

Puma predation subsidizes an obligate scavenger in the high Andes

Paula L. Perrig^{1*}, Emiliano Donadio², Arthur D. Middleton^{3†} and Jonathan N. Pauli¹

¹Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Linden 1630, Madison, WI 53706, USA; ²INIBIOMA, UNcoma, CONICET, Junín de los Andes, Neuquén 8371, Argentina; and ³School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA

Summary

1. The ungulate–carnivore–vulture complex is a key trophic module of many terrestrial ecosystems, but one that is globally under threat. Few have explored cross-species dependencies in this module, and the degree to which vultures rely on trophic facilitation by apex carnivores is rarely known and almost never quantified.

2. We investigated the importance of puma *Puma concolor* predation on its native camelid prey, vicuñas *Vicugna vicugna* and guanacos *Lama guanicoe*, in food provisioning for Andean condors *Vultur gryphus* in the high Andes of north-western Argentina. We evaluated the origin of wild food sources through carcass surveys. We quantified condor feeding habits via foraging observations and through the analysis of pellet contents and stable isotopes from moulted feathers.

3. Of the 102 fresh camelid carcasses we monitored, nearly all (94%) resulted from puma predation, and the majority (85%) of camelid carcasses used by condors were killed by pumas. Camelids represented 88% of the prey items identified from 183 condor pellets, and isotopic analyses of moulted feathers from 86 individuals identified via multilocus genotyping revealed that camelids and Small livestock were the most important prey items, representing 45–58% and 28–38% of condor assimilated biomass, respectively.

4. *Synthesis and applications.* Our results show that puma predation plays a key role in the foraging ecology of Andean condors, and highlight the importance of predatory processes that make carrion available to scavengers. We contend that targeting the conservation of ungulate–carnivore–vulture modules, rather than a species-specific approach, will be a more effective strategy to ensure the long-term persistence of Andean condors and other obligate scavengers.

Key-words: Argentina, camelids, carnivore, condor, predator, puma, scavenger, trophic facilitation, ungulates, vulture

Introduction

Identifying and conserving trophic interactions is critical to the maintenance of biodiversity. Predation, in particular, has been recognized as a major shaping force of community structure and ecosystem function (Estes *et al.* 2011). While focus has primarily been on their top-down effects, predators can also have upwelling effects on upper trophic levels (Moleón *et al.* 2014). By hunting frequently

and over a broad range, apex predators provide access to essential food resources for many species of scavengers (Wilmers & Getz 2004) and generate crucial, multitrophic links in food webs that intersect at the production and consumption of carrion (Moleón *et al.* 2014). Although intuitive and highly relevant, these linkages have barely been explored (Pereira, Owen-Smith & Moleón 2014).

The ungulate–carnivore–vulture complex is a major predation–scavenging system of terrestrial ecosystems (Moleón *et al.* 2014). Vultures have evolved to feed on the carrion of large ungulates (Ruxton & Houston 2004), which are often available only episodically as a pulsed and ephemeral resource. In Africa's Serengeti ecosystem, for example, ungulates dying from malnutrition constitute

*Correspondence author. E-mail: perrig@wisc.edu

†Present address: Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720, USA

the principal food for scavengers, and carrion availability varies strongly both temporally and spatially (Houston 1974). In this region, vultures select areas featuring high ungulate mortality rather than abundance, which suggests that carrion predictability is the driver of vulture habitat use (Kendall *et al.* 2014).

Carnivores often serve as a crucial linkage between scavengers and carrion, providing spatial and temporal consistency to its availability. Following wolf *Canis lupus* extirpation in North America (Wilmers *et al.* 2003) and Europe (Wikenros *et al.* 2013), carrion availability occurred primarily as function of autumn hunter harvests or winter die-offs; but following wolf recovery, carrion consistency increased both seasonally and interannually, with significant benefits for scavengers such as bears and ravens (Wilmers & Getz 2004). Solitary and ambush predators may be even more consequential to vertebrate scavengers than social and coursing ones (Elbroch & Wittmer 2012; Allen *et al.* 2014), because prolonged prey consumption makes solitary predators more susceptible to kleptoparasites (Krofel, Kos & Jerina 2012; Elbroch & Wittmer 2013; Elbroch *et al.* 2014b). Furthermore, their hunting success depends less on the seasonal vulnerability of prey (Pereira, Owen-Smith & Moleón 2014).

The ecological role of apex predators is waning globally (Oriol-Cotterill *et al.* 2015), affecting not only lower trophic levels (Estes *et al.* 2011) but also many species of scavengers through altered patterns of carrion availability (Wilmers & Getz 2004). Additionally, changes in land use and the intensification of agricultural production have reduced the abundance of wild and domestic ungulates that have sustained vulture populations (Ogada, Keesing & Virani 2011). More importantly, carrion sources increasingly harbour novel toxicological risks, such as lead in hunted game, lingering pharmaceutical drugs in cattle and poison intentionally deployed for carnivores (Ogada, Keesing & Virani 2011). Consequently, vultures are currently the most threatened group of birds in the world (Ogada, Keesing & Virani 2011), and the availability of reliable food resources is paramount to their conservation.

The largest obligate scavenger of the world, Andean condors *Vultur gryphus*, inhabits the puna ecosystem of the high Andes. Only one study, through the analysis of pellet contents, has quantitatively described the diet of condors (Lambertucci *et al.* 2009). Along with anecdotal accounts (Wallace & Temple 1988) and movement patterns (Lambertucci *et al.* 2014), it appears that Andean condors feed on both terrestrial and marine mammals. The two wild ungulates in this system are the South American native camelids – guanacos *Lama guanicoe* (mean adult body weight = 120 kg) and vicuñas *Vicugna vicugna* (40 kg). Pumas *Puma concolor* are the largest carnivores in the puna and the only native predators capable of killing adult camelids (Walker & Novaro 2009). They are considered key in making carrion biomass available to native scavengers, including the Andean condor (Elbroch

& Wittmer 2012). At our study site, camelids are the main prey of pumas (Donadio *et al.* 2010) and may also represent important carrion resources for condors. However, biomass from livestock in nearby ranches and marine mammals from the Pacific coast are also potentially available to the local condor population. We hypothesized that Andean condors benefit from the puma–camelid predatory interaction to secure food resources, creating tight trophic linkages among condors, pumas and camelids (Fig. 1). Herein, we used a suite of non-invasive methods to assess whether the main prey of condors at our study site were native camelids and whether condors primarily used carrion resulting from puma predation. Specifically, we evaluated the origin of wild food sources through field carcass investigation and studied condor foraging habits through direct observations at feeding sites, the analysis of pellet contents and the quantification of stable isotopes from individually identified moulted feathers. This integrative approach allowed us to quantify the importance of the puma–camelid relationship as a mechanism of food provisioning to Andean condors at the core of their distribution, providing insight into potential conservation strategies.

Materials and methods

STUDY SITE

Our research was conducted at San Guillermo National Park (SGNP), Argentina (−29.07° S, −69.35° W). Along with two contiguous reserves, Laguna Brava and San Guillermo Provincial Reserves, the park constitutes the San Guillermo-Laguna Brava landscape: ~1.4 million ha protected in the high Andes (Fig. 1). SGNP encompasses 166 000 ha at 2000–5600 m above sea level. The climate is cold and dry (100–500 mm year^{−1}), with annual temperatures ranging between 27 and −23 °C (Salvioli 2007). Warmer temperatures and occasional rains define the wet season (December–April), whereas low temperatures and water limitation characterize the dry season during the remaining months (Salvioli 2007; Donadio, Buskirk & Novaro 2012). Along with Andean condors, mountain caracaras *Phalacrocorax macrorhynchos*, and culpeo *Lycalopex culpeus* and grey foxes *L. gymnocercus* are common vertebrate scavengers. Non-native species are limited to a low-density population of European hares *Lepus europaeus* (2.5 ± 0.6 ind. km^{−2}, Di Martino and Donadio 2009, unpubl. data) and few (<21 individuals) feral cattle (Donadio *et al.* 2010).

ORIGIN AND USE OF CAMELID CARCASSES

From 2008 to 2011 and in 2013, we conducted surveys from a vehicle along ~30 km of permanent transects 5 days per week while in the field, and located fresh carcasses of yearling (12–24 months old) and adult (>24 months old) camelids either by direct observation or by investigating sites where avian scavengers were observed (Donadio, Buskirk & Novaro 2012). Extensive open plains with virtually no vegetation cover constitute 81% of the landscape, allowing us to rapidly locate carcasses from a distance of up to 1 km; we also conducted intensive on-foot surveys of carcasses within meadows and narrow canyons. Time since

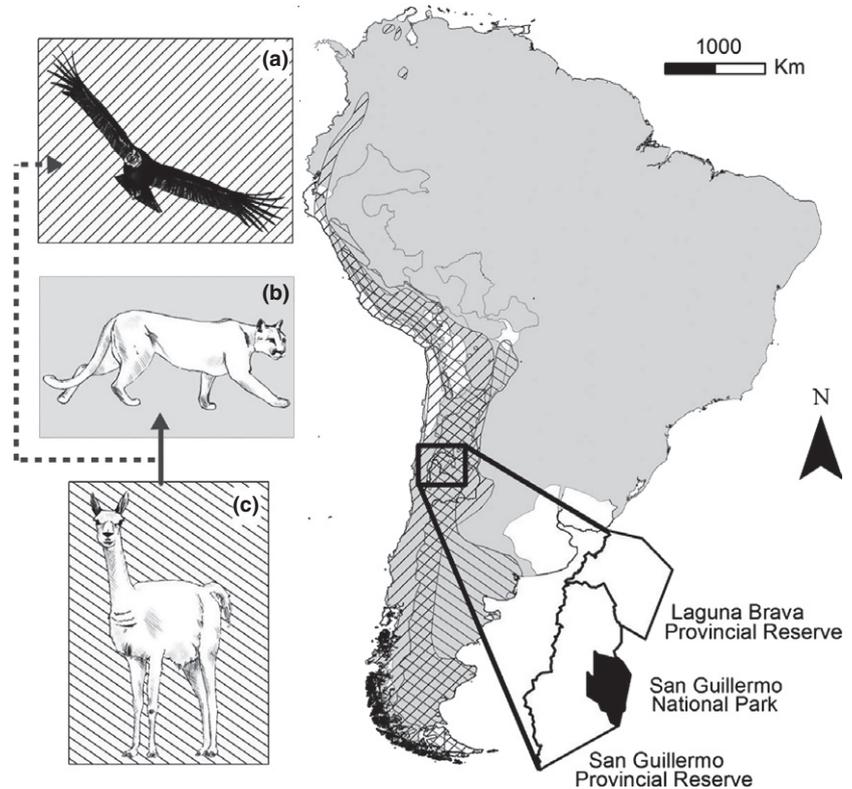


Fig. 1. Distribution of (a) Andean condors, (b) pumas and (c) native camelids across South America (IUCN 2014). These species co-occur in the Andes of central Argentina, where they are protected by the San Guillermo-Laguna Brava landscape: ~1.4 million ha comprising San Guillermo National Park (SGNP), San Guillermo Provincial Reserve and Laguna Brava Provincial Reserve. This study was conducted within SGNP. Here, we hypothesized that Andean condors rely on the puma–camelid predatory interaction to acquire food resources.

death was estimated based on our frequent surveys of the study area and carcass stiffness. For each carcass we found <72 h after death, we determined mortality cause as puma predation when we found puma signs (e.g. dragging marks, canine punctures in hide or skull, cached carcass, broken and chewed large bones and ribs, puma tracks) and non-predation when puma signs were not detected (given that pumas rarely scavenge; Elbroch *et al.* 2014a). When we were unable to attribute death to either of the above-mentioned categories, we recorded cause of death as uncertain (Donadio, Buskirk & Novaro 2012). For each carcass, we registered presence of scavengers via direct observation, inspection of signs (footprints, feathers, scats) or camera trap surveillance. Carcass field investigations were conducted with different sampling intensity across years; however, we did not find temporal differences in the number of carcasses scavenged by condors (Fisher's exact tests; $P = 0.68$) and we combined data across years for our analysis.

ANDEAN CONDOR PELLET CONTENT

In summer 2013, we collected 183 Andean condor pellets from an active roosting site in the park. In the laboratory, pellets were oven-dried at 55 °C for 48 h, weighed, covered with water and broken up in a Petri dish. Prey items were identified microscopically via guard hair morphology using reference materials and keys (Chehébar & Martín 1989). Prey was grouped in five categories: camelid (vicuñas and guanacos), small livestock (goat/sheep), large livestock (cow/horse), European hare and mountain vizcacha *Lagidium viscacia*. Results are presented as (i) percentage of occurrence (number of times a prey species occurred divided by the total number of prey items in all pellets), and (ii) percentage volume of each prey item, estimated visually.

We used a rarefaction approach to analyse the number of samples required for a precise estimate of condor diet diversity. We bootstrapped the data (1000 replicates) and computed Levins' index (Colwell & Futuyma 1971) with 95% confidence intervals at increasing sampling sizes (20–500 by 10 pellets) and evaluated the standard error of the mean in relation to the mean value (Williams, Goodenough & Stafford 2012). We conducted statistical analyses using program R 2.11.1 (R Development Core Team 2010).

GENETIC PROFILE OF SHED FEATHERS

We collected moulted feathers from Andean condors in feeding sites and roosting site sampled for pellets. Feathers were stored in envelopes at room temperature and classified according to size as large ($\bar{x} \pm 1$ SE; 46 cm \pm 11 cm; $n = 64$), medium (24 cm \pm 6 cm; $n = 23$) and small (11 cm \pm 3 cm; $n = 64$). To avoid pseudoreplication, we identified individuals from the collected feathers via multilocus genotypes. DNA was extracted from the 1 cm basal tip of the calamus and from the superior umbilicus (Horváth *et al.* 2005); for large feathers, we only used the superior umbilicus. We followed a standard DNA extraction protocol (QIAamp DNA Micro Kit, QIAGEN, Valencia, CA, USA; which includes DTT). Extractions were performed in a pre-PCR clean room dedicated to low-quality samples, and tubes without samples were included to monitor for contamination through the procedure.

Extracted samples were genotyped at five polymorphic microsatellite markers (Vg001, Vg007, Vg015, Vg022 and Vg025; see Supporting Information for details). Amplified PCR products were scored via fluorescent DNA fragment analysis on ABI 3730xl DNA analyzer (Applied Biosystems, Foster City, CA, USA) and scored with GENEMAPPER v5 software (Applied

Biosystems). We initially screened all samples with one microsatellite (Vg015); 16 samples failed to amplify and were removed for subsequent steps. The remaining samples were genotyped twice.

Allele frequencies, observed and expected heterozygosities, and probability of identity (PID_{umb}) were calculated in GIMLET 1.3.3 (Valière 2002). We used a $PID_{umb} = 0.01$ as a cut-off to call individual condors (Mills *et al.* 2000). We used MICRO-CHECKER (Van Oosterhout *et al.* 2004) to detect samples likely containing genotyping errors, to estimate null alleles, allelic dropout and to evaluate Hardy–Weinberg equilibrium. Amplification success was estimated for each locus as the proportion of PCR leading to a readable genotype. We identified unique individuals using the software ALLELEMATCH (Galpern *et al.* 2012), allowing one mismatch between pairwise comparison, and unique genotypes were manually reviewed. We tested for linkage disequilibrium with GENEPOP (Raymond & Rousset 1995), applying a sequential Bonferroni correction.

Molecular sexing was accomplished by amplification of sex-chromosome-link CHD genes through the universal primers P2 and P8 (Griffiths *et al.* 1998). We included both positive and negative controls in PCR amplifications (see Supporting Information for details).

STABLE ISOTOPE ANALYSIS

We sampled 5 cm of the distal extreme of one feather per individual bird. Since the discriminatory power and reliability of estimates decreases with overparametrization of isotopic mixing models (Phillips *et al.* 2014), we only considered potentially relevant terrestrial food sources as prey items occurring in $\geq 10\%$ of the analysed pellets or that represented $\geq 30\%$ of pellet volume. Hair from potential terrestrial food sources was collected within

and near our study area from carcasses or live animals: cow *Bos taurus* ($n = 10$), goat *Capra hircus* ($n = 4$), vicuña ($n = 7$) and guanaco ($n = 7$). To evaluate whether condors utilized marine resources, we used published $\delta^{13}C$ and $\delta^{15}N$ values from Central Chile (*Otaria flavescens*; Hückstädt, Rojas & Antezana 2007).

All samples were rinsed three times with 2:1 chloroform:methanol solution to remove surface oils and contaminants, homogenized with scissors and dried for 72 h at 55 °C. Samples were weighed, placed in tin capsules and analysed for ^{13}C and ^{15}N with a Costech 4010 elemental analyzer attached to a Thermo Finnigan DeltaPLUS XP or V Flow Isotope Ratio Mass Spectrometer. Results are provided in per mil [parts per thousand (‰)] notation relative to the international standards of Pee Dee Belemnite (PDB) and atmospheric nitrogen (AIR) with calibrated internal laboratory standards. We evaluated measurement precision by randomly selecting half of the samples for duplicate analysis.

We employed K nearest neighbour randomization test to evaluate differences in isotopic signature of condor potential prey items (all pairwise $P < 0.05$, Rosing, Ben-David & Barry 1998). We identified four isotopically distinct and biologically meaningful prey groups: large livestock (cows), small livestock (goat), camelids (vicuñas and guanacos) and marine mammals. We used trophic enrichment factors of $3.1\text{‰} \pm 0.1$ for $\delta^{15}N$ and $0.4\text{‰} \pm 0.4\text{‰}$ for $\delta^{13}C$ observed for Californian condors on a controlled feeding trial (Kurler *et al.* 2013). We evaluated the mixing space qualitatively (Fig. 2a), plotting convex hulls using package Stable Isotope Bayesian Ellipses in R (SIBER, Jackson *et al.* 2011) and through simulated mixing polygons (Smith *et al.* 2013; Fig. 2b). Because we did not detect a strong marine signal among Andean condors (Fig. 2), we eliminated marine mammals as a prey item to improve the discriminatory power of our mixing models. From the resulting mixing space, three samples showed

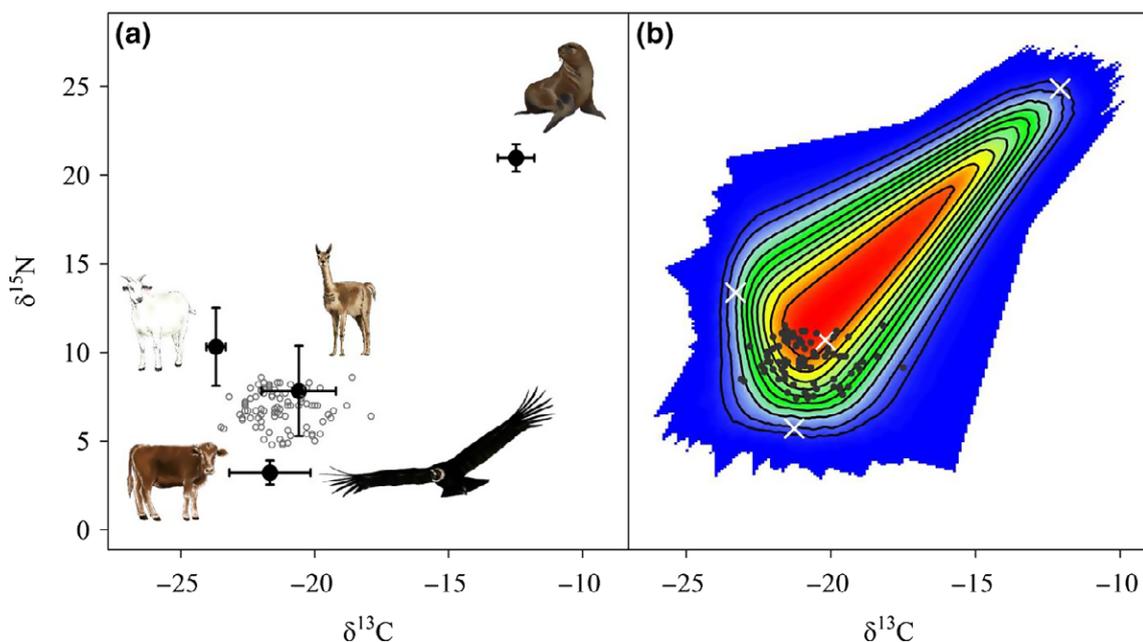


Fig. 2. Evaluation of proposed mixing space for Andean condor moulted feathers and its main food sources detected by pellet content analysis at San Guillermo National Park (Argentina). (a) Biplot of $\delta^{13}C$ and $\delta^{15}N$ signature of individual birds (coloured circles, corrected for trophic discrimination) and its main food sources (mean \pm SD); and (b) Monte Carlo simulation of polygons for the biplot (Smith *et al.* 2013). Contours show the proportion of polygons simulated that can satisfy the geometry of mixing models for each consumer (black dots) at 5% (outermost contour) and every 10% level. Average prey signatures are shown as white crosses.

<5% probability that a combination of those food sources could explain their isotopic signature (Fig. 2), and were excluded from the consumer's final data set. Visual analysis of the final mixing space corroborated that the remaining samples (belonging to 86 of the 89 identified birds) fell within the proposed convex polygon.

To quantify the relative contribution of each prey group to the diet of Andean condors, we used Bayesian stable isotope mixing models in the package Stable Isotope Analysis in R (SIAR, Parnell *et al.* 2010). We used informative priors from our pellet content analysis (camelids = 94%, small livestock = 4.2%, and large livestock = 1.8%) and also ran a second model with uninformative priors to explore the influence of our developed priors on dietary estimates. We also used SIAR to explore sexual differences in condor diet. We reported the mean and 95% credible interval to statistically summarize the isotopic mixing space and the marginal posterior distribution calculated by all models.

Results

ORIGIN AND USE OF CAMELID CARCASSES

We found 102 fresh camelid carcasses; the majority (94%) showed signs of puma predation (Fig. 3a). Most carcasses found were scavenged (Fig. 3b), of which 35% were used by Andean condors. We assessed presence of condors by direct observation ($n = 29$), presence of signs ($n = 5$) and camera trap records ($n = 2$). We found an equal number of camelid carcasses in the dry and wet seasons ($n = 51$ each season), and condors' use of carrion did not differ seasonally (Fisher's exact tests; $P = 0.12$). We found signs of puma predation in most of the carcasses fed upon by condors throughout the year (Fig. 3c).

ANDEAN CONDOR PELLET CONTENT

Our rarefaction analysis illustrated that after 40 pellets all prey items were detected, and our sample provided an estimate of condor diet diversity with a standard deviation equal to 20.3% of the mean value (Levin's index = 0.069, 95% CI = 0.042–0.096; Fig. S1, Supporting information). Native camelids were the most frequent food item,

representing 88% of the total prey found (Fig. 4). Second in importance in terms of frequency was the European hare, although present in relatively small volumes, followed by small livestock (Fig. 4).

GENETIC PROFILE OF SHED FEATHERS

We did not detect significant deviations from Hardy–Weinberg expectations, linkage disequilibrium or allelic dropout. However, there was evidence of null alleles at two loci (Table S1). The mean probability of mis-assigning a feather sample to an individual was small (multilocus $PID_{\text{unb}} = 0.0002$). Of 135 feathers, 60 were genotyped at all 5 loci, 53 at 4, 20 at 3 and 2 at 2 loci. The genotyping error rate was 3%. Of the 135 analysed samples, we were able to assign 131 feathers to individuals with a $PID_{\text{unb}} < 0.01$, from which we genetically tagged 89 individuals with an average of 1.3 (range 1–5) feathers genotyped per bird. Of the 86 individuals analysed for stable isotopes, molecular sexing revealed that 65% were females.

STABLE ISOTOPE ANALYSIS

Average difference between duplicate samples was 0.06‰ and 0.09‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Our dietary estimates derived from mixing models (Table S2) revealed that camelids were the most important prey in the diet of condors, representing 45–58% of their assimilated biomass (Table 1). Small livestock was the second most important prey category, accounting for 28–38% of condor diet. For all models, large livestock represented a relatively insignificant food source. Dietary items had a similar importance for female and male birds, although males appeared to consume slightly more camelids and less livestock than females (Table 1).

Discussion

Our findings revealed a strong, trophic dependency of a vertebrate scavenger on the interaction between an apex

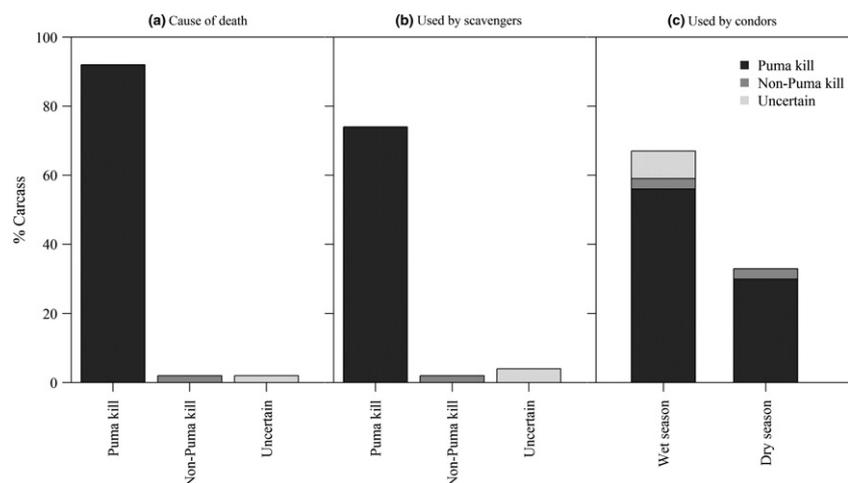


Fig. 3. Origin and use of camelid carcasses found at San Guillermo National Park (Argentina). (a) Specific mortality causes of camelids determined through field investigations of fresh carcasses ($n = 102$); (b) scavenger use of those carcasses in relation to cause of death ($n = 102$); (c) camelid carcasses fed upon by Andean condors by season and cause of mortality ($n = 36$).

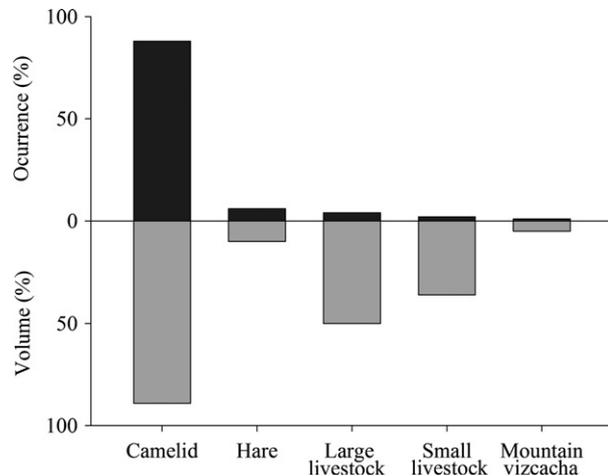


Fig. 4. Content of Andean condor pellets collected in San Guillermo National Park (Argentina) during 2013 presented as percentage of occurrence of prey items (number of times a prey item occurred divided by the total number of prey items in all pellets) and percentage volume of each item estimated visually.

carnivore and its native ungulate prey. Puma predation accounted for the vast majority of camelid mortalities (95%) and of the carcasses used by condors (85%). Camelids represented 88% and 45–58% of the prey items consumed by Andean condor according to pellet content and stable isotope analysis, respectively. Altogether, then, our results strongly support that the puma–camelid trophic interaction provides a significant source of carrion for Andean condors.

Our complementary diet analysis integrates Andean condor foraging across spatiotemporal scales, providing a robust evaluation of the food habits of this wide-ranging scavenger. Pellet contents, in particular, were dominated by camelids. Pellets reflect a relatively constrained spatial and temporal scale, and likely reveal prey consumption around perching sites within SGNP (Lambertucci *et al.* 2009). Our stable isotope analysis, however, provided estimates of assimilated diet over a longer time period (~3 months) than the ‘snapshot’ provided by pellets, and likely encompassed forays further away from the park. Isotopic mixing models assume that all condor food sources had been identified, which is difficult to achieve with a species as wide-ranging as the Andean condor (Lambertucci *et al.* 2014). Condor consumption of exotic

species – virtually absent in SGNP (Donadio *et al.* 2010) – reveals that condors are almost certainly foraging outside the park. Nevertheless, we found no evidence of an important marine contribution and complete reliance on terrestrial food sources in the 86 individual condors we sampled. It is interesting that condors did not use marine-derived food resources despite their relative proximity to the Pacific Coast, and future research should be aimed and exploring possible reasons for this.

In many systems, the degree to which populations of obligate scavengers derive their diet from predator-killed carrion may be unclear because of anthropogenic disturbances. Our study area, in contrast, provides a reference for relatively intact prey–predator–scavenger interactions. Hunting is prohibited in the San Guillermo-Laguna Brava complex. Though some poaching has been reported in the two reserves surrounding SGNP, poachers typically remove the carcasses of hunted animals (Donadio & Buskirk 2006), rendering this an unlikely source of carrion for Andean condors. In SGNP, neither diseases nor weather events appear to be an important mortality cause for camelids (Wallace & Temple 1988; Bank *et al.* 2002; Shaw, Galaz & Marquet 2012): since 1978, only one pulsed, winter-related camelid mortality event has been documented (Cajal & Ojeda 1994). Therefore, pumas appear to act as an important resource buffer for condors by providing carrion across seasons and years. While old world vultures rely primarily on non-predatory causes of ungulate mortality (Houston 1974; Kendall *et al.* 2014), scavengers in northern ecosystems receive important subsidies from apex carnivores, including pumas (Allen *et al.* 2014) and wolves (Wilmers *et al.* 2003; Wikenros *et al.* 2013). Our work illuminates the key bottom-up effects that apex predators have in a food web once widespread in arid landscapes of South America.

Nevertheless, our results also show that even in a pristine and remote landscape (Sanderson *et al.* 2002), a key scavenger relies partly upon domestic species despite studies indicating livestock are rare in and surrounding our study area (Wurstten, Novaro & Walker 2014), and not an important food resource for pumas (Donadio *et al.* 2010). This finding highlights both the remarkable foraging requirements for condors and the challenge of protecting such a highly mobile species from potential threats. Indeed, poisoning by toxin-laced carcasses (Lambertucci

Table 1. Mean isotopic values of Andean condors’ food sources detected by pellet content analysis and their estimated proportional contribution to Andean condor diet at San Guillermo National Park (Argentina) as calculated by informed isotopic mixing models in SIAR (Stable Isotope Analysis in R)

Diet groups	SI values (Mean [SD])		Contribution to diet (Mean [95% CI])		
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Population	Males	Females
Camelids	−20.59 (1.39)	7.83 (2.55)	0.51 (0.45–0.58)	0.63 (0.49–0.75)	0.51 (0.43–0.60)
Small Livestock	−21.67 (1.52)	3.22 (0.67)	0.33 (0.28–0.38)	0.31 (0.20–0.41)	0.31 (0.24–0.37)
Large Livestock	−23.69 (0.37)	10.32 (2.21)	0.15 (0.10–0.17)	0.06 (0.00–0.14)	0.17 (0.11–0.24)

2007) and lead intoxication from ingestion of lead bullet fragments in hunted animals (Lambertucci *et al.* 2011) represent main risks to condor conservation. Furthermore, domestic food sources can fluctuate greatly based on public policies and global markets that drive livestock availability in the landscape (Margalida *et al.* 2010). Consequently, policies recognizing the importance of reliable and safe food sources – and the ecological processes that provision it – may be paramount for condor conservation (Lambertucci *et al.* 2011).

Ultimately our work demonstrates that maintaining populations of interactive large carnivores and their wild ungulate prey is key for the long-term persistence of the iconic Andean condor in South America. Indeed, puma kills are not haphazardly consumed by scavengers (Elbroch & Wittmer 2012; Allen *et al.* 2014), but represent a significant food source for this obligate necrophagous species. The high mobility of condors forces a ‘thinking large’ approach to biodiversity preservation (Lambertucci *et al.* 2014). Therefore, an important long-term goal for effective condor conservation may be a network of protected areas that ensure consistent availability of safe carrion resources via native predator–prey interactions. In this vein, we call for a conservation approach focused on community intactness, aimed at long-term and simultaneous conservation of the puma–camelid–condor assemblage.

Acknowledgements

We thank SGNP, especially to J. Gallo, for providing valuable logistical support and to J. Cayuela, B. Avila and other volunteers for their assistance during field and laboratory work. We are grateful to B. D. Varela, S. A. Lambertucci and R. Palacios for valued discussions and assistance. Research permits were issued by the Argentinean National Park Service and the Argentine Ministry of Environmental and Sustainable Development. Financial support was provided by National Birds of Prey Trust; Conservation, Research and Education Opportunities International (CREOI); Hawk Mountain Sanctuary; Association of Zoos and Aquariums; National Geographic Society (CRE # 8399-08); and Rufford Foundation.

Data accessibility

Molecular markers uploaded as online supporting information.

Stable isotope data available from Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.7nk90> (Perrig *et al.* 2016).

References

- Allen, M.L., Elbroch, L.M., Wilmers, C.C. & Wittmer, H.U. (2014) Trophic facilitation or limitation? Comparative effects of pumas and black bears on the scavenger community. *PLoS ONE*, **9**, e102257.
- Bank, M.S., Sarno, R.J., Campbell, N.K. & Franklin, W.L. (2002) Predation of guanacos (*Lama guanicoe*) by southernmost mountain lions (*Puma concolor*) during a historically severe winter in Torres del Paine National Park, Chile. *Journal of Zoology*, **258**, 215–222.
- Cajal, J.L. & Ojeda, R.A. (1994) Camelidos silvestres y mortalidad por tormentas de nieve en la cordillera frontal de la provincia de San Juan, Argentina. *Mastozoología Neotropical*, **1**, 81–88.
- Chehébar, C. & Martín, S. (1989) Guía para el reconocimiento microscópico de los pelos de los mamíferos de la Patagonia. *Doñana Acta Vertebrata*, **16**, 247–291.
- Colwell, R.K. & Futuyma, D.J. (1971) On the measurement of niche breadth and overlap. *Ecology*, **52**, 567–576.
- Donadio, E. & Buskirk, S.W. (2006) Flight behavior in guanacos and vicuñas in areas with and without poaching in western Argentina. *Biological Conservation*, **127**, 139–145.
- Donadio, E., Buskirk, S. & Novaro, A.J. (2012) Juvenile and adult mortality patterns in a vicuña (*Vicugna vicugna*) population. *Journal of Mammalogy*, **93**, 1536–1544.
- 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.
- Elbroch, L.M. & Wittmer, H.U. (2012) Table scraps: inter-trophic food provisioning by pumas. *Biology Letters*, **8**, 776–779.
- Elbroch, L.M. & Wittmer, H.U. (2013) Nuisance ecology: do scavenging condors exact foraging costs on pumas in patagonia? *PLoS ONE*, **8**, 1–8.
- Elbroch, L.M., Allen, M.L., Lowrey, B.H. & Wittmer, H.U. (2014a) The difference between killing and eating: ecological shortcomings of puma energetic models. *Ecosphere*, **5**, 1–16.
- Elbroch, L.M., Lendrum, P.E., Allen, M.L. & Wittmer, H.U. (2014b) Nowhere to hide: pumas, black bears, and competition refuges. *Behavioral Ecology*, **26**, 247–254.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.
- Galpern, P., Manseau, M., Hettinga, P., Smith, K. & Wilson, P. (2012) Allelematch: an R package for identifying unique multilocus genotypes where genotyping error and missing data may be present. *Molecular Ecology Resources*, **12**, 771–778.
- Griffiths, R., Double, M., Orr, K. & Dawson, R. (1998) A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.
- Horváth, M., Martínez-Cruz, B., Negro, J.J., Kalmár, L. & Godoy, J.A. (2005) An overlooked DNA source for non-invasive genetic analysis in birds. *Journal of Avian Biology*, **36**, 84–88.
- Houston, D.C. (1974) The role of griffon vultures *Gyps africanus* and *Gyps ruppellii* as scavengers. *Journal of Zoology*, **172**, 35–46.
- Hückstädt, L.A., Rojas, C.P. & Antezana, T. (2007) Stable isotope analysis reveals pelagic foraging by the Southern sea lion in central Chile. *Journal of Experimental Marine Biology and Ecology*, **347**, 123–133.
- IUCN. (2014) The IUCN Red List of Threatened Species. Version 2015.1., <http://www.iucnredlist.org>.
- Jackson, A.L., Inger, R., Parnell, A.C. & Bearhop, S. (2011) Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, **80**, 595–602.
- Kendall, C.J., Virani, M.Z., Hopcraft, J.G.C., Bildstein, K.L. & Rubenstein, D.I. (2014) African vultures don't follow migratory herds: scavenger habitat use is not mediated by prey abundance. *PLoS ONE*, **9**, e83470.
- Krofel, M., Kos, I. & Jerina, K. (2012) The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology*, **66**, 1297–1304.
- 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. *Condor*, **115**, 492–500.
- Lambertucci, S. (2007) Biología y conservación del Cóndor Andino (*Vultur gryphus*) en Argentina. *El Hornero*, **22**, 149–158.
- Lambertucci, S.A., Trejo, A., Di Martino, S., Sánchez-Zapata, J.A., Donazar, J.A. & Hiraldo, F. (2009) Spatial and temporal patterns in the diet of the Andean condor: ecological replacement of native fauna by exotic species. *Animal Conservation*, **12**, 338–345.
- Lambertucci, S.A., Donazar, J.A., Huertas, A.D., Jiménez, B., Sáez, M., Sánchez-Zapata, J.A. & Hiraldo, F. (2011) Widening the problem of lead poisoning to a South-American top scavenger: lead concentrations in feathers of wild Andean condors. *Biological Conservation*, **144**, 1464–1471.
- Lambertucci, S.A., Alarcón, P.A.E., Hiraldo, F., Sánchez-Zapata, J.A., Blanco, G. & Donazar, J.A. (2014) Apex scavenger movements call for transboundary conservation policies. *Biological Conservation*, **170**, 145–150.
- Margalida, A., Donazar, J.A., Carrete, M. & Sánchez-Zapata, J.A. (2010) Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology*, **47**, 931–935.
- Mills, L.S., Citta, J.J., Lair, K.P., Schwartz, M.K. & Tallmon, D.A. (2000) Estimating animal abundance using noninvasive DNA sampling: promise and pitfalls. *Ecological Applications*, **10**, 283–294.
- Moleón, M., Sánchez-Zapata, J.A., Selva, N., Donazar, J.A. & Owen-Smith, N. (2014) Inter-specific interactions linking predation and

- scavenging in terrestrial vertebrate assemblages. *Biological Reviews of the Cambridge Philosophical Society*, **1045**, 1042–1054.
- Ogada, D.L., Keasing, F. & Virani, M.Z. (2011) Dropping dead: causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences*, **1249**, 57–71.
- Oriol-Cotterill, A., Valeix, M., Frank, L.G., Riginos, C. & Macdonald, D.W. (2015) Landscapes of Coexistence for terrestrial carnivores: the ecological consequences of being downgraded from ultimate to penultimate predator by humans. *Oikos*, **124**, 1263–1273.
- Parnell, A.C., Inger, R., Bearhop, S. & Jackson, A.L. (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE*, **5**, e9672.
- Pereira, L.M., Owen-Smith, N. & Moleón, M. (2014) Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mammal Review*, **44**, 44–55.
- Perrig, P.L., Donadio, E., Middleton, A. & Pauli, J.N. (2016) Puma predation subsidizes an obligate scavenger in the high Andes. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.7nk90>
- 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.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raymond, M. & Rousset, F. (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248–249.
- Rosing, M.N., Ben-David, M. & Barry, R.P. (1998) Analysis of stable isotope data: a K nearest-neighbors randomization test. *The Journal of Wildlife Management*, **62**, 380–388.
- Ruxton, G.D. & Houston, D.C. (2004) Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology*, **228**, 431–436.
- Salvioli, G. (2007) Caracterización hidrometeorológica. *Diversidad Biológica y Cultural de los Altos Andes Centrales de Argentina—Línea de Base de la Reserva de Biosfera San Guillermo, San Juan* (ed. E. Martínez Carretero), pp. 63–87. Fundación Universidad Nacional de San Juan, San Juan, Argentina.
- Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. & Woolmer, G. (2002) The human footprint and the last of the wild. *BioScience*, **52**, 891–904.
- Shaw, A.K., Galaz, J.L. & Marquet, P.A. (2012) Population dynamics of the vicuña (*Vicugna vicugna*): density-dependence, rainfall, and spatial distribution. *Journal of Mammalogy*, **93**, 658–666.
- Smith, J.A., Mazumder, D., Suthers, I.M. & Taylor, M.D. (2013) To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons ed G. Bowen. *Methods in Ecology and Evolution*, **4**, 612–618.
- Valière, N. (2002) GIMLET: a computer program for analysing genetic individual identification data. *Molecular Ecology Notes*, **2**, 377–379.
- Van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M. & Shipley, P. (2004) Micro-Checker: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes*, **4**, 535–538.
- Walker, S. & Novaro, A. (2009) The world's southernmost Pumas in Patagonia and the southern Andes. *Cougar: Ecology and Conservation* (eds M. Hornocker & S. Negri), p. 306. The University of Chicago Press, Chicago, IL, USA.
- Wallace, M. & Temple, S. (1988) Impacts of the 1982–1983 El Niño on population dynamics of Andean Condors in Peru. *Biotropica*, **20**, 144–150.
- Wikens, C., Sand, H., Ahlqvist, P. & Liberg, O. (2013) Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. *PLoS ONE*, **8**, e77373.
- Williams, R.L., Goodenough, A.E. & Stafford, R. (2012) Statistical precision of diet diversity from scat and pellet analysis. *Ecological Informatics*, **7**, 30–34.
- Wilms, C.C. & Getz, W.M. (2004) Simulating the effects of wolf-elk population dynamics on resource flow to scavengers. *Ecological Modelling*, **177**, 193–208.
- Wilms, 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.
- Wurstten, A., Novaro, A.J. & Walker, R.S. (2014) Habitat use and preference by guanacos, vicuñas, and livestock in an altitudinal gradient in northwest Argentina. *European Journal of Wildlife Research*, **60**, 35–43.

Received 11 May 2016; accepted 26 September 2016

Handling Editor: Susan Cheyne

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Details for genotyping and molecular sexing of Andean condors.

Fig. S1. Rarefaction curve illustrating reliability for estimating Andean condor diet with regurgitated pellets.

Table S1. Microsatellite markers used to obtain multilocus genotypes of Andean condor moulted feathers.

Table S2. Estimated proportional contribution of prey items to Andean condor diet from isotopic mixing models.