarnes & Herszage, 2017; University of California, Davis, USA). Given that we detected no differences between these two approaches in either  $\delta^{15}\text{N}$  in glutamic acid and phenylalanine (multivariate analysis of variance [MANOVA]  $F_{2,13} = 1.54$   $p = 0.25$ ) or estimated TP values (Welch's  $t_{4,5} = 1.85$ ,  $p = 0.13$ ), we pooled condor CSIA data in subsequent analyses.

We estimated the trophic position for plants, vicuñas, guanacos, pumas, condor and camelid carrion based on the  $\delta^{15}\text{N}$  values of glutamic acid ( $\delta^{15}\text{N}_{\text{glu}}$ ) and phenylalanine ( $\delta^{15}\text{N}_{\text{phe}}$ ) using the equation: 
$$\text{TP} = \frac{\delta^{15}\text{N}_{\text{glu}} - \delta^{15}\text{N}_{\text{phe}} + \beta}{\Delta_{\text{glu-phe}}} + \lambda$$
 (Chikaraishi et al., 2009), where  $\beta$  corrects for the difference in  $\delta^{15}\text{N}$  values between glutamic acid and phenylalanine in  $\text{C}_3$  plants;  $\Delta_{\text{glu-phe}}$  represents the net trophic discrimination between glutamic acid and phenylalanine (7.2; Steffan et al., 2015, 2017); and  $\lambda$  represents the basal trophic level (1). A TP estimate can be improved by using a  $\beta$  value that has been empirically derived from the study system (Steffan et al., 2013). While most terrestrial  $\text{C}_3$  plant  $\beta$  are assumed to be near 8.4‰ (Chikaraishi et al., 2014), we measured our system-specific  $\beta$  to be 8.35‰ ( $\pm \text{SD} = 0.80$ ). We tested for normality in our TP estimates using the Shapiro–Wilk test and for homoscedasticity with a Bartlett test (Bartlett's  $K^2$ ) with subsequent pairwise comparisons. To compare TP among all trophic entities we used Welch's ANOVA. We then conducted pairwise comparisons between

camelid carrion and living camelids, and between pumas and male and female condors using Welch's *t*-test. We compared observed TP values to expected TP categories with a one sample *t*-test.

Research permits were issued by the Argentine National Park Administration (#DRC265 and DCM255 and subsequent renewals) and the Argentine Ministry of Environmental and Sustainable Development under CITES permit No. 15US94907A/9.

## Results

Camelids were the most common dietary item found in Andean condor pellets, constituting 98.3% of occurrence and 86.9% (mean  $\pm$  21.9 SD) of volumetric content (Table 1). Plant matter was the second most important dietary item, found in 57.6% of the pellets analyzed, which on average constituted 9.9% ( $\pm$  15.8) of the pellet volumetric content. Other sources of food, such as livestock, hares and mountain viscachas were present only in 12.9% of the pellets and accounted for 3.1% ( $\pm$  4.2) of volumetric content.

Our dietary mixing model involving bulk  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for the subset of condors that we also analyzed TP (Fig. 2), suggested that the diet of male condors was 65.2% (median, 95% credible interval [35-89]) camelids, whereas the diet of females was 53.1% [26-75] camelids. Additionally, livestock and plants represented 24.3% [3-58] and 7.8% [1-28] of male diet, respectively, while the diet of females were 32.6% [7-65] livestock and 13.0% [2-33] plants (Fig. 2b). When we analyzed the entire dataset of condors, mixing models revealed the same ranked importance in diet items at the population level (Table 1): camelids, followed by livestock and then plant matter, with sex and age-based differences in proportional diets overlapping (Table S2).

Our TP estimates for discrete trophic entities differed predictably ( $F_{5,11} = 284.9, p < 0.001$ ), with plants (TP =  $1.01 \pm 0.11$  [SD]) at the base of the food web, camelids (TP =  $2.02 \pm 0.05$ ) registering as primary consumers, and pumas (TP =  $3.00 \pm 0.04$ ) as strict consumers of herbivores. Camelid carrion was significantly elevated relative to living camelids (TP =  $2.26 \pm 0.1$ ;  $t_{3,8} = -3.91, p = 0.02$ ). TP estimates for male (TP =  $3.09 \pm 0.34$ ) and female condors (TP =  $2.83 \pm 0.15$ ) did not differ ( $t_{8,1} = -1.70, p = 0.13$ ; condor population TP =  $2.9 \pm 0.29$ ). However, the TP of pumas was significantly higher than the TP for female condors ( $t_9 = 2.67, p = 0.027$ ), and marginally lower than male condors ( $t_6 = -0.64, p = 0.054$ ). Indeed, TP of female condors

represent a non-integer value ( $t_7 = -2.85, p = 0.025$ ), lower than strict carnivory (3.0), while male condor TP was indistinguishable from strict carnivory ( $t_6 = 0.64, p = 0.549$ ). Among all the trophic groups in this Andean food-web, Andean condors exhibited the widest range of TP values, from 2.6 to 3.8 (Fig. 3), and had a significantly greater variance compared to that found in pumas ( $K^2 = 7.70, p = 0.006$ ). TP variance was marginally higher in male than female condors ( $K^2 = 3.63, p = 0.057$ ).

## Discussion

Our results reveal that carcasses are not just meat to obligate scavengers but represent a heterogeneous pool of resources that span taxa and trophic positions. In the process, the consumption of a carcass and the attendant necrobiome effectively integrates the macro- and microbiome within scavenger populations. Indeed, we found that plant material was common within regurgitated pellets of condors and assimilated in relatively large amounts by these scavengers. Our estimates of TP suggested that carcasses also have non-trivial amounts of microbial matter and that there was a detectable, and important, consumption of microbes by condors. Finally, our non-integer estimates of TP for condors, as well as the high level of inter-individual variation in TP estimates, demonstrates that this highly specialized scavenger is, indeed, a “trophic omnivore” (Steffan & Dharampal, 2019) and consumes multiple trophic levels.

Andean condor diet partitioning among sexes and age classes has been widely debated. Strong sexual dimorphism and hierarchical dominance structures have been suggested as potential mechanisms that drive partitioning of space and time (Alarcón et al., 2017; Donazar et al., 1999), with eventual implications for the diet. However, evidence documenting sex-based dietary partitioning in condors is inconsistent between sites (Perrig et al., 2021). Our results show some support for dietary partitioning between the sexes. Similar to Perrig et al. (2017), but with the inclusion of plants, we did not detect difference in the assimilated diet between age-sex classes, nor did we detect TP differences between the sexes. On the other hand, adult male condors possessed TP estimates indistinguishable from strict carnivory (TP - 3.0), while females had lower TP estimates attributable to trophic omnivory. This aligns with studies showing that adult males can exert control and gain priority over high quality sites (Alarcón et al., 2017; Marinero et al., 2018; Wallace & Temple, 1987) and, therefore the highest-quality food, as well

Accepted Article

as with the observation that males have less pigments derived from plant material in the blood (Blanco et al., 2013). The lack of consistent evidence of partitioning between sexes may be due to high unpredictability in resource availability in the landscape (Mancini et al., 2013). That is to say, the camelid carcasses regularly provisioned by pumas contain varying amounts of residual meat (Elbroch et al., 2014), which could modulate the potential dietary differentiation. Hence, future research should evaluate the impact of carcass quality (i.e. amount of remaining meat) at a finer scale.

Diet estimates obtained from bulk isotopes and mixing model differed from those derived from pellets. Notably, bulk isotopes estimated greater reliance on livestock and less consumption of camelids. However, camelids remained the most important diet item regardless of the approach. This difference in point estimates is likely a result of the different integration times that these methods reflect: isotopes from feathers reveal assimilated diet over a wider spatio-temporal frame (~3 months), while the pellets reflect more immediate foraging events. Additionally, estimates of the mixing model could be affected by the wide range  $^{15}\text{N}$  found in the plant material, inflating error estimates. However, a previous study that did not include plants as a potential diet item, found similar results in the relative contribution of camelids and livestock (Perrig et al., 2017).

We found that condors consumed a considerable amount of plant biomass. The ingestion of plant material may be incidental (Duclos et al., 2020) and associated with the consumption of the guts of the carcass. However, its consistent presence in the diet of condors could link this feeding habit to other functions. It is possible that plant consumption allows the assimilation of carotenoids (Blanco et al., 2013), which can be important in social hierarchies for Andean condors (Marinero et al., 2018) and associated with their immune response (Plaza et al., 2020). Also, plant digesta and associated volatile fatty acids produced in the rumen of camelids may provide nutritional inputs that would otherwise be unavailable and limiting to condors, given that vultures do not possess the capacity for fermentation and the cecum is vestigial or absent (Clench & Mathias, 1995). Additionally, plant digesta can be a source of water, as moisture is retained for longer periods in the internal tissues of the carcass (Carter et al., 2007; Schotsmans et al., 2011), which might be a relevant factor in arid and semiarid environments. It is also possible that plant material is ingested not only for nutrition or digestion but also as an emetic, as suggested

for other vultures (Thomson et al. 2013). Regardless of the ultimate function of plant ingesta, it showed as a non-trivial and consistent item across the condor population.

As predicted, camelid carrion exhibited an inflated TP of 2.26, most likely produced by microbial consumption of the carrion (Steffan et al., 2017). As microbes consume carrion and propagate through the carcass, they stockpile  $^{15}\text{N}$  within certain amino acid pools, including glutamic acid (Steffan et al. 2013, 2015). This compound-specific enrichment is how microbes cause trophic inflation within a detrital mass (Steffan et al. 2017; Steffan & Dharampal 2019). Autolytic processes during decomposition produce a general isotopic enrichment of bulk  $^{15}\text{N}$  in carrion as volatilized compounds such as ammonia are lost (Keenan & DeBruyn, 2019), although the role in  $^{15}\text{N}$  enrichment of glutamic acid over phenylalanine should be minor. Glutamic acid newly synthesized, and enriched in  $^{15}\text{N}$ , is unexpected to happen by itself in a dying tissue. Indeed, enrichment of bulk  $^{15}\text{N}$  is only perceptible in tissues with a prolonged decomposition stage (Keenan & DeBruyn, 2019; Yurkowski et al., 2017) when microbes are dominant. Intra-trophic enrichment of glutamic acid  $^{15}\text{N}$  and elevation of TP by catabolic processes has been documented in living organisms, sometimes generating *de novo* tissues, that sustain these processes for prolonged periods like hibernation, starvation, and egg production in animals (Whiteman et al., 2021) or flowers and bud development in plants (Takizawa et al., 2017). Because the primary cause of mortality of camelids in San Guillermo NP is puma predation, and all carrion we sampled were the result of predation, trophic elevation of camelid carrion due to prior starvation is highly unlikely; rather it is far more plausible that the trophic elevation of carrion was driven by microbial decomposition. While trophic inflation of decomposed tissues colonized by microbes has been described uniquely in detritus of vegetation and invertebrates (Steffan et al., 2017; Steffan & Dharampal, 2019) and bulk  $^{15}\text{N}$  enrichment has been reported in decaying vertebrate tissue (Keenan & DeBruyn, 2019); this study provides the first evidence for trophic position inflation of vertebrate tissue using CSIA.

Even though condors consumed and assimilated measurable amounts of plant material, their average TP was close to that of pumas (3.0), suggesting that condors are also eating non-trivial quantities of secondary consumer biomass (i.e., the microbes embedded in carcasses that are trophically analogous to pumas). Thus, it appears the consumption of the microbes likely elevates the condor TP, effectively neutralizing the depressive effects of the plant digesta. Given that condors unlikely scavenge on pumas due to their lower population density in relation to

Accepted Article

camelids, and that camelid carrion has an already inflated TP of 2.26, it is almost certain that condors are eating the heterotrophic microbes of the carrion as secondary consumers. This is one of the few studies to report trophic inflation (i.e. higher TP due to consumption of detritivores organisms) in a terrestrial vertebrate consumer (Pauli et al., 2019) and the first suggesting microbivory for a large vertebrate. These findings highlight the importance of CSIA in trophic positions and necrobiomes where regular bulk isotopes analysis have shown variable differences (Burrows et al., 2014; Keenan & DeBruyn, 2019; Payo-Payo et al., 2013; Yurkowski et al., 2017). It is notable that estimated TPs of pumas showed little variability around 3.0, suggesting little-to-no ingestion of microbial-colonized tissues. Pumas in our study site abandon carcasses shortly after killing (on average 34 hours), which may be insufficient for microbial trophic inflation. Andean condors, in contrast, consume carcasses after pumas have given up and up to 3-7 days after death. It is possible that other organisms, notably scavenging insects, could have been also consumed by condors; however, the complete absence of insect remains or chitin in pellets, their infrequent occurrence on puma-killed carcasses and the fact that carrion is trophically inflated suggests that the TP of condors came primarily from microbes on the carrion.

Puma predation provides obligate scavengers not only with a regular supply of carrion (Barry et al., 2019; Elbroch & Wittmer, 2013) but also with other dietary components as plant digesta and high concentration of microbes. This is especially important given that vulture reliance on landfills or other artificial food sources is increasingly common (Duclos et al., 2020; Moreno-Opo et al., 2015; Plaza & Lambertucci, 2017) and these sources do not always provide all the components of naturally occurring carcasses. The existence of microbivory in vultures requires further study, as it could represent a link between scavenger gut microbiota and the microbiome of the carrion, as shown for other taxa (Weatherbee et al., 2017). Vulture gut microbiota similarly to other scavenger, the American alligator, is composed mainly of Clostridia and Fusobacteria (Keenan & Elsey, 2015; Roggenbuck et al., 2014), generally considered pathogenic for other vertebrates and associated with flesh decomposition (Zepeda Mendoza et al., 2018). It could be that condors and other scavengers exploit microbes from carrion to inoculate gut flora and increase digestion efficiency, which is critical for birds that feed on patchy and ephemeral food resources (Grémillet et al., 2012). Our study represents an initial contribution to the understanding of the trophic heterogeneity found within a carcass and the role of scavengers in uniting the macro- and micro-biome, emphasizing the utility of multifaceted



approaches in reconstructing the diets of free-ranging animals within their natural habitat. Our work also highlights how the integration of microbes into food webs can help resolve the trophic identities and dietary differences for large vertebrates and that resolving interkingdom interactions can shed light on the necrobiome functioning.

## References

- Alarcón, P. A. E., Morales, J. M., Donázar, J. A., Sánchez-Zapata, J. A., Hiraldo, F., & Lambertucci, S. A. (2017). Sexual-size dimorphism modulates the trade-off between exploiting food and wind resources in a large avian scavenger. *Scientific Reports*, *7*, 11461. <https://doi.org/10.1038/s41598-017-11855-0>
- Ballejo, F., Lambertucci, S. A., Trejo, A., & De Santis, L. J. M. (2018). Trophic niche overlap among scavengers in Patagonia supports the condor-vulture competition hypothesis. *Bird Conservation International*, *28*, 390–402. <https://doi.org/10.1017/S0959270917000211>
- Barceló, G., Perrig, P. L., Dharampal, P., Donadio, E., Steffan, S. A., & Pauli, J. N. (2022). More than just meat: Carcass decomposition shapes trophic identities in a terrestrial vertebrate. *Dryad, Dataset*, <https://doi.org/10.5061/dryad.vhmgqnrj>
- Barry, J. M., Elbroch, L. M., Aiello-Lammens, M. E., Sarno, R. J., Seelye, L., Kusler, A., Quigley, H. B., & Grigione, M. M. (2019). Pumas as ecosystem engineers: ungulate carcasses support beetle assemblages in the Greater Yellowstone ecosystem. *Oecologia*, *189*, 577–586. <https://doi.org/10.1007/s00442-018-4315-z>
- Benbow, M. E., Barton, P. S., Ulyshen, M. D., Beasley, J. C., DeVault, T. L., Strickland, M. S., Tomberlin, J. K., Jordan, H. R., & Pechal, J. L. (2019). Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. *Ecological Monographs*, *89*, e01331. <https://doi.org/10.1002/ecm.1331>
- Blanco, G., Hornero-Méndez, D., Lambertucci, S. A., Bautista, L. M., Wiemeyer, G., Sanchez-Zapata, J. A., Garrido-Fernández, J., Hiraldo, F., & Donázar, J. A. (2013). Need and seek for dietary micronutrients: Endogenous regulation, external signalling and food sources of carotenoids in New World vultures. *PLoS ONE*, *8*, e65562. <https://doi.org/10.1371/journal.pone.0065562>
- Blanke, C. M., Chikaraishi, Y., Takizawa, Y., Steffan, S. A., Dharampal, P. S., & Vander Zanden, M. J. (2017). Comparing compound-specific and bulk stable nitrogen isotope trophic discrimination factors across multiple freshwater fish species and diets. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*, 1291–1297. <https://doi.org/10.1139/cjfas-2016-0420>
- Buechley, E. R., & Şekercioğlu, Ç. H. (2016). The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions. *Biological Conservation*, *198*,

220–228. <https://doi.org/10.1016/j.biocon.2016.04.001>

- Burkepile, D. E., Parker, J. D., Woodson, C. B., Mills, H. J., Kubanek, J., Sobecky, P. A., & Hay, M. E. (2006). Chemically mediated competition between microbes and animals: Microbes as consumers in food webs. *Ecology*, *87*, 2821–2831. [https://doi.org/10.1890/0012-9658\(2006\)87\[2821:CMCBMA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2821:CMCBMA]2.0.CO;2)
- Burrows, D. G., Reichert, W. L., & Bradley Hanson, M. (2014). Effects of decomposition and storage conditions on the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope values of killer whale (*Orcinus orca*) skin and blubber tissues. *Marine Mammal Science*, *30*, 747–762. <https://doi.org/10.1111/mms.12076>
- Cajal, J. L. (1989). Uso de hábitat por vicuñas y guanacos en la Reserva San Guillermo, Argentina. *Vida Silvestre Neotropical*, *2*, 21–31.
- Carter, D. O., Yellowlees, D., & Tibbett, M. (2007). Cadaver decomposition in terrestrial ecosystems. *Naturwissenschaften*, *94*, 12–24. <https://doi.org/10.1007/s00114-006-0159-1>
- Chikaraishi, Y., Kashiyama, Y., Ogawa, N. O., Kitazato, H., & Ohkouchi, N. (2007). Metabolic control of nitrogen isotope composition of amino acids in macroalgae and gastropods: Implications for aquatic food web studies. *Marine Ecology Progress Series*, *342*, 85–90. <https://doi.org/10.3354/meps342085>
- Chikaraishi, Y., Ogawa, N. O., Kashiyama, Y., Takano, Y., Suga, H., Tomitani, A., Miyashita, H., Kitazato, H., & Ohkouchi, N. (2009). Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnology and Oceanography: Methods*, *7*, 740–750. <https://doi.org/10.4319/lom.2009.7.740>
- Chikaraishi, Y., Steffan, S. A., Ogawa, N. O., Ishikawa, N. F., Sasaki, Y., Tsuchiya, M., & Ohkouchi, N. (2014). High-resolution food webs based on nitrogen isotopic composition of amino acids. *Ecology and Evolution*, *4*, 2423–2449. <https://doi.org/10.1002/ece3.1103>
- Clench, M. H., & Mathias, J. R. (1995). The avian cecum: A review. *The Wilson Bulletin*, *107*, 93–121.
- Corr, L. T., Berstan, R., & Evershed, R. P. (2007). Development of N-acetyl methyl ester derivatives for the determination of  $\delta^{13}\text{C}$  values of amino acids using gas chromatography-combustion- isotope ratio mass spectrometry. *Analytical Chemistry*, *79*, 9082–9090. <https://doi.org/10.1021/ac071223b>
- Dharampal, P. S., Carlson, C., Currie, C. R., & Steffan, S. A. (2019). Pollen-borne microbes

shape bee fitness. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182894.  
<https://doi.org/10.1098/rspb.2018.2894>

Donadio, E., Novaro, A. J., Buskirk, S. W., Wursten, A., Vitali, M. S., & Monteverde, M. J. (2010). Evaluating a potentially strong trophic interaction: Pumas and wild camelids in protected areas of Argentina. *Journal of Zoology*, 280, 33–40.  
<https://doi.org/10.1111/j.1469-7998.2009.00638.x>

Donadio, Emiliano, Buskirk, S. W., & Novaro, A. J. (2012). Juvenile and adult mortality patterns in a vicuña (*Vicugna vicugna*) population. *Journal of Mammalogy*, 93, 1536–1544.  
<https://doi.org/10.1644/12-MAMM-A-062.1>

Donazar, J. A., Travaini, A., Ceballos, O., Rodríguez, A., Delibes, M., & Hiraldo, F. (1999). Effects of sex-associated competitive asymmetries on foraging group structure and despotic distribution in Andean condors. *Behavioral Ecology and Sociobiology*, 45, 55–65.

Duclos, M., Sabat, P., Newsome, S. D., Pavez, E. F., Galbán-malagón, C., Jaksic, F. M., & Quirici, V. (2020). Latitudinal patterns in the diet of Andean condor (*Vultur gryphus*) in Chile: Contrasting environments influencing feeding behavior. *Science of the Total Environment*, 741, 140220. <https://doi.org/10.1016/j.scitotenv.2020.140220>

Elbroch, L. M., Allen, M. L., Lowrey, B. H., & Wittmer, H. U. (2014). The difference between killing and eating: Ecological shortcomings of puma energetic models. *Ecosphere*, 5, 53.  
<https://doi.org/10.1890/ES13-00373.1>

Elbroch, L. M., & Wittmer, H. U. (2013). Nuisance ecology: Do scavenging condors exact foraging costs on pumas in Patagonia? *PLoS ONE*, 8, e53595.  
<https://doi.org/10.1371/journal.pone.0053595>

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pickett, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., ... Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, 333, 301–306.  
<https://doi.org/10.1126/science.1205106>

Ferguson-Lees, J., & Christie, D. A. (2001). Raptors of the world. [https://doi.org/10.1111/j.1557-9263.2006.00078\\_1.x](https://doi.org/10.1111/j.1557-9263.2006.00078_1.x)

Grémillet, D., Prudor, A., le Maho, Y., & Weimerskirch, H. (2012). Vultures of the seas: Hyperacidic stomachs in wandering albatrosses as an adaptation to dispersed food

resources, including fishery wastes. *PLoS ONE*, 7, e37834.

<https://doi.org/10.1371/journal.pone.0037834>

- Hyodo, F., Matsumoto, T., Takematsu, Y., & Itioka, T. (2015). Dependence of diverse consumers on detritus in a tropical rain forest food web as revealed by radiocarbon analysis. *Functional Ecology*, 29, 423–429. <https://doi.org/10.1111/1365-2435.12357>
- Keenan, S. W., & Elsey, R. M. (2015). The good, the bad, and the unknown: Microbial symbioses of the American alligator. *Integrative and Comparative Biology*, 55, 972–985. <https://doi.org/10.1093/icb/icv006>
- Keenan, S. W., & DeBruyn, J. M. (2019). Changes to vertebrate tissue stable isotope ( $\delta^{15}\text{N}$ ) composition during decomposition. *Scientific Reports*, 9, 9929. <https://doi.org/10.1038/s41598-019-46368-5>
- Kurle, C. M., Finkelstein, M. E., Smith, K. R., George, D., Ciani, D., Koch, P. L., & Smith, D. R. (2013). Discrimination factors for stable isotopes of carbon and nitrogen in blood and feathers from chicks and juveniles of the California condor. *The Condor*, 115, 492–500. <https://doi.org/10.1525/cond.2013.120107>
- Mancini, P. L., Bond, A. L., Hobson, K. A., Duarte, L. S., & Bugoni, L. (2013). Foraging segregation in tropical and polar seabirds: Testing the intersexual competition hypothesis. *Journal of Experimental Marine Biology and Ecology*, 449, 186–193. <https://doi.org/10.1016/j.jembe.2013.09.011>
- Marinero, N. V., Cailly-Arnulphi, V. B., Lambertucci, S. A., & Borghi, C. E. (2018). Pigmentation and not only sex and age of individuals affects despotism in the Andean condor. *PLoS ONE*, 13, e0205197. <https://doi.org/10.1371/journal.pone.0205197>
- Moleón, M., & Sánchez-Zapata, J. A. (2015). The living dead: Time to integrate scavenging into ecological teaching. *BioScience*, 65, 1003–1010. <https://doi.org/10.1093/biosci/biv101>
- Moleón, M., Sánchez-Zapata, J. A., Selva, N., Donázar, J. A., & Owen-Smith, N. (2014). Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews*, 89, 1042–1054. <https://doi.org/10.1111/brv.12097>
- Moreno-Opo, R., Trujillano, A., Arredondo, Á., Mariano, L., & Margalida, A. (2015). Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. *Biological Conservation*, 181, 27–35. <https://doi.org/10.1016/j.biocon.2014.10.022>

- Parmenter, R. R., & Macmahon, J. A. (2009). Carrion decomposition and nutrient cycling in a semiarid shrub-steppe ecosystem. *Ecological Monographs*, *79*, 637–661.  
<https://doi.org/10.1890/08-0972.1>
- Pauli, J. N., Donadio, E., & Lambertucci, S. A. (2018). The corrupted carnivore: How humans are rearranging the return of the carnivore-scavenger relationship. *Ecology*, *99*, 2122–2124.  
<https://doi.org/10.1002/ecy.2385>
- Pauli, J. N., Manlick, P. J., Dharampal, P. S., Takizawa, Y., Chikaraishi, Y., Niccolai, L. J., Grauer, J. A., Black, K. L., Garces Restrepo, M., Perrig, P. L., Wilson, E. C., Martin, M. E., Rodriguez Curras, M., Bougie, T. A., Thompson, K. L., Smith, M. M., & Steffan, S. A. (2019). Quantifying niche partitioning and multichannel feeding among tree squirrels. *Food Webs*, *21*, e00124. <https://doi.org/10.1016/j.fooweb.2019.e00124>
- Pavez, E. F., Duclos, M., Rau, J. R., Sade, S., & Jaksic, F. M. (2019). Evidence of high consumption of waste by the Andean condor (*Vultur gryphus*) in an anthropized environment of Chile. *Ornitología Neotropical*, *30*, 185–191.  
<https://journals.sfu.ca/ornneo/index.php/ornneo/article/view/439>
- Payo-Payo, A., Ruiz, B., Cardona, L., & Borrell, A. (2013). Effect of tissue decomposition on stable isotope signatures of striped dolphins *Stenella coeruleoalba* and loggerhead sea turtles *Caretta caretta*. *Aquatic Biology*, *18*, 141–147. <https://doi.org/10.3354/ab00497>
- Pechal, J. L., Crippen, T. L., Cammack, J. A., Tomberlin, J. K., & Benbow, M. E. (2019). Microbial communities of salmon resource subsidies and associated necrophagous consumers during decomposition: Potential of cross-ecosystem microbial dispersal. *Food Webs*, *19*, e00114. <https://doi.org/10.1016/j.fooweb.2019.e00114>
- Perrig, P. L., Donadio, E., Middleton, A. D., & Pauli, J. N. (2017). Puma predation subsidizes an obligate scavenger in the high Andes. *Journal of Applied Ecology*, *54*, 846–853.  
<https://doi.org/10.1111/1365-2664.12802>
- Perrig, P. L., Lambertucci, S. A., Alarcón, P. A. E., Middleton, A. D., Padró, J., Plaza, P. I., Blanco, G., Zapata, J. A. S., Donazar, J. A., & Pauli, J. N. (2021). Limited sexual segregation in a dimorphic avian scavenger, the Andean condor. *Oecologia*,  
<https://doi.org/10.1007/s00442-021-04909-8>.
- Perrig, P. L., Lambertucci, S. A., Donadio, E., Padró, J., & Pauli, J. N. (2019). Monitoring vultures in the 21st century: The need for standardized protocols. *Journal of Applied*

*Ecology*, 56, 796–801. <https://doi.org/10.1111/1365-2664.13348>

- Phillips, D. L., Inger, R., Bearhop, S., Jackson, A. L., Moore, J. W., Parnell, A. C., Semmens, B. X., & Ward, E. J. (2014). Best practices for use of stable isotope mixing models in food-web studies. *Canadian Journal of Zoology*, 92, 823–835. <https://doi.org/10.1139/cjz-2014-0127>
- Plaza, P. I., Blanco, G., Wiemeyer, G., López-Rull, I., Hornero-Méndez, D., Donázar, J. A., Hiraldo, F., & Lambertucci, S. A. (2020). Plasma carotenoids and immunity in a despotic avian scavenger. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 333, 569–578. <https://doi.org/10.1002/jez.2397>
- Plaza, P. I., & Lambertucci, S. A. (2017). How are garbage dumps impacting vertebrate demography, health, and conservation? *Global Ecology and Conservation*, 12, 9–20. <https://doi.org/10.1016/j.gecco.2017.08.002>
- Ritchie, E. G., Elmhagen, B., Glen, A. S., Letnic, M., Ludwig, G., & McDonald, R. A. (2012). Ecosystem restoration with teeth: What role for predators? *Trends in Ecology and Evolution*, 27, 265–271. <https://doi.org/10.1016/j.tree.2012.01.001>
- Roggenbuck, M., Bærholm Schnell, I., Blom, N., Bælum, J., Bertelsen, M. F., Pontén, T. S., Sørensen, S. J., Gilbert, M. T. P., Graves, G. R., & Hansen, L. H. (2014). The microbiome of New World vultures. *Nature Communications*, 5, 5498. <https://doi.org/10.1038/ncomms6498>
- Ruxton, G. D., & Houston, D. C. (2004). Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology*, 228, 431–436. <https://doi.org/10.1016/j.jtbi.2004.02.005>
- Salvioli, G. (2007). Caracterización hidrometeorológica. In E. Martínez Carretero (Ed.), *Diversidad biológica y cultural de los altos Andes centrales de Argentina—línea de base de la Reserva de Biosfera San Guillermo, San Juan* (pp. 63–87). Editorial Fundación Universidad Nacional de San Juan.
- Schotsmans, E. M. J., Van de Voorde, W., De Winne, J., & Wilson, A. S. (2011). The impact of shallow burial on differential decomposition to the body: A temperate case study. *Forensic Science International*, 206, e43–e48. <https://doi.org/10.1016/j.forsciint.2010.07.036>
- Sergio, F., Newton, I., Marchesi, L., & Pedrini, P. (2006). Ecologically justified charisma: Preservation of top predators delivers biodiversity conservation. *Journal of Applied*

*Ecology*, 43, 1049–1055. <https://doi.org/10.1111/j.1365-2664.2006.01218.x>

Shukla, S. P., Plata, C., Reichelt, M., Steiger, S., Heckel, D. G., Kaltenpoth, M., Vilcinskas, A., & Vogel, H. (2018). Microbiome-assisted carrion preservation aids larval development in a burying beetle. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 11274–11279. <https://doi.org/10.1073/pnas.1812808115>

Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., Bidder, O. R., & Middleton, A. D. (2019). Habitat complexity mediates the predator–prey space race. *Ecology*, 100, e02724. <https://doi.org/10.1002/ecy.2724>

Steffan, S. A., Chikaraishi, Y., Currie, C. R., Horn, H., Gaines-Day, H. R., Pauli, J. N., Zalapa, J. E., & Ohkouchi, N. (2015). Microbes are trophic analogs of animals. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 15119–15124. <https://doi.org/10.1073/pnas.1508782112>

Steffan, S. A., Chikaraishi, Y., Dharampal, P. S., Pauli, J. N., Guédot, C., & Ohkouchi, N. (2017). Unpacking brown food-webs: Animal trophic identity reflects rampant microbivory. *Ecology and Evolution*, 7, 3532–3541. <https://doi.org/10.1002/ece3.2951>

Steffan, S. A., Chikaraishi, Y., Horton, D. R., Ohkouchi, N., Singleton, M. E., Miliczky, E., Hogg, D. B., & Jones, V. P. (2013). Trophic hierarchies illuminated via amino acid isotopic analysis. *PLoS ONE*, 8, e76152. <https://doi.org/10.1371/journal.pone.0076152>

Steffan, S. A., & Dharampal, P. S. (2019). Undead food-webs: Integrating microbes into the food-chain. *Food Webs*, 18, e00111. <https://doi.org/10.1016/j.fooweb.2018.e00111>

Stevens, C. E., & Hume, I. D. (1998). Contributions of microbes in vertebrate gastrointestinal tract to production and conservation of nutrients. *Physiological Reviews*, 78, 393–427. <https://doi.org/10.1152/physrev.1998.78.2.393>

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ*, 2018, e5096. <https://doi.org/10.7717/peerj.5096>

Stock, B. C., & Semmens, B. X. (2016). Unifying error structures in commonly used biotracer mixing models. *Ecology*, 97(10), 2562–2569.

Takizawa, Y., Dharampal, P. S., Steffan, S. A., Takano, Y., Ohkouchi, N., & Chikaraishi, Y. (2017). Intra-trophic isotopic discrimination of  $^{15}\text{N}/^{14}\text{N}$  for amino acids in autotrophs: Implications for nitrogen dynamics in ecological studies. *Ecology and Evolution*, 7, 2916–



2924. <https://doi.org/10.1002/ece3.2866>

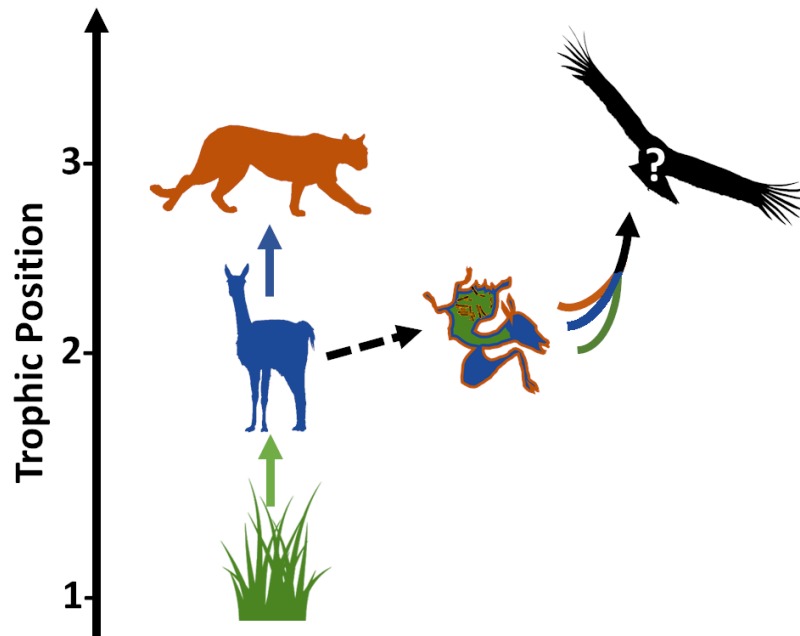
- Takizawa, Y., Takano, Y., Choi, B., Dharampal, P. S., Steffan, S. A., Ogawa, N. O., Ohkouchi, N., & Chikaraishi, Y. (2020). A new insight into isotopic fractionation associated with decarboxylation in organisms: implications for amino acid isotope approaches in biogeoscience. *Progress in Earth and Planetary Science*, 7, 50.  
<https://doi.org/10.1186/s40645-020-00364-w>
- Thomson, N., Stehn, H., & Bridgford, P. (2013). Observations of white-backed vultures eating plant material in Namibia. *Vulture News*, 64, 61–65.
- Wallace, M. P., & Temple, S. A. (1987). Competitive Interactions within and between species in a guild of avian scavengers. *The Auk*, 104, 290–295.
- Wallach, A. D., Ripple, W. J., & Carroll, S. P. (2015). Novel trophic cascades: Apex predators enable coexistence. *Trends in Ecology and Evolution*, 30, 146–153.  
<https://doi.org/10.1016/j.tree.2015.01.003>
- Weatherbee, C. R., Pechal, J. L., & Benbow, M. E. (2017). The dynamic maggot mass microbiome. *Annals of the Entomological Society of America*, 110, 45–53.  
<https://doi.org/10.1093/aesa/saw088>
- Whiteman, J. P., Newsome, S. D., Bustamante, P., Cherel, Y., & Hobson, K. A. (2021). Quantifying capital versus income breeding: New promise with stable isotope measurements of individual amino acids. *Journal of Animal Ecology*, 90, 1408–1418.  
<https://doi.org/10.1111/1365-2656.13402>
- Wilmers, C. C., Crabtree, R. L., Smith, D. W., Murphy, K. M., & Getz, W. M. (2003). Trophic facilitation by introduced top predators: Grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology*, 72, 909–916. <https://doi.org/10.1046/j.1365-2656.2003.00766.x>
- Wilson, E. E., & Wolkovich, E. M. (2011). Scavenging: How carnivores and carrion structure communities. *Trends in Ecology and Evolution*, 26, 129–135.  
<https://doi.org/10.1016/j.tree.2010.12.011>
- Yarnes, C. T., & Herszage, J. (2017). The relative influence of derivatization and normalization procedures on the compound-specific stable isotope analysis of nitrogen in amino acids. *Rapid Communications in Mass Spectrometry*, 31, 693–704.  
<https://doi.org/10.1002/rcm.7832>

Yurkowski, D. J., Hussey, A. J., Hussey, N. E., & Fisk, A. T. (2017). Effects of decomposition on carbon and nitrogen stable isotope values of muscle tissue of varying lipid content from three aquatic vertebrate species. *Rapid Communications in Mass Spectrometry*, *31*, 389–395. <https://doi.org/10.1002/rcm.7802>

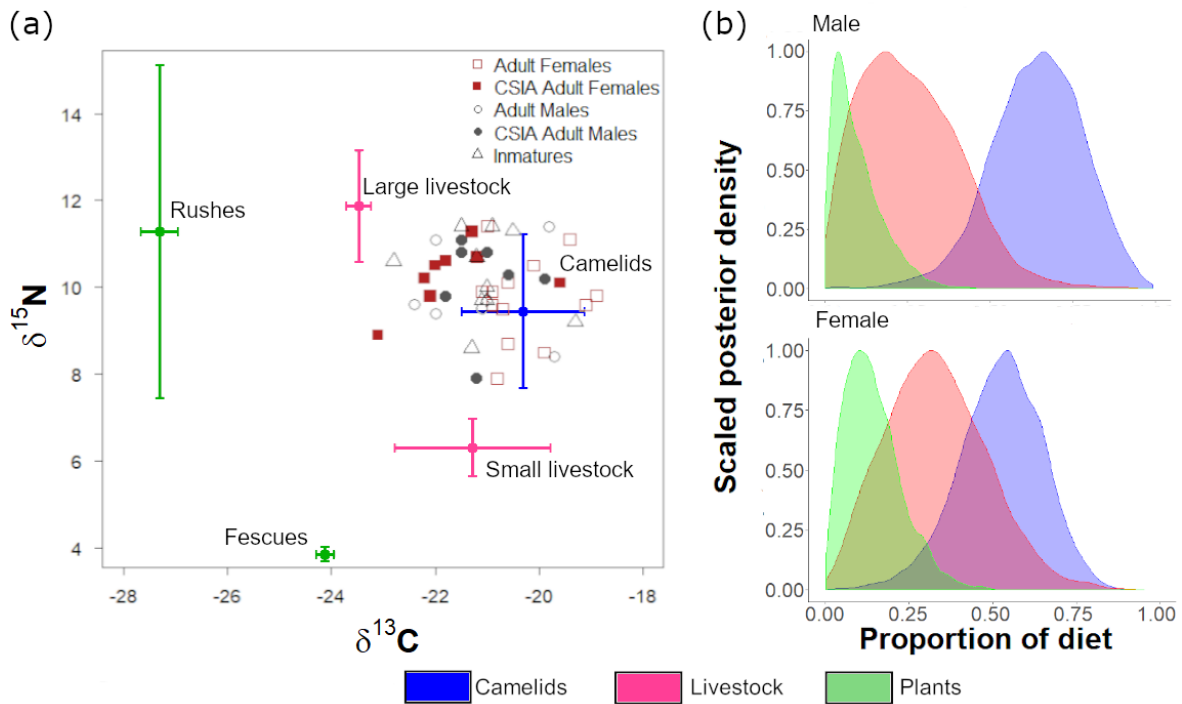
Zepeda Mendoza, M. L., Roggenbuck, M., Manzano Vargas, K., Hansen, L. H., Brunak, S., Gilbert, M. T. P., & Sicheritz-Pontén, T. (2018). Protective role of the vulture facial skin and gut microbiomes aid adaptation to scavenging. *Acta Veterinaria Scandinavica*, *60*, 61. <https://doi.org/10.1186/s13028-018-0415-3>

Table 1: Mean diet estimates of Andean condors based on isotopic mixing models ( $n = 47$ ;  $\pm 95\%$  credible interval) and the volumetric content in the pellets ( $n = 177$ ;  $\pm 95\%$  confidence interval) from San Guillermo National Park, Argentina, 2013. Diet components consisted of camelids (*Vicugna vicugna*, *Lama guanicoe*), plants (*Juncus* sp., *Festuca* spp.), livestock (*Bos taurus*, *Capra aegagrus*, *Ovis aries*, *Equus ferus*) and others (*Lagidium viscacia*, *Lepus europeus*).

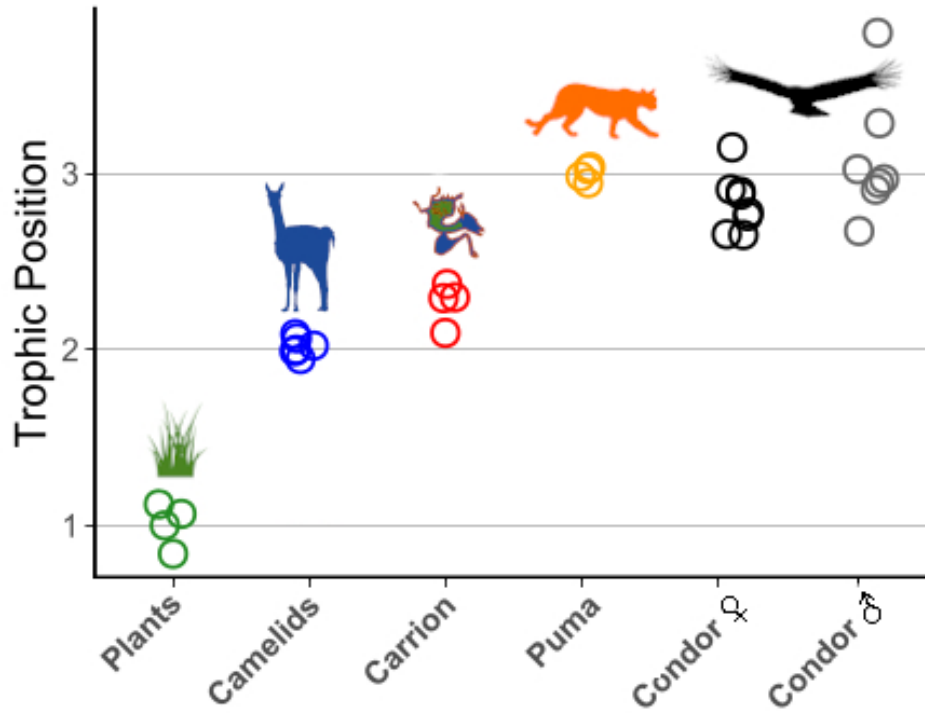
Diet items	Bulk stable isotope (% diet)	Pellets (% volume)
Camelids	68.8 (44.5 – 84.8)	86.9 (83.6 – 90.1)
Plants	8.3 (1.5 – 22.8)	9.9 (7.6 – 12.2)
Livestock	22.1 (3.9 – 47.3)	2.5 (1.1 – 03.9)
Others	-	0.7 (0.0 - 1.3)



**Fig. 1** The trophic relationships and positions of food web members in the high Andes of Argentina: primary producers (TP = 1: rushes [*Juncus* sp.] and fescues [*Festuca* spp.]; green), primary consumers (TP = 2: vicuñas [*Vicugna vicugna*] and guanacos [*Lama guanicoe*]; blue), secondary consumer (TP = 3: pumas [*Puma concolor*] and microbes; orange). Dashed line represents predator provisioning camelids for scavengers and decomposers. The carcass is a conglomerate of three trophic positions (TP): plant digesta (TP ~ 1), camelid meat (TP = 2) and microbes (TP ~ 3) of which we predict Andean condors (*Vultur gryphus*) is consuming across.



**Fig. 2** (a) Stable isotope signatures ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of Andean condors (*Vultur gryphus*; adult males (circles), adult females (squares), and immature males and females (triangles). Individuals analyzed also for bulk only (open), and for bulk and CSIA-AA (filled). Also shown are the main food sources for Andean condors in our study system (mean  $\pm$  SD, corrected by trophic discrimination factor): plants (in green; fescues, *Festuca* sp.; and rushes *Juncus* sp.), large livestock (in red; *Bos taurus*), small livestock (in red; *Capra aegagrus*) and camelids (in blue; *Vicugna vicugna* and *Lama guanicoe*). (b) Proportion of camelids, livestock, and plants in the diet of male and female condors, estimated from Bayesian mixing model based on a uniform prior from individuals analyzed for CSIA-AA.



**Fig. 3** Trophic positions estimated through the analysis of  $\delta^{15}\text{N}$  in glutamic acid and phenylalanine of each component of the Andean food web: plants (*Festuca* sp. and *Juncus* sp.; green), camelids (*Vicugna vicugna* and *Lama guanicoe*; blue), camelid carrion (red), Andean condor (*Vultur gryphus*; females in black, males in gray) and puma (*Puma concolor*; orange).