Apex scavengers in a changing world:
historical demography and future conservation of Andean condors

By

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Dissertation abstract

Scavening is a ubiquitous, crucial and yet poorly understood ecological process that is being rapidly altered by human-induced environmental changes. These changes have the potential to alter the structure and energy flow of food webs, reduce community stability, and jeopardize human and wildlife health. While the economic, environmental and cultural consequences of these disruptions are being increasingly recognized, the most specialized and efficient vertebrate scavengers, vultures, are among the most imperiled guilds on earth. For my dissertation, I focused on Andean condor (*Vultur gryphus*) trophic and spatial ecology to inform conservation measures for the persistence of large vultures in the Anthropocene.

Chapter 1 explores pre-historic dynamics of scavenger-predator-prey community modules. Through the reconstruction of demographic trajectories via genetic-based approaches, I found independent historical demography of pumas (*Puma concolor*), Andean condors and wild camelids (*Vicugna vicugna* and *Lama guanicoe*) in southern South America from the late Pleistocene to modern times. My results also indicate an increase in population sizes of Andean condors in South America, California condors (*Gymnogyps californianus*) in North America, and white-backed vultures (*Gyps africanus*) in Africa. These results suggest that flexible foraging strategies of extant vultures allowed them to thrive despite large environmental changes.

Chapter 2 develops an integrative spatial prioritization model for contemporary populations of Andean condors. I used GPS locations of birds tracked across two regions in central Argentina and Chile to analyze how landscape predictors influence condor habitat selection during foraging, flying and roosting, while accounting for regional and individual differences. I assembled this information into a model of spatial priorities across ~30% of condor distribution and found that most reserves are not located in areas of relevance for condor conservation. While my work has particular implications for Andean condors, this approach could be used to direct management efforts on unprotected landscapes for other wide-ranging species.

Chapter 3 evaluates trophic and spatial segregation between Andean condor adult females and males across a spectrum of human-altered landscapes featuring different prey diversity. Male condors weight up to 50% more and are socially dominants over females. This has been suggested as a mechanism by which the sexes partition space and limit intra-specific competition. My analyses of stable isotopes on molted feathers and space use of GPS-tracked birds, however, revealed a lack of sexual differences in home range overlap, feeding locations, and trophic partitioning. Scattered carrion resources and social information transfer might prevent sexual segregation in condors despite their despotic behaviors.

Chapter 4 provides guidance for range-wide and long-term monitoring programmes for vulture conservation globally. I reviewed the common techniques use to study vulture populations around the globe and compared them using Andean condors as a case study. I found that most studies are restricted to specific regions and species, preventing international collaboration and comparison of estimated demographic parameters. I identified the use of shed feathers as the most robust method for monitoring avian scavengers and developed an efficient protocol for identifying individual Andean condors through feathers collected in a non-invasive way. I call for the implementation of this and similar protocols to monitor vultures at continental scales.

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Demography of avian scavengers after Pleistocene megafaunal extinction

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Abstract

The late Quaternary megafauna extinctions reshaped species assemblages, yet we know little about how extant obligate scavengers responded to this abrupt ecological change. To explore whether obligate scavengers persisted by depending on contemporary community linkages or via foraging flexibility, we tested the importance of the trophic interaction between pumas (*Puma concolor*) and native camelids (*Vicugna vicugna* and *Lama guanicoe*) for the persistence of Andean condors (*Vultur gryphus*) in southern South America, and compared the demographic history of three vultures in different continents. We sequenced and compiled mtDNA to reconstruct past population dynamics. Our results suggest that Andean condors increased in population size >10 KYA, whereas vicuñas and pumas showed stable populations and guanacos a recent (<10 KYA) demographic expansion, suggesting independent trajectories between species. Further, vultures showed positive demographic trends: white-backed vultures (*Gyps africanus*) increased in population size, matching attenuated community changes in Africa, and California condors (*Gymnogyps californianus*) exhibited a steep demographic expansion ~20 KYA largely concurrent with North American megafaunal extinctions. Our results suggest that dietary plasticity of extant vulture lineages allowed them to thrive despite historical environmental changes. This dietary flexibility, however, is now detrimental as it enhances risk to toxicological compounds harbored by modern carrion resources.

Keywords

Scavenger, Megafauna, Andean condor, California condor, White-backed vulture, South America.

Introduction

Historical species assemblages can provide insight into the contemporary structure and functioning of communities (Galetti et al. 2017). Pleistocene communities, in particular, sustained diverse vertebrate assemblages of mega-carnivores and -herbivores (average body size ≥ 44kg; Anderson 1984, Barnosky et al. 2004) that provided plentiful carrion resources for scavenging (Ruxton and Houston 2003). These carrion resources precipitated a rapid radiation of avian obligate scavengers (Rich 1983, Johnson et al. 2006, 2016) that varied in morphology and body size according to different feeding strategies (Hertel 1994). Climatic changes and human impacts during the Pleistocene-Holocene transition triggered a massive loss of megafauna (Lorenzen et al. 2011, Metcalf et al. 2016, van der Kaars et al. 2017): only ~5% of megaherbivores, 40% of megacarnivores (Koch and Barnosky 2006), and ~41% of obligate scavengers (Rich 1983, Tyrberg 2008) genera persisted. The near-complete disassembly of Pleistocene communities radically transformed ecological interactions for those species that went through the extinction epoch (Galetti et al. 2017). Yet, the mechanisms by which species survived ecological changes are poorly understood, especially for guilds tightly linked to mega-mammals.

The Pleistocene megafaunal extinctions were a globally heterogeneous phenomenon (Koch and Barnosky 2006, Stuart 2015). Across Africa and southeast Eurasia, where large-bodied species had a deep history of coevolution with hominids, loss of megafauna was relatively moderate and gradual (Sandom et al. 2014). For example, in Sub-Saharan Africa most of the Pleistocene megafauna persist today, including 31 genera of mega-herbivores and 5 mega-carnivores (Koch and Barnosky 2006). Unsurprisingly, then, Africa (*n* = 11) and southern Asia (*n* = 10) support the greatest diversity of the largest obligate scavengers (Wilburg and Jackson 1983) which rely upon carrion from herds of ungulates that die primarily from non-predatory causes (Houston 1974, Kendall et al. 2014). In contrast, the megafauna of the Americas experienced a punctuated wave of extinctions, losing 70-80% of Pleistocene megafauna genera (Lyons et al. 2004, Koch and Barnosky 2006) from a combination of climate changes and human arrival (Grayson 2007, Lorenzen et al. 2011, Metcalf et al. 2016). In North America, this extinction wave drove the disappearance of at least seven genera of vultures (Emslie 1998, Stucchi and Emslie 2005). The California condor (*Gymnogyps californianus*), however, persisted into the Holocene by relying on marine-derived food resources (Chamberlain et al. 2005, Fox-Dobbs et al. 2006).

The megafauna extinctions in South America were more extensive than on any other continent with the complete loss of mega-herbivores, 50% of megacarnivores (Koch and Barnosky 2006, Svenning and Faurby 2017), and at least 50% of vultures (Alvarenga et al. 2008, Cenizo et al. 2015, Stucchi et al. 2015). Notably, however, a tightly-linked community module of pumas (*Puma concolor*) preying largely on wild camelids, guanacos (*Lama guanicoe*) and vicuñas (*Vicugna vicugna*), emerged in Patagonia and the southern Andes (Prevosti and Martin 2013). Moreover, these species exhibited a demographic expansion (increased effective population size) in the mid-Holocene (Marín et al. 2007, Marin et al. 2013, Matte et al. 2013), leading to a rapid reorganization of the ecological community to one that became dominated by mid-sized vertebrates (Prevosti and Martin 2013, Van Valkenburgh et al. 2015). The largest extant scavenger of South America, the Andean condor (*Vultur gryphus*), currently relies almost exclusively on terrestrial food resources (Perrig et al. 2017, Lambertucci et al. 2018). In areas where native ungulates have been extirpated, Andean condors now forage on an array of exotic prey (livestock [*Ovis aries*, *Bos Taurus*], European hares [*Lepus europaeus*], red deer [*Cervus elaphus*]) (Lambertucci et al. 2009, Ballejo et al. 2017). Comparatively, in pristine landscapes Andean condors show a strong dependency on puma-killed camelids, indicating a tight ecological association among these species (Perrig et al. 2017). It is unknown, however, whether this trophic linkage to the puma-camelid predatory interaction occurred historically and played a role in sustaining Andean condors during the Pleistocene extinctions. Further, it is unknown how these two different contemporary foraging strategies affect the long-term viability and persistence of Andean condor populations.

The demography of obligate scavengers are generally linked to the availability of carrion resources (Margalida and Colomer 2012). Apex predators can impact the abundance of scavenger populations by hunting large prey continuously through time, thus providing spatially and temporarily reliable access to carrion (Wilmers and Getz 2004, Elbroch et al. 2017, Walker et al. 2018). If necrophagous birds rely on predators provisioning the carrion of mammalian herbivores, their historic demographic trajectories should mirror that of the species they depended upon. Alternatively, if carrion availability is from other resources (e.g., marine; Chamberlain et al. 2005) or other sources of ungulate mortality (e.g., malnutrition, disease, extreme weather events; Kendall et al. 2014), there should be independent population size changes between predators, scavengers and ungulates. To test these competing hypotheses, we first explored past trophic linkages in South American communities. We hypothesized that if the puma-camelid predator-prey interaction sustained Andean condor populations in southern South America from the early Holocene to historical times, the demographic trajectories for Andean condors, pumas, vicuñas and guanacos would be coupled and have expanded synchronously in the early Holocene. On the other hand, if Andean condors persisted through the Pleistocene extinctions by consuming other dietary resources, their paleo-demographic trajectories would not be synchronized with those of pumas, vicuñas and guanacos, indicating that Andean condors persisted into the Holocene thanks to a plastic foraging behavior. Secondly, we reconstructed the demographic trajectory of other vulture species that share similar life history strategies to Andean condors, but experienced different historical changes to their communities: white-backed vultures (*Gyps* *africanus*) in Africa and California condors in North America. Given that white-backed vultures are dependent on African ungulates, which experienced relatively attenuated community changes in the late Pleistocene (Sandom et al. 2014, Kendall et al. 2014), we predicted that these vultures will exhibit a relatively stable population size over time. For California condors, which persisted through the late Quaternary extinctions by shifting from terrestrial to marine food resources (Chamberlain et al. 2005), we predicted that they would exhibit similar historical demographic dynamics to Andean condors given that both species had to rely upon alternative food resources after the collapse of megafauna. To test our predictions, we implemented three complementary analytical methods that infer past population dynamics from contemporary gene sequences. In particular, we sequenced mitochondrial (mtDNA) and nuclear loci (nDNA) of Andean condors and compiled available mtDNA sequences from GenBank to study changes in population size of pumas, Andean condors, vicuñas, guanacos, California condors and white-backed vulture via neutrality tests, mismatch distributions, and Extended Bayesian Skyline Plot coalescent models (EBSP).

Results

For Andean condors, we amplified 522-538 base pairs of the c-myc gene, and 1502 - 1639 bp of mitochondrial control region and partial 12S (table 1). The c-myc nuclear gene presented only one variable nucleotide, resulting in low haplotype diversity (0.09) and insignificant values of neutrality test statistics (table 2). CR1 showed the highest number of variable nucleotides compared to CR2 and 12S (21 vs 12 and 4) and the highest haplotype diversity (0.88 vs 0.087 and 0.17, Supplementary Table S1). Neutrality tests with concatenated mitochondrial and nuclear loci were significant and negative (table 1), indicating population expansion of Andean condors. A unimodal distribution of pairwise differences from mismatch analysis (Supplementary Fig. S1) also indicated that a demographic expansion affected neutrality, with an estimated time since expansion of ~12

KYA ($\tau = 0.732$). The EBSP plot exhibited a slight and steady increase in population size since ~100 KYA (Fig. 1), and the majority of EBSP chains detected one or more population changes (Supplementary Fig. S2). Yet, the null hypothesis of population stability could not be completely rejected since the 95% highest posterior density (HPD) of population changes included zero (95% HPD 0-3, Supplementary Fig. S2).

For guanacos, significant neutrality tests (table 2), largely unimodal mismatch distributions, and EBSP analysis with 95% HPD of population changes excluding zero (Fig. 1, 95% HPD 1-4) corroborated previous reports of guanacos undergoing a recent population expansion (<10 KYA). However, we did not find this pattern for vicuñas and pumas inhabiting southern South America. In particular, pumas yielded positive neutrality statistics (table 2), a bimodal mismatch distribution (Supplementary Fig. S1) and a flat EBSP plot with 95% HPD including zero (Supplementary Fig. S2), overall indicative of a stable population size. Similar results were obtained for vicuñas in their current southern range (table 2; Supplementary Fig. S2 and S3). The independence of the demographic histories of Andean condors, pumas, and camelids is evident even when EBSP analyses were conducted fixing molecular evolution rates at the lower, median and upper values estimated (Supplementary Fig. S4).

Skyline analysis revealed population expansion of California condors since ~20 KYA (as indicated by the median effective population size [Fig. 2], and 95% HPD of population changes excluding zero) which was supported by significant neutrality tests (table 2) and a unimodal mismatch distribution (Supplementary Fig. S1). Similarly, a smooth and unimodal mismatch analysis (Supplementary Fig. S1) along with negative and significant Fu's and Tajima's D values indicate that white-backed vultures experienced population expansion, although Fu and Li D* value was non-significant (table 2). Visual inspection of the EBSP plot indicates a slightly increasing population trend since ~30 KYA (Fig. 2), although 95%

HPD interval of population changes overlapped zero (Supplementary Fig. S2). Mismatch distributions suggested an expansion ~ 47.4 KYA ($\tau = 1.36$).

Discussion

We found independent historical demographic trajectories among pumas, condors and wild camelids in southern South America, and no support for the condor-puma-camelid being a historical relationship that allowed the persistence of Andean condors despite the loss of megafauna. In particular, our neutrality tests and mismatch analysis indicated an increase in Andean Condors ~12 KYA. While the 95% highest posterior density of population changes for our EBSP analysis overlapped zero (Heled and Drummond 2008), we attribute this to a lack of power to detect slight demographic changes from a small sample size (n = 23) (Grant 2015). In contrast to EBSP, neutrality tests are robust to small sample sizes and reflect either the effects of natural selection or recent demographic changes (Grant 2015). Given the long generation time, low genetic diversity, and lack of population structure in the Andean condor (Hendrickson et al. 2003, Padró et al. 2018), we are confident that our results are driven by a demographic change and not by natural selection. In contrast to Andean condors, vicuñas and pumas showed stable populations, and guanacos a steep and recent (<10 KYA) demographic expansion. These results corroborate previous work that has shown increasing guanaco populations during the early-Holocene (Marin et al. 2013) and nominal change for vicuñas when restricted to southern South America (Marín et al. 2007). It is notable that vicuña populations in northern Peru exhibited recent demographic expansion (Supplementary Fig. S2) (Marín et al. 2007, Casey et al. 2018). Our finding that pumas were stable during the late Pleistocene-Holocene differs from previous work showing demographic expansion of South American pumas (Matte et al. 2013). We attribute these different conclusions to sampling design: while Matte *et al.* (Matte et al. 2013) combined puma samples from across the continent – pooling five subspecies (Culver et al. 2000, Matte et al.

2013) – we targeted pumas within Argentina and Chile. It is possible that relatively moderate changes in total mammal biomass (Doughty et al. 2016, Svenning et al. 2016) along with expanding human populations that competed with pumas for prey (Goldberg et al. 2016, Root-Bernstein and Svenning 2016), prevented significant demographic changes in the puma population. Accurate inference of the timing of historical demographic change relies on estimating a species-specific substitution rate (Grant 2015). As a consequence of the previously reported time-dependency of mitochondrial substitution rates (Ho et al. 2011), the timing of events inferred in our study (including the ~12 KYA onset of expansion in Andean condors) may be overestimated. Regardless, our discordant neutrality tests (table 2), mismatch analyses (Supplementary Fig. S1) and Skyline-plots (Fig. 2), all point to independent demographic histories of Andean condors, pumas and camelids. Thus, carrion subsidies from puma-killed camelids do not seem to explain the demographic trajectory of Andean condors, suggesting that food availability was not a limiting factor for its population in southern South America.

While extant lineages of Andean condors appear to have expanded along the Andes, condor populations in their eastern range went extinct after the Pleistocene (Lambertucci 2007), and the reasons for this range contraction remain unclear. On one hand, Andean condors depend upon uplift wind to soar in search for carcasses in open habitats (Shepard and Lambertucci 2013). Thus, climatic changes could have had a great impact on condor populations (Tonni and Noriega 1998). In the early Holocene, hotter and more humid conditions in eastern South America resulted in decreased thermal uplifts, landscapes with more vegetative cover (Tonni and Noriega 1998), and faster decomposition of carrion (DeVault et al. 2003), all of which could have contributed to the loss of large soaring birds adapted to scavenging in arid environments (Tonni and Noriega 1998). On the other hand, Andean condor populations could have been driven to extinction by a reduced availability of carrion resources after the loss of megafauna (Cenizo et al. 2015), which was the case for most North American vultures and raptors (Fox-Dobbs et al. 2006). California condors were able to survive Quaternary extinctions due to marine subsidies; by the early Holocene, those condors were confined to the Pacific coast of North America where marine mammals offered the only remaining source of large animal carcasses (Chamberlain et al. 2005, Fox-Dobbs et al. 2006). It is unknown if Andean condor foraging history mirrors that of California condors. Historical samples indicate that marine remains were more important to Andean condors in the 19th century compared to now (Lambertucci et al. 2018). Quantifying Andean condor diet during the early Holocene (Chamberlain et al. 2005) would help to reveal if marine subsidies were consumed and contributed to the persistence of Andean condors during the late Quaternary extinctions. Regardless of exact foraging mechanism, persisting Andean condors do not appear to have experienced a population bottleneck (Padró et al. 2018), which is supported by archeological records indicating that the species was common across their current range until the 19th century. Overall, then, reductions in extant Andean condor populations seem to be recent (< 500 years), and largely caused by anthropogenic impacts (Lambertucci 2007).

As with Andean condors in South America, our results suggest an increase in vulture populations in North America and Africa despite significant climatic and ecological changes (Syverson and Prothero 2010). Notably, California condors appear to have undergone a steep demographic expansion ~20 KYA, which could explain their high mitochondrial DNA diversity (D'Elia et al. 2016). California condors possibly benefited from relaxed competition due to the extinction of other avian scavengers during the particularly abrupt megafaunal extinctions that occurred in North America during the Pleistocene-Holocene transition (Van Valkenburgh and Hertel 1998, Tyrberg 2008, Barnosky et al. 2015). Contrary to our expectation, our neutrality tests and mismatch analysis suggested that the most widespread and common African vulture, the white-backed vulture (Wilburg and Jackson 1983), also experienced a demographic expansion ~47 KYA, which is supported by previous studies showing high genetic diversity in historically large populations (van Wyk et al. 2001, Arshad et al. 2009b). As with Andean condors, though, EBSP 95% highest posterior density of population changes overlapped zero (Supplementary Fig. S2), which we attribute to low diversity in the gene fragment analyzed. Losses of African megafauna were substantial but happened earlier than the period studied (Koch and Barnosky 2006), so white-backed vultures possibly benefited from a constant carrion supply from wild ungulates (Kendall et al. 2014). Our analyses, then, suggest that extant vultures – in the Americas and Africa – not only persisted but increased in population size despite large ecological shifts.

Most vertebrates that survived the last Quaternary extinction possessed flexible foraging behaviors (Van Valkenburgh and Hertel 1998). Indeed, extinct vultures were generally larger and possessed more extreme skull morphologies compared to extant species, indicating that intermediate sized scavengers were more likely to survive into the Holocene (Hertel 1994). Extant vultures show high flexibility in foraging, as evidenced by their ability to exploit small carcasses (Collins et al. 2000, Lambertucci et al. 2009, Donázar et al. 2010, Ballejo et al. 2017) and a diversity of human-related carrion resources (Margalida and Marín-arroyo 2013, Plaza and Lambertucci 2017). As human land-use intensifies, vultures have increasingly taken advantage of novel food sources. Unfortunately, these new foraging opportunities are often associated with toxicological risks, such as lead from hunted animals (Plaza and Lambertucci 2019), pharmaceutical compounds in livestock (Pain et al. 2008), or poison intentionally deployed on carrion remains (Ogada et al. 2016). Further, vultures' consumption of human-related food resources results in direct persecution. Both dietary toxins and persecution associated with current-day carrion sources are the main threat for vultures worldwide (Buechley and Şekercioğlu 2016). Thus, the flexible foraging strategy appears to be a “double-edged sword” – a behavioral trait that enabled lineages of vultures to persist through the Pleistocene epoch but now enhances their risks to modern threats.

While the impact of megafauna extinctions over carnivore and herbivore communities has received a great deal of attention, only a handful of studies have assessed the loss of large vertebrates over scavengers to date (Kane et al. 2017, Galetti et al. 2017). We found evidence that suggests vultures responded demographically to changes in mammal communities, but no support for predator-prey interactions driving the historical demographic trajectory of obligate scavengers. These findings do not diminish the importance of carrion resources from mammalian predatory interactions (Elbroch et al. 2017), but stress the behavioral plasticity of large vultures responding to ecological changes and the overestimated effect of food availability as a natural-limiting factor of some vulture populations. A consequence of the late Quaternary extinctions is that many extant species present large dietary breadths, even within specialized guilds (Galetti et al. 2017). Our findings suggest that, until recently, large avian scavengers survived because of this flexibility. This plastic foraging behavior, though, now exposes them to a suite of threats associated with current carrion resources (Pauli et al. 2018).

Methods

To understand how changes in community composition impacted obligate scavengers, we evaluated the historical demography (100 KYA to mid-Holocene) of a tightly linked scavenger-predator-prey community module of southern South America. Additionally, we explored and compared how historical community changes affected the demographic trajectory of three large obligate scavengers inhabiting different continents that share life history strategies with long-generation times, and lifestyles involving social roosting and feeding habits, large individual home ranges and dependence on soaring flight (Buechley and Şekercioğlu 2016).

Laboratory analysis

We extracted DNA from molted feathers of individual Andean Condors in 2013 from active roosting sites in northwestern Argentina: San Guillermo National Park (*n* = 11; -29.07°S, -69.35°W), La Payunia Provincial Reserve (*n* = 6; -36.40°S, -69.23°W) and Auca Mahuida reserve (*n* = 6; -38°S, -68.70°W) (Perrig et al. 2017, Padró et al. 2018). We amplified the mitochondrial (mtDNA) complete Glu and partial control region with primers L16652-H621 (hereafter CR1), control region with L798-H1455 (hereafter CR2), and complete Phe and partial 12S with L798-H1795 (hereafter 12S) (Hendrickson et al. 2003). Additionally, we amplified exon 3 of the nuclear gene c-myc with the primers mycEX3D-RmycEX3D and mycEX3A-RmycEX3A (Ericson et al. 2006). Details on laboratory analyses are presented in the Supplementary material.

Compiled datasets

We compiled mtDNA sequences from vicuñas (Marín et al. 2007), guanacos (Marin et al. 2013), pumas (Culver et al. 2000, Matte et al. 2013), California condor (D'Elia et al. 2016), white-backed vulture (Arshad et al. 2009a) and outgroup species (*Puma yaguaroundi* and *Gyps ruepelli*) from GenBank (Supplementary Table S2). For demographic reconstruction of South American species, we selected samples that overlapped the geographic region with our Andean condor sampling sites based on haplotype structure from previous studies. In particular, puma samples came from southwestern South America, vicuña samples from Argentina and their southern Chilean range, and for guanacos we only considered the subspecies *L. g. guanicoe*. Samples of California condors were collected across their historical range (D'Elia et al. 2016) and samples of white-backed vultures were collected in Africa, primarily Namibia (Arshad et al. 2009a) (Supplementary Table S2). We tested for population panmixia by conducting exact test of population differentiation in

Arlequin v3.5 (Excoffier and Lischer 2010) with 100,000 Markov chain, and eliminated samples of significantly segregated populations.

Data analysis

We obtained Andean condor haplotype statistics via DNAsp v6.10.1 (Rozas et al. 2017). For all following analysis, we used the Akaike information criterion corrected for sample size (AICc) to find the best fit evolutionary model with jModeltest 2.1.4 (Darriba et al. 2012). Skylines plots and analyses for estimation of molecular clock rates were implemented in BEAST v.2.4.7 (Bouckaert et al. 2014). Convergence to the stationary distribution and sufficient effective sampling sizes (>200) for each estimated parameter were checked using Tracer v1.5 (Rambaut and Drummond 2007), and four independent runs were combined using Log Combiner v2.4.7, a software implemented in BEAST2.

Substitution rates

We estimated clock rates for Andean and California condors implementing a Bayesian multispecies coalescent tree in *BEAST2 (Ogilvie et al. 2017) using available mtDNA control region sequences from historical samples of California condors (D'Elia et al. 2016) and Andean condor sequence generated in this study via CR1. The resulting molecular substitution rate for the Andean condor was used to estimate molecular evolution rates for CR2, 12S and c-myc via a coalescent constant population model process implemented in BEAST2. To estimate site and species-specific substitution rates for pumas, we also constructed multispecies coalescent analyses for loci ATP8 and NADH5 with *Puma yaguaroundi* as an outgroup (Culver et al. 2000). We conducted a similar analysis to estimate cytochrome b oxidase I (cyt-b) substitution rate of *Gyps africanus* using *Gyps ruepelli* as an outgroup. For vicuñas and guanacos, mtDNA sequences from fossil samples and associated dates estimated by Metcalf et al. (Metcalf et al. 2016) were used for calibration of fossilized birth-death models (Heath et al. 2014) implemented in BEAST2 using the Sampled Ancestors add-on package (Gavryushkina et al. 2014). For all analyses we compared the performance of a strict and uncorrelated relaxed lognormal clock model; we subsequently combined results of two independent runs of the best model (see details on the analysis in the Supplementary material).

Demographic analysis

We used three complimentary methods to infer changes in population size over time in our study species. We conducted neutrality tests, against null hypothesis of a constant population size, using Tajima's *D* (Tajima 1989), Fu's *Fs* (Fu 1997), Fu and Li D* statistics in DNAsp v6.10.1 (Rozas et al. 2017) with 10,000 coalescent simulations to calculate significance values. Second, we tested deviations from null models of constant populations via the distribution of pairwise sequence differences, or mismatch distribution, using the same software as above; observed versus expected results were plotted in R v3.4.2 (R Development Core Team 2017). For pumas and Andean condors, these two methods were implemented for concatenated mtDNA sequences. Finally, we estimated the timing and degree of population changes with Extended Bayesian Skyline Plot coalescent models (EBSP; Heled and Drummond 2008). These analyses depend on the estimation of evolutionary rates, which rely heavily on the statistical methods used to calibrate the clock (Ho et al. 2011). To account for some of the uncertainty around the rates estimated, EBSP analyses were run using estimated molecular clock rates via log normal priors informed by median and 95% HPD values from initial analyses (see table 1 for further model details). We computed the posterior distribution of the number of demographic changes between runs, and formally rejected the null hypothesis of a constant population size when the 95% high posterior density (HPD) of population changes excluded zero (Heled and Drummond 2008). For species with conflicting results between EBSPs and neutrality test (Andean condors and white-backed vultures, see results), we obtained an approximated time since expansion based on mismatch analysis using the formula $t = \tau/2\mu$, where $\mu = m\mu$ is the mutation rate (as described previously) of the entire segment of m base pairs and τ is estimated based on the crest of the mismatch distribution (Rogers and Harpending 1992, Schenekar and Weiss 2011). Because we did not have a mutation rate for our entire mtDNA sequence of Andean Condors, we calculated the mean rate of the 3 fragments analyzed ($\mu_{aver} = 0.02$), which was equal to the widely used substitution rate for mtDNA of birds (Weir and Schluter 2008).

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Data accessibility

Details of laboratory and data analyses, and GenBank sequences used in analyses have been uploaded as part of the Supplementary material. Additionally, Andean condor sequences will be uploaded to GenBank data repository upon acceptance.

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Table 1. Number of samples (n), gene length in base pairs (bp), reference for samples obtained via GenBank, estimated median and 95% highest probability density (HPD) mutation rate for each species, and model parameters for Bayesian Extended Skyline plot analyses (evolutionary model for the sequence, mean in real space and standard deviation for log normal clock prior, and generation length and sampling interval of Markov Chain Monte Carlo chains).

						EBSP model parameters		
Species	*n*	Gene	GenBank	Bp	Mutation rate	Evol. Model	Clock prior; mean (sd)	MCMC
Andean condor	23	CR1		621 – 622	0.0129 (0.0006-0.0295)	HKY+I[1]	0.013(0.6)	$10x10^8$; $25x10^2$
		CR2		353 – 479	0.0169 (0.0063-0.029)	TrN	0.025(0.45)	
		12S		528 – 538	0.0031 (0.00051-0.0063)	F81	0.003(0.6)	
		c-myc		522 – 538	0.0002 (0.00003-0.0005)	F81	0.0002(0.7)	

California condor	75	D-loop	D'Elia et al. 2016	569	0.0129 (0.0006-0.0296)	HKY+I[2]	0.013(0.5)	$10x10^8$; $3x10^3$
White-backed vulture	77	Cyt-b	Arshad et al. 2009	1026	0.014 (0.0003-0.046)	HKY	0.014(1.2)	$9x10^7$; $25x10^2$
Puma	45	NAD5	Matte el at. 2013 Culver et al. 2000	313	0.0221 (0.0080-0.0464)	TN93	0.022(0.4)	$9x10^7$; $25x10^2$
	22	ATP8		191	0.0155 (0.006-0.0322)	HKY	0.015(0.5)	
Vicuña	23	CR	Marin et al. 2007	513	0.0379 (0.0112-0.0929)	HKY+I[3]	0.04(0.63)	$8x10^7$; $25x10^2$
Guanaco	196	D-loop	Marin et al. 2013	442	0.0493 (0.0238-0.0841)	JC	0.05(0.3)	$26x10^7$; $10x10^2$

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1. Proportion invariant = 0.868
2. Proportion invariant = 0.805
3. Proportion invariant = 0.929

Table 2. Results of Tajima's *D* (D_T), Fu's *Fs* and Fu and Li's D* (D_{FL}) neutrality tests under assumptions of constant population size, and *p* - values from 10,000 coalescent simulations. Statistically significant results are shown in bold.

Species	D_T	p-value	Fu's Fs	p-value	D_{FL}	p-value
Andean condor - complete	-1.68	**0.01**	-3.6	**<0.01**	-2.21	**0.02**
Andean condor - mtDNA	-2.06	**<0.01**	-7.50	**<0.01**	-2.40	**0.02**
Andean condor - nDNA	-1.16	0.27	-0.99	0.35	-1.59	0.06
California condor	-1.49	**0.05**	-9.44	**<0.01**	-4.76	**<0.01**
White-backed vulture	-1.59	**0.03**	-7.33	**<0.01**	-1.49	0.09
Puma	1.98	0.97	2.43	0.88	1.01	0.86
Vicuña	1.79	0.98	-0.29	0.47	1.16	0.95
Guanaco	-2.33	**<0.01**	-21.84	**<0.01**	-2.67	**0.01**

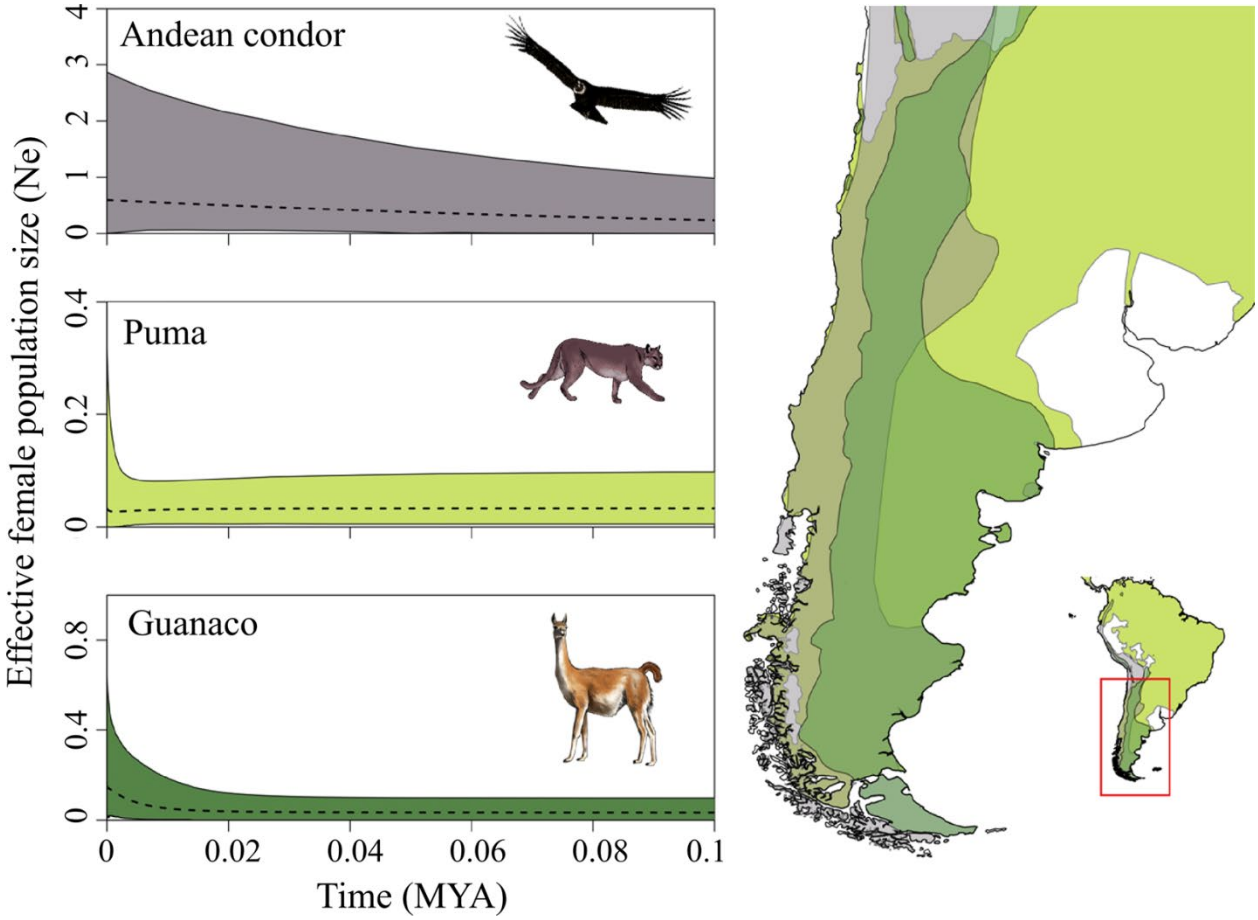

Figure 1. Extended Bayesian Skyline Plots illustrating female effective population size by generation time on a scale of millions of years (MYA) using combined nuclear and mitochondrial DNA sequences of Andean condors, and mitochondrial DNA of pumas and guanacos in southern South America. Dotted line depicts median values; shaded region represents 95% highest posterior density.

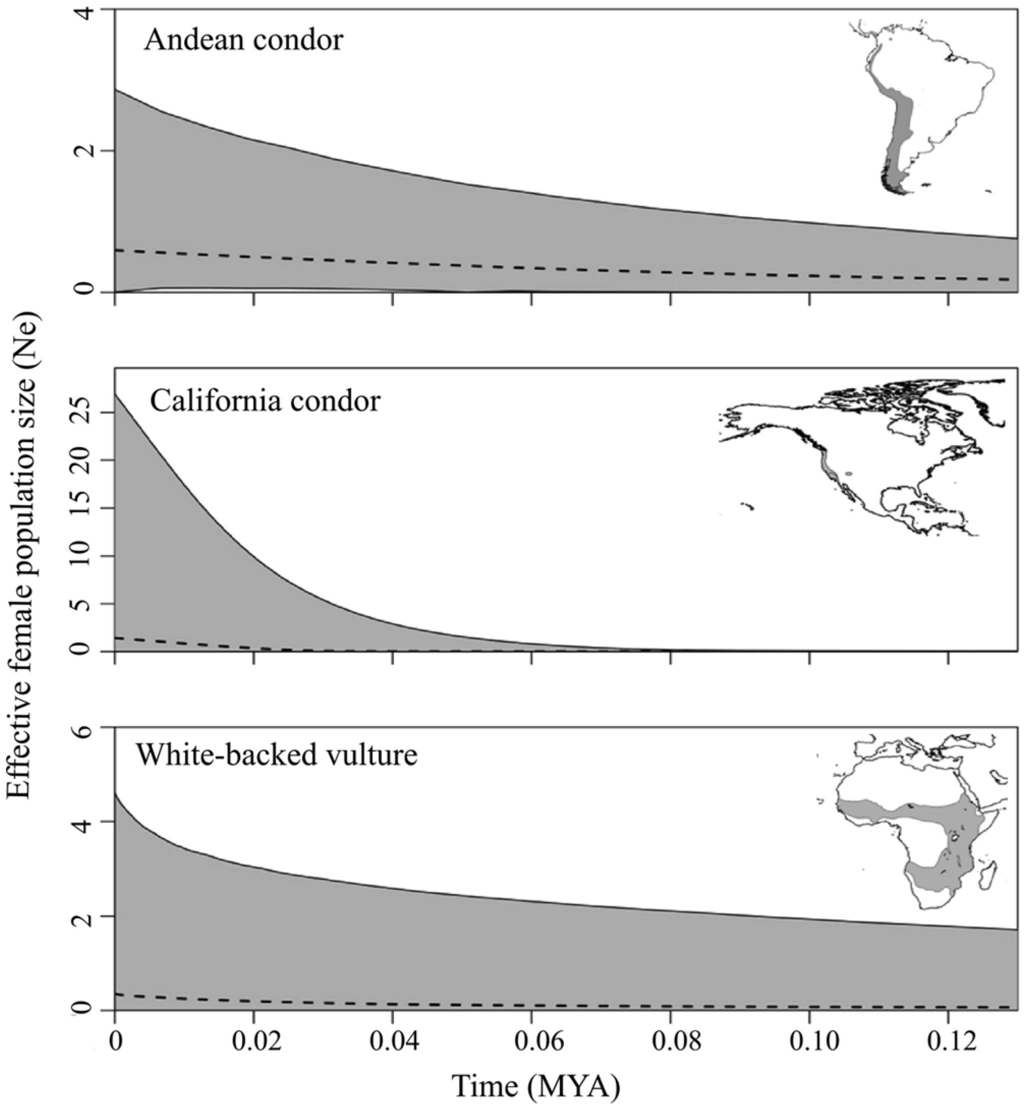

Figure 2. Extended Bayesian Skyline Plots illustrating female effective population size by generation time on a scale of millions of years (MYA) for Andean condors, California condors and white-backed vultures. Dotted lines depict median values; shaded region represents 95% highest posterior density.

Supplementary Information

Sequencing of Andean condor samples

We extracted DNA from 23 Andean condor samples collected non-invasively by removing the blood clot at the superior umbilicus of each feather shaft (Horváth et al. 2005). We performed genomic isolation with QIAamp DNA Micro Kit (QIAGEN, Valencia, CA, USA) in a pre-PCR cleanroom facility at Wisconsin University dedicated to low template DNA, and included negative controls during the extractions. We amplified mitochondrial DNA (mtDNA), including the complete Glu and partial control region with primers L16652-H621 (CR1), control region with L798-H1455 (CR2), and complete Phe and partial 12S with L798-H1795 (12S) (Hendrickson et al. 2003). All PCRs were performed in a final volume of 20µl containing 2 µL template DNA, 1X PCR buffer, 0.25 mM dNTPs, 0.3µM of forward and reverse primer, and 0.025U taq polymerase (201203, Qiagen), and additional 0.5 µg/µl BSA for CR1 and CR2. For 12S, the PCR parameters consisted of 3 m denaturation at 94°C, 35 cycles of 30 s at 94°C, 30 s at 52°C and 30 s at 72°C, and a final extension step of 10 m at 72°C. For CR2 and CR1 the thermal profile included the same steps with an annealing temperature of 50°C and 54°C, respectively. Additionally, exon 3 of the nuclear gene c-myc was amplified with the primers mycEX3D-RmycEX3D and mycEX3A-RmycEX3A (Ericson et al. 2006). PCR products were purified using ExoSAPII (78201, Affymetrix) purification kit according to the manufacturer’s instructions. We pair-end sequenced the fragments on an ABI 3730xl DNA analyzer at the Biotechnology Center, University of Wisconsin-Madison. Sequences were visually aligned using MEGA v7.0.26 (Kumar et al. 2016) except for CR2 which was automatically aligned via webprank (Löytynoja and Goldman 2010) under the default settings due to the presence of variable repeats.

Estimation of substitution rates

To estimate species-specific clock rates for condors, we combined available mtDNA control region sequences from historical samples of California condors (collected between 1825-1980; table S2) with our Andean condor sequences in a Bayesian multispecies coalescent analysis implemented in *BEAST2 (Ogilvie et al. 2017). We trimmed the data to have the same base pair length (sequence length 524 bp; California condors, n = 65, Andean condor, n = 23). The best fitting substitution model for the dataset was HKY+G (gamma shape 0.418) as estimated by JModeltest 2.1.4 (Darriba et al. 2012). A calibrated Yule tree prior was implemented with root height constrained at the estimated time of divergence of condors clade following Johnson et al. (Johnson et al. 2016) by using a normal distribution with mean = 9.5 and std dev =1.6, and groups enforced as monophyletic. The MCMC was run for 90 million generations, sampling every 3000th generation. An improper Jeffrey's prior (1/X) was placed on the clock to allow calibration date to inform the clock rate. For this and all subsequent analysis, evaluation of model performances (convergence to the stationary distribution and effective sampling sizes >200) and resulting substitution rates were obtained using Tracer v1.5 (Rambaut and Drummond 2007). Samples from two independent runs with a relaxed log normal clock were pooled and, after discarding the initial 20% as burn-in, a maximum clade credibility tree was compiled in TreeAnnotator v2.4.7 (included in the BEAST package) summarizing mean node heights. The tree was analyzed via FigTree to obtain median rates of sequence evolution and associated 95% HPD intervals for Andean and California condors independently.

The resulting molecular substitution rate for the Andean condor was used to estimate molecular evolution rates for CR2, 12S and nuclear gene c-myc using a coalescent constant population model process implemented in BEAST2. The model was run linking gene trees for mitochondrial loci and unlinked for nuclear locus, unlinked substitution and site models, and fix substitution rate of 0.0129 for CR1 (as informed by previous analysis). The clock rate for the remaining loci was estimated from the CR1 clock using uniform clock rate priors (0 - ∞). Evolutionary models were HKY+I (prop. Inv. = 0.8680) for CR1, TN93 for CR2, and HKY for 12S and c-myc. The root height was constrained as described above. The MCMC was run for 90 million generations, sampling every 2500th generation. We pooled two independent runs of the model under a strict clock to obtain median and associated 95% HPD substitutions rates.

Two multispecies coalescent models were implemented to estimate substitution rates for pumas using the genes NADH5 (Culver et al. 2000, Matte et al. 2013) and ATP8 (Culver et al. 2000) from individuals across the Americas (n = 287) with *Puma yaguaroundi* as an outgroup (Culver et al. 2000). We trimmed both datasets to have the same base pair length. To inform the tree, we grouped the haplotypes as North America, Central America and South America based on a neighbor joining tree created in Mega7 (Kumar et al. 2016) and haplotype structure from previously published studies (Culver et al. 2000, Caragiulo et al. 2013, Matte et al. 2013). Both processes were run using an analytical population size model and a calibrated yule prior, with TRN evolutionary model for NADH and HKY model for ATP8, using a Jeffrey's prior (1/X) for clock rate estimates, a normal prior on the Most Recent Common Ancestor of the tree with mean 4.17 and standard deviation of 1 following Johnson et al. (Johnson et al. 2006b), and groups enforced as monophyletic (Culver et al. 2000). Both MCMC were run for 90 million generations, sampling every 2500th generation. Models were tested under a strict and relaxed lognormal clock. Due to the standard deviation on the relaxed clock rate having a mean close to zero, as assessed in Tracer, we used a strict molecular clock. Two independent runs were pooled to obtain final substitution rates.

We estimated a substitution rate for cytochrome b (cytb) for *Gyps africanus* (n = 77) implementing a multispecies coalescent analysis in *BEAST2 along with sequences of *Gyps ruepelli* (n = 6, 1026 bp). The process was run under an analytical size integration population model, calibrated yule tree prior with a birth rate of 3.67, Jeffrey's prior (1/X) clock rate, normal prior on the Most Recent Common Ancestor with mean 1 and standard deviation of 0.8, and with groups enforced as monophyletic (Johnson et al. 2006a). The MCMC was run for 100 million generations, sampling every 3000th generation. Model performance was compared under a strict and relaxed log normal clock, and samples from two independent runs under a strict clock were pooled.

For both vicuñas and guanacos, mitochondrial DNA sequences from contemporary fossil samples (n = 3 and n = 25 samples of vicuñas and guanacos, respectively) and associated dates estimated by Metcalf et al. (Metcalf et al. 2016) were used for calibration of fossilized birth-death models (Heath et al. 2014) implemented in BEAST2 using the Sampled Ancestors add-on package (Gavryushkina et al. 2014). Since the guanaco subspecies were paraphyletic (Marin et al. 2013), we only used data for *Lama guanicoe guanicoe* for estimating substitution rates (n = 265, 443 bp). For vicuñas, we did not find evidence of subspecies' differentiation, so we modelled all available data (n = 72, 458bp). Both analysis were parametrized using a origin date of species of 1.5 MYA according to (Lameiro 2016); thus, origin FBD was modeled in real space with mean 1.04, standard deviation 0.19, and offset 0.01062 for guanacos and 0.0215 for vicuñas. Sampling proportion prior had a beta distribution with both parameters set at 2 while diversification rate had an exponential prior with mean 1. We performed each analysis using 80 x 10^7 MCMC generations, sampling every 2500 generations, and two independent runs with a strict clock rate were combined to obtain a final rates for each camelid species.

Table S1. Substitution sites (S), number of haplotypes (h), haplotype diversity (hd), Tajima's *D* (D_T) and Fu's *Fs* (Fs) value and significance (bolded numbers) from coalescent simulations for 3 mitochondrial loci and one nuclear gene sequenced from 23 Andean condor samples collected in Central Argentina.

	S	h	hd	D_T	p-value	Fs	p-value
c-myc	1	2	0.08	-1.16	0.270	-0.99	0.349
CR1	21	14	0.88	-1.82	**0.016**	-7.50	**<0.01**
CR2	12	2	0.08	-2.35	**<0.01**	3.21	0.905
12S	4	3	0.17	-1.88	**<0.01**	-0.78	0.378

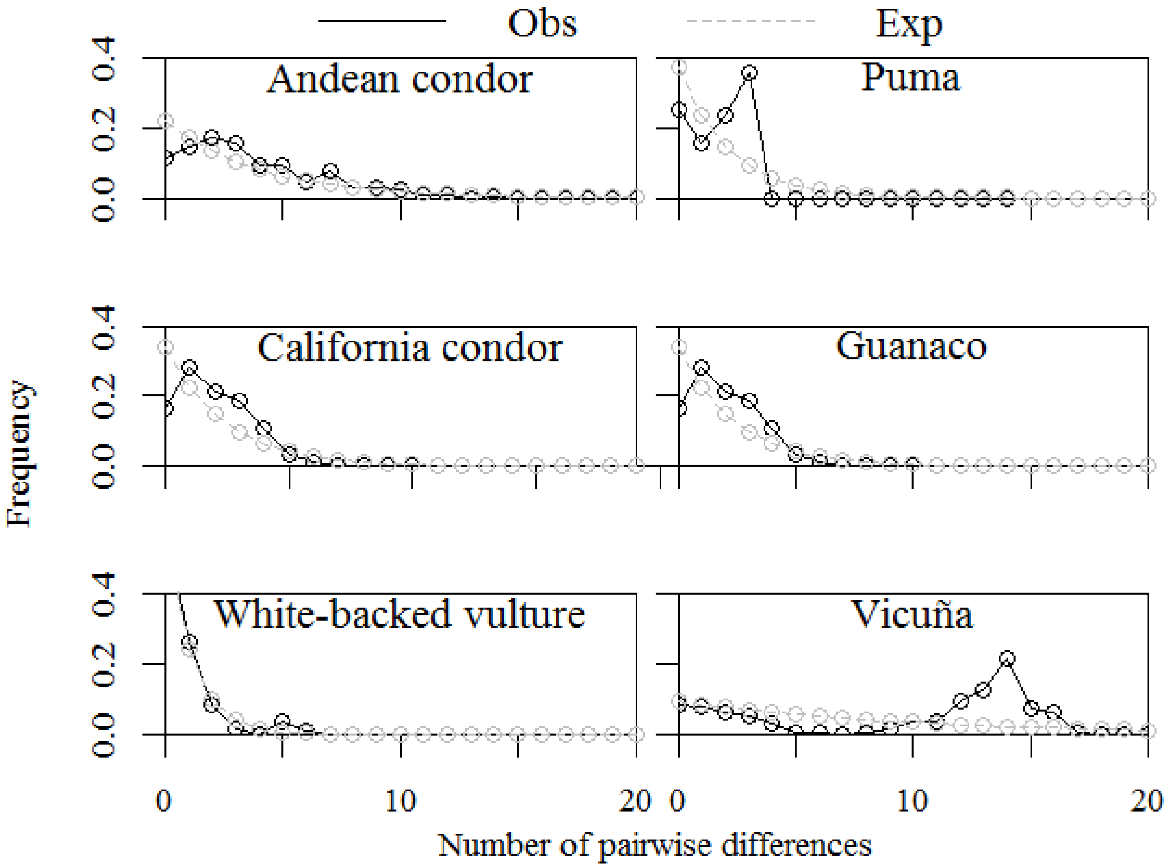

Figure S1. Observed and expected mismatch distribution for mitochondrial genes of all study species.

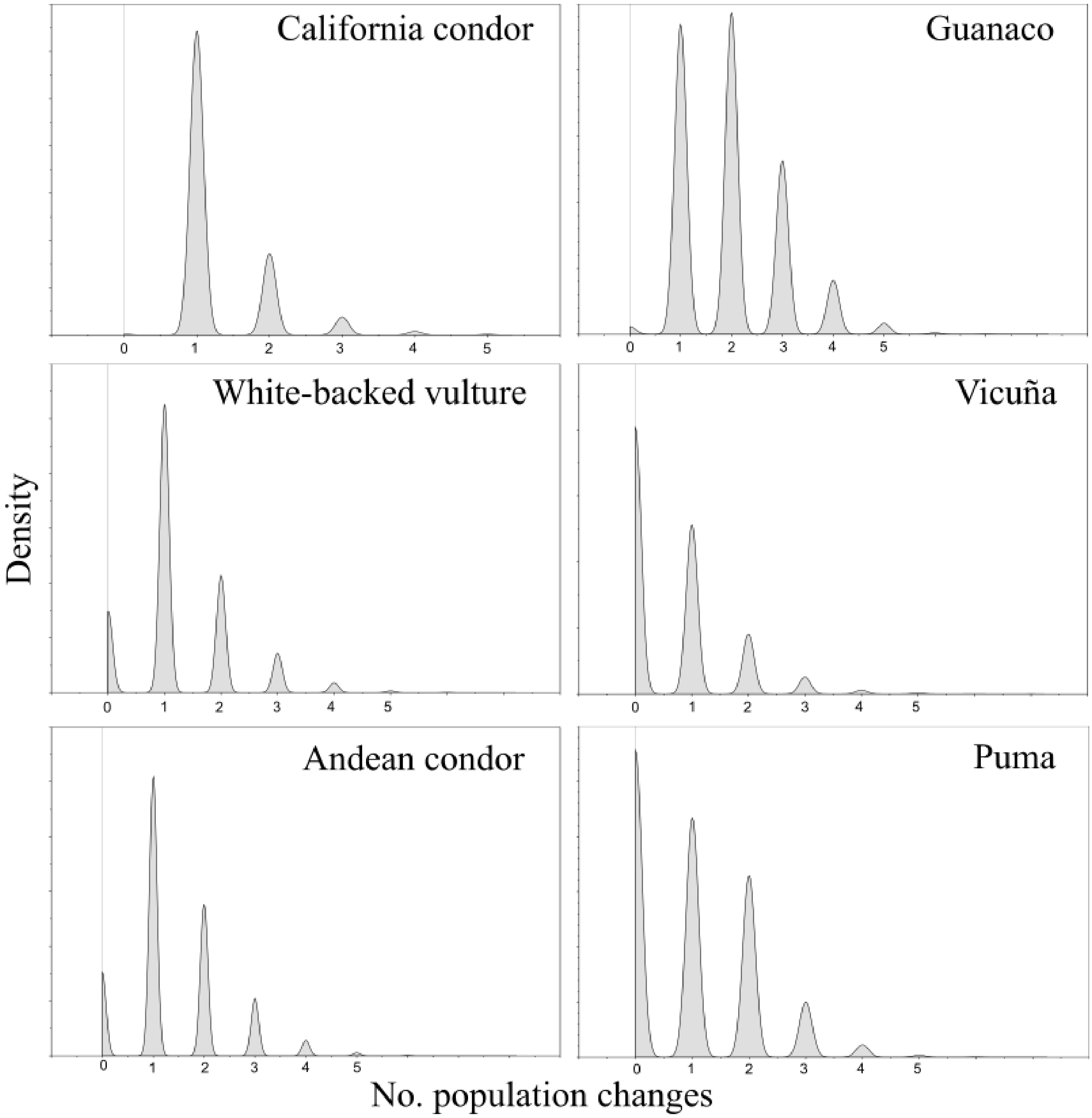

Figure S2. Number of population changes in the posterior distribution of Extended Bayesian Skyline Plots. A constant size coalescent model can be rejected when 0 population changes is outside the 95% Highest Posterior Density interval (HPD) (Heled and Drummond 2008). This was the case for California condors (median of population changes = 1, 95% HPD = 1-3) and guanacos (2, 1-4), whereas we cannot rejected the null hypothesis of a constant population for white-backed vultures (1, 0-3), vicuñas (0, 0-2), Andean condors (1, 0-3) and pumas (1, 0-3).

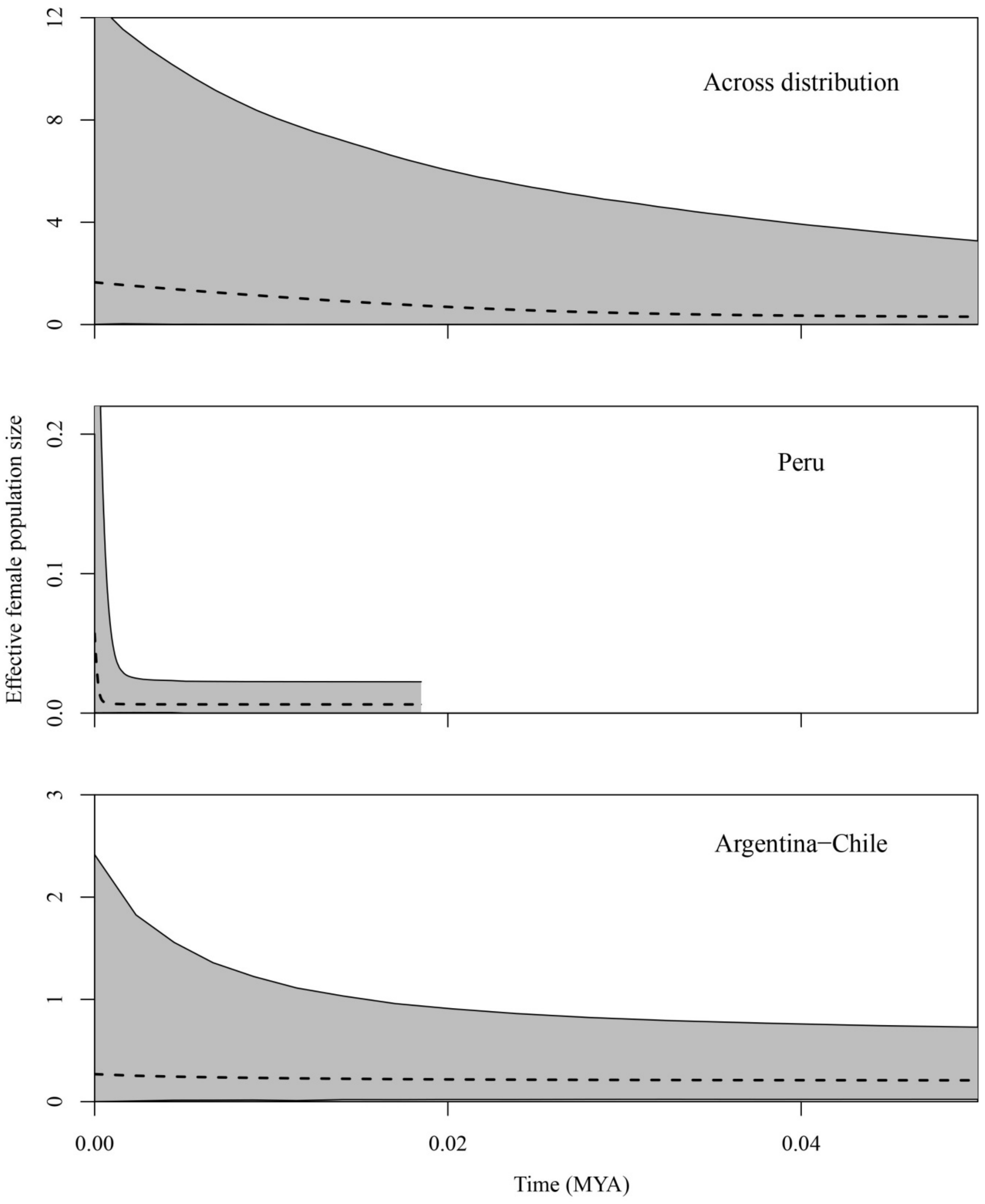

Figure S3. Extended Bayesian Skyline plots for vicuñas implemented with readily available D-loop sequences from (a) the complete species distribution (n = 72, 458 bp), (b) Perú (n = 206, 328 bp), and (c) southern range of vicuña distribution encompassing Chile and Argentina. The models were parametrized as described in main text, except for the best evolutionary model that was HKY and 0.79 proportion invariant for Peruvian populations, and HKY with 0.024 gamma shape for the complete vicuña dataset. It is worth mentioning that pooling sequences from across the species distribution (a) can yield misleading results (Grant 2015).

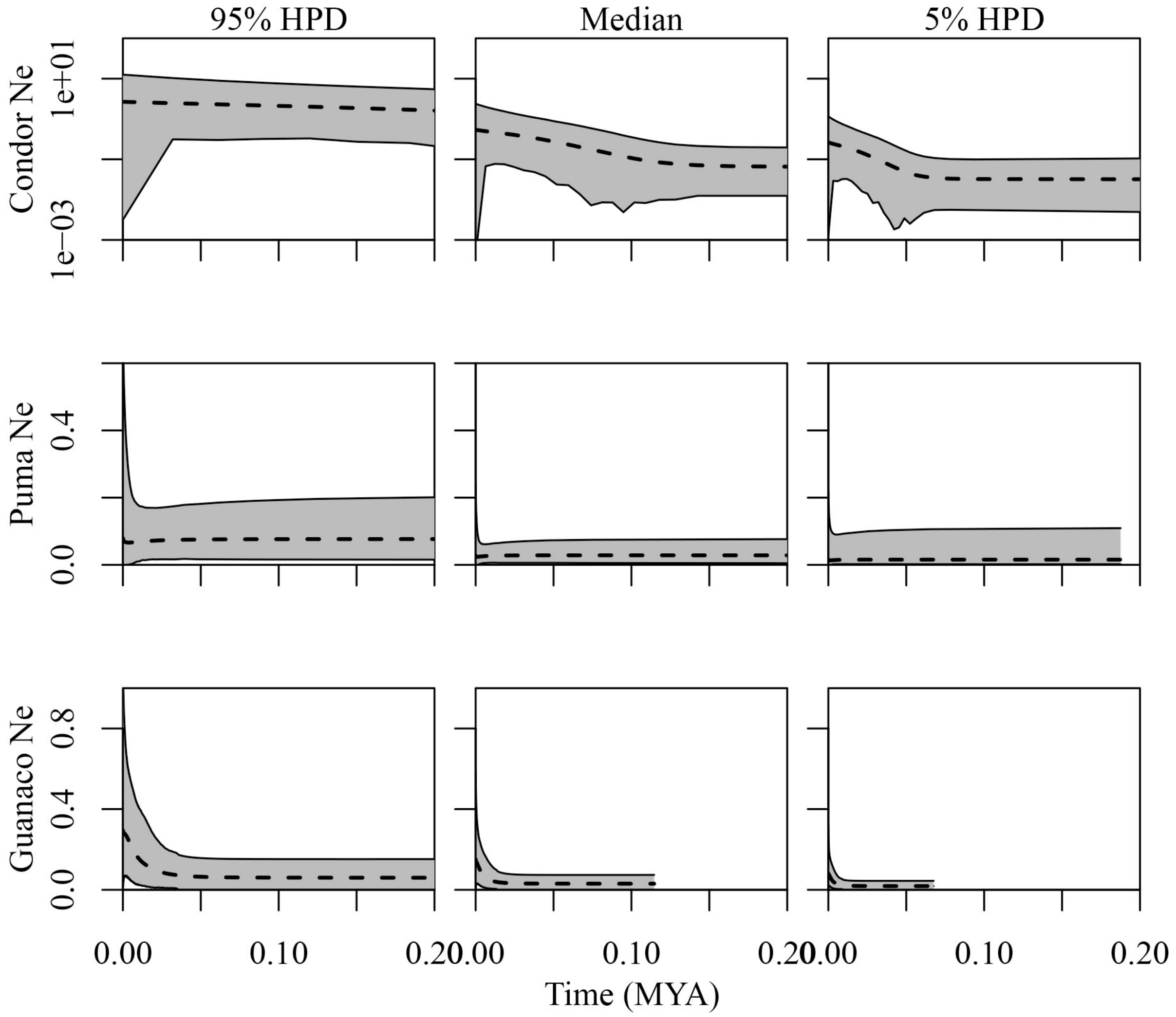

Figure S4. Evaluation of substitution rate effects on Extended Bayesian Skyline Plot (EBSP) analyses of Andean condors, pumas and guanacos' mitochondrial codons. The y-axis represents the female effective population size (Ne) multiplied by generation time, in log scale for Andean condors. EBSP analysis were conducted as described in main text but fixing molecular evolution rates at the lower (5% HPD), median and upper (95% HPD) values estimated in this study. Each plot shows the result of 4 independent runs combined after accounting for a 20% burn-in.

Table S2. Details of sequences retrieved from GenBank

Species	Haplotype	Origin	Locus	GenBank Accession #	# Inds	Reference
Vicugna vicugna		Argentina	CR	AY856304- AY856309, AY856319- AY856323	11	Marín et al. 2007
		Chile	CR	AY856310- AY856318, AY856339- AY856324	17	
		Peru	CR	AY856303- AY856270	33	
		Peru	D-loop	EF197725- EF197535	190	
		Chile	D-loop	EF197534- EF197502	30	
		Peru, Argentina	CR	KU753702- KU753673	4	Metcalf et al. 2016
Lama guanicoe		Argentina	CR	JX678410- JX678536, JX678400- JX678409	136	Marin et al. 2013
		Chile	CR	JX678537- JX678399, JX678301- JX678351	188	
		Bolivia	CR	JX678321- JX678340	19	
		Peru	CR	JX678291- JX678300	10	

		Argentina	CR	KU753671, KU753676- KU753679, KU753711- KU753715, KU753717, KU753718, KU753720-KU753722, KU753724, KU753725,	17	Metcalf et al. 2016
		Chile	CR	KU753701, KU753700, KU753707, KU753660	4	
		Peru	CR	KU753705, KU753706, KU753709, KU753710	4	
Puma concolor	Haplotype 18	South America	NADH5	KF460513	11	Matte et al. 2013
	Haplotype 19	South America	NADH5	KF460514	7	
	Haplotype 07	South America	NADH5	KF460502	5	
	Haplotypes A, L, F	South America	NADH5	AF241860	49	Culver et al. 2000
	Haplotype B	South America	NADH5	AF241861	1	

	Haplotype C	Central America	NADH5	AF241862	2	
	Haplotype D	South America	NADH5	AF241863	4	
	Haplotype E	South America	NADH5	AF241864	2	
	Haplotypes G, H	South America	NADH5	AF241865	10	
	Haplotypes I, J	South America	NADH5	AF241866	23	
	Haplotype K	South America	NADH5	AF241867	1	
	Haplotype M	North America	NADH5	AF241868	190	
	Haplotype N	North America	NADH5	AF241869	4	
	Haplotype A	South America	ATP8	AF241854	1	
	Haplotype B, D, E, F, G, K, L	South America	ATP8	AF241855	57	
	Haplotype C	Central America	ATP8	AF241856	2	
	Haplotypes H, I	South America	ATP8	AF241857	13	
	Haplotype J	South America	ATP8	AF241858	19	
	Haplotypes M, N	North America	ATP8	AF241859	194	
Puma yaguaroundi	JHA	Indet	Genome	KP202279	1	Li et al. Unpubl.

Gyps ruepelli	haplotype GR52	France	Cytb	EU496452	1	Arshad et al. 2009
	haplotype GR51	South Africa	Cytb	EU496451	1	
	haplotype GR50	France	Cytb	EU496450	2	
	haplotype GR53	Gambia	Cytb	DQ908973	1	Johnson et al. 2006a
	haplotype GR54	Gambia	Cytb	AY987260	1	Lerner and Mindell 2005
Gyps africanus	Haplotype GA1	Indet	Cytb	DQ908972	1	Johnson et al. 2006a
	Haplotype GA2	Indet	Cytb	AY987263	1	Lerner and Mindell 2005
	haplotype GA14	South Africa	Cytb	EU496414	1	Arshad et al. 2009
	haplotype GA1	Namibia	Cytb	EU496401	31	
	haplotype GA2	Namibia	Cytb	EU496402	18	
	haplotype GA3	Namibia	Cytb	EU496403	10	
	haplotype GA4	Namibia	Cytb	EU496404	3	
	haplotype GA5	Namibia	Cytb	EU496405	2	
	haplotype GA6	Namibia	Cytb	EU496406	2	

	haplotype GA7	Namibia	Cytb	EU496407	2	
	haplotype GA8	Namibia	Cytb	EU496408	1	
	haplotype GA9	Namibia	Cytb	EU496409	1	
	haplotype GA10	Namibia	Cytb	EU496410	1	
	haplotype GA11	Namibia	Cytb	EU496411	1	
	haplotype GA12	Namibia	Cytb	EU496412	1	
	haplotype GA13	Namibia	Cytb	EU496413	1	
Gymnogyps californianus	Haplotype H18	USA	D-loop	KX379736	1	D’Elia et al. 2016
	Haplotype H17	USA	D-loop	KX379735	1	
	Haplotype H16	USA	D-loop	KX379734	1	
	Haplotype H15	USA	D-loop	KX379733	1	
	Haplotype H14	USA	D-loop	KX379732	1	
	Haplotype H13	USA	D-loop	KX379731	1	
	Haplotype H12	USA	D-loop	KX379730	1	
	Haplotype H11	USA	D-loop	X379729	1	
	Haplotype H10	USA	D-loop	KX379728	1	

Haplotype H9	USA	D-loop	KX379727	1
Haplotype H8	USA	D-loop	KX379726	3
Haplotype H7	USA	D-loop	KX379725	9
Haplotype H6	USA	D-loop	KX379724	8
Haplotype H5	USA	D-loop	KX379723	3
Haplotype H4	USA	D-loop	KX379722	13
Haplotype H3	USA	D-loop	KX379721	1
Haplotype H2	USA	D-loop	KX379720	1
Haplotype H1	USA	D-loop	KX379719	20

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A regional analysis of habitat selection identifies conservation priority areas for the Andean condor

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Abstract

Mobile species face an array of human threats across political boundaries, and their protection relies on identifying and prioritizing areas for conservation. Large avian scavengers are one of the widest ranging and most threatened species globally, and efforts to preserve them have come to the forefront of wildlife management. Vultures require access to functionally distinct habitats for roosting, foraging and flying, yet behavior-specific habitat modelling has been overlooked in management planning. Herein, we developed a spatial prioritization model for the threatened Andean condor (*Vultur gryphus*) that integrates activity-specific habitat selection across heterogeneous landscapes. We tracked 35 individuals across two regions of Argentina and Chile differing in topography and vegetation composition, and analyzed how landscape covariates influence where condors roost, forage and fly, while accounting for individual differences. We found that individuals responded differently to environmental covariates during each behavior, and identified regional differences for some covariates dependent on behavioral state. We also found important individual differences in habitat selection between birds inhabiting each region. We combined these results into an ensemble spatial prioritization model, and found that most areas of high priority for Andean condor conservation are not under protection. The strategic implementation of conservation measures in these priority areas could have important implications for the recovery of this species. Our study illustrates the value of integrating behavior-specific habitat analyses into spatial conservation planning, and points to opportunities for effective management of threatened vultures.

Keywords

South America, vultures, scavenger conservation, functional habitat, Individual variation, spatial conservation planning.

Introduction

Highly mobile species can be particularly sensitive to anthropogenic threats as an individual organism can span a range of environmental conditions and human boundaries (Nandintsetseg et al., 2019). For mobile species, then, conservation challenges and opportunities are spatially-linked across broad geographic regions, and traditional site-level management actions are insufficient for their protection (Runge et al., 2014). A number of landscape-level conservation measures have been proposed in replacement, such as establishing networks of protected areas (Runge et al., 2016), increasing landscape permeability and connectivity (Nandintsetseg et al., 2019), and developing temporally and spatially dynamic management actions (Reynolds et al., 2017). The success of these conservation efforts relies on identifying critical areas for the focal species (Runge et al., 2014). In particular, identifying the functional value of habitats can lead to improved conservation of mobile and migratory species (Sawyer and Kauffman, 2011). Yet, the importance of recognizing and integrating habitats with different functional value into landscape-level management planning remains overlooked (Frans et al., 2018).

While conservation efforts take place at the population level, individuals can exhibit markedly different habitat-selection patterns (Merrick and Koprowski, 2017). Inter-individual variability in habitat selection not only can arise between sexes (van Toor et al., 2011) and ages (Stillman et al., 2019), but also due to varying personalities within demographic groups (Montgomery et al., 2018). Some individuals outperform others in certain environmental conditions, and conserving behavioral differences within populations can be critical for the persistence of species under environmental changes (Merrick and Koprowski, 2017). Furthermore, individuals can exhibit high variability in habitat selection in different times. An individual can select the same area differently between years (Nandintsetseg et al., 2019), seasons (Osipova et al., 2019), and even within days. In particular, the daily habitat requirements of many species are defined by features that are spatially segregated (Law and Dickman, 1998), forcing individuals to travel on a daily basis; for example, an animal's use of feeding grounds and waterholes (Valls-Fox et al., 2018) or breeding sites (Frans et al., 2018). Maintaining landscape heterogeneity and complexity has been proposed as a way to account and manage for inter- and intra-individual differences in habitat selection (Merrick and Koprowski, 2017). Yet, habitat selection can vary with environmental context, complicating generalizations across areas (William et al., 2018). Understanding how habitat selection vary across individuals within populations is relevant for effective management (Berger-Tal et al., 2016). Yet, these analyses were unfeasible until recent technological and analytical advances in the field of movement ecology, which are now opening avenues for the conservation of highly mobile species in anthropogenic landscapes (Alarcón and Lambertucci, 2018).

Large avian scavengers are among the widest ranging and most threatened species globally (Buechley and Şekercioğlu, 2016). Causes of vulture declines include human-derived contaminants, persecution, habitat destruction, and decreasing food availability (Buechley and Şekercioğlu, 2016). Vultures are the focus of intensive conservation efforts due to these declines and to the irreplaceable ecosystem services that they provide (Botha et al., 2017). Management for the conservation of vultures often involves approaches like augmented feeding (so-called "vulture restaurants"; Cortés-Avizanda et al. 2016), increasing the accessibility and safety of carrion resources (Botha et al., 2017), and conserving populations of wild ungulates (Santangeli et al., 2018) and their predators (Cortés-avizanda et al., 2015). Vultures have also benefited from networks of protected areas, either existing (Ogada et al., 2016) or created specifically for their conservation (Arrondo et al., 2018). Site-based interventions, however, have had limited success to conserve vultures, partially because of behavior-specific habitat requirements not being captured by these networks of reserves (Morales-Reyes et al., 2016). Identifying areas of high conservation value for threatened vultures requires habitat modelling at the large landscape scale while accounting for activity-specific habitat selection.

The Andean condor (*Vultur gryhus*) is a near-threatened species distributed across the Andes (Houston, 1994). Similar to other vultures, Andean condors face unintentional poisoning (Wiemeyer et al. 2017, Plaza et al. 2019), persecution (Cailly Arnulphi et al., 2017) and habitat loss (Lambertucci, 2007). Although highly threatened in their northern range, larger populations in southern South America range widely in search for carrion from domestic and wild ungulates (Lambertucci et al., 2009; Perrig et al., 2017). In general, Andean condors have extensive home ranges, where they soar in areas featuring thermal and orographic uplift, feed in open habitats with high ungulate density, and roost and nest in cliffs and mountains (Houston, 1994; Lambertucci et al., 2014). Andean condor habitat selection across heterogeneous landscapes remains unexplored, limiting the development of transboundary conservation efforts.

Herein, we developed an ecologically-based spatial prioritization model for Andean condors across ~30% of the species' distributional range. To this end, we tracked with GPS devices 35 individuals in southern South America, and quantified how habitat covariates drive Andean condor foraging, roosting and flying behaviors across 2 regions encompassing heterogeneous landscapes. From these analyses, we built a prioritization model to guide future planning efforts aimed at protecting this ecologically important species of conservation concern.

Methods

Study area and field methods

Our study area encompassed Andean condor distribution in Argentina and Chile (Birdlife International 2016) between ~ -26° and -46° S (~ 2000 km from north to south). We analyzed Andean condor space use in two separate regions: Cuyo and Patagonia (Fig. 1). The geography of both areas is dominated by the high Andes, which reaches altitudes close to 7000 meters in Cuyo. Cuyo region encompasses temperate climate west of the Andes, with Mediterranean-type shrubland and woodland ecosystems, and arid and semi-arid climate with Puna and Monte ecosystems to the east (Veblen et al., 2015). Patagonia is dominated by dense forests in the western range, and grassland-steppes to the east (Veblen et al., 2015). Both regions are sparsely populated, yet include large urban areas including Santiago in Chile and Mendoza in Argentina.

We trapped Andean condors in Argentina with baited cannon net traps. In Cuyo, we captured and tagged 12 adult Andean condors at San Guillermo National Park, San Juan province (29°25’S - 69°15’W) during 2015-2017. We tagged birds with 70 or 50 g solar Argos/GPS PTT tags (Microwave Telemetry Inc.). In Patagonia, we captured 23 adult birds during 2011-2013 near Bariloche city, Rio Negro province (41°09’S - 71°18’W). We tagged 10 individuals with 50 g. solar Argos/GPS PTT tags and 13 with 100 g Solar GPS–GSM CTT-1070-1100 tags (CellTrack Tech.; see Lambertucci et al. 2014 for details). We programmed PTT units to transmit every 60 minutes, and 15 minutes for CTT tags (minimum interval allowed by these units) from dawn to dusk daily.

Animal locations and behavioral states

Condor locations were processed in R (R Core Team 2018) using the *move* (version 1.3-1; Kranstauber and Smolla 2015) and *maptools* packages (version 0.9-5; Bivand and Lewin-Koh, 2019). We retained GPS locations with horizontal dilution of precision (HDOP) lower than 10 to increase spatial accuracy. Because we were interested only in spatial differences in habitat selection, to avoid pseudo replication and increase computational efficiency, we only considered one used location per 500 m^2 grid cell (our resolution for habitat covariate) for each individual.

We assigned vetted locations (Appendix, Table S1) to one of three behavioral states: roosting, foraging, and flying. We assumed individuals were roosting when point locations were recorded at night (defined as two hours after sunset to sunrise) and had zero velocity. Because we tracked adults, roosting also include nesting locations. Andean condors require open areas to descend to feed (Houston, 1994), and forage predominantly at midday (Alarcón et al., 2017). Thus, we assigned point locations as foraging when recorded 5-8 hours after sunrise with zero velocity, and away from roosting locations (i.e. found outside a 5 km-buffer surrounding roosting locations, which represents the 25 percentile of distance travelled by condors in an hour). We also eliminated locations in Patagonia that were surrounded (1.5 km^2) by forest based on MODIS land cover type since Andean condors are not able to feed in this habitat type (Houston, 1994). Thus, "foraging" includes data in which feeding was likely the birds' main purpose, but also likely includes instances of individuals perched or resting on the ground. We captured flying via condor paths that included at least three consecutive daytime locations with velocity higher than 3 m/s (Appendix, figure S1) at 1-hour intervals.

We assessed how individuals' foraging, roosting and flying behaviors differed in the selection of landscape covariates within their home range (Johnson's third order selection; Johnson, 1980) via a matched case-control design. Specifically, each used roosting and foraging location was matched with 9 random locations within a 64 km-buffer (the median daily distance travelled by condors) that defined the available landscape. For flying, we created nine matched available paths of identical topology to the utilized path, which were randomly rotated between 0 - 360° and shifted a random distance in x and y between 0 and 43 km, the 95 percentile of the distance travelled by hour across individuals.

Landscape covariates

Topographic measures included elevation (m), slope (degrees) and terrain ruggedness derived from a Digital Elevation Model (DEM) extracted using the *raster* package in R (version 2.8-19; Hijmans, 2019). Primary production was inferred from Dynamic Habitat Indices (DHI) based on the normalized difference vegetation index (NDVI) for the year 2015 (Radeloff et al., 2019), used here as a proxy for carcass availability. DHI captures the seasonal nature of NDVI by providing annual cumulative greenness (productivity capacity of the landscape during a year), annual minimum productivity (lowest point of productivity in the year), and seasonal variation in productivity (Radeloff et al., 2019). Finally, we included habitat types from the land cover MODIS product (Friedl and Sulla-Menashe, 2015) as single variables characterized as a proportion of the cover type in an area of 1.5 km surrounding each cell. We removed croplands and wetlands since they lacked sufficient coverage across the study area to be informative (prevalence < 0.2).

We described soaring conditions with surface temperature and wind power (W/m^2). Because thermals emerge over land heated by solar radiation (Bohrer et al., 2012), we used land surface temperature (LST) as proxy for the presence of thermal uplift, which was obtained from a global climatology dataset on LST derived from MOD11A1 product based on years 2003-2014 (Bechtel and Benjamin, 2015). We characterized high-wind areas for potential orographic uplift using a wind power density product (https://globalwindatlas.info/).

Covariates describing land-use changes driven by human activities included a Human Footprint Index (Sanderson et al., 2002), and distance to buildup areas and paved highways. Distance to buildup (i.e., urban) areas was calculated using the MODIS land cover product, and distance to paved highways from Argentina and Chile road networks (Appendix, table S1) using QGIS (version 2.18.23; QGIS Development Team 2019).

We resampled or averaged covariates (Appendix, table S1) to a consistent 500 m grid cell resolution in R (R Core Team 2018). We extracted cell values for each predictor at used and available roosting and foraging locations, and averaged them along used and available flying paths. We evaluated collinearity between explanatory variables using a Pearson correlation coefficient based on the common threshold |r| < 0.7 using the *usdm* R package (version 1.1-18; Naimi et al. 2014). We also calculated variance inflation factor (VIF) of all the remaining covariates and confirmed that none of the retained covariates had a VIF < 10 (Harrison et al., 2018). We standardized variables to zero mean and unit variance to improve model convergence and allow direct comparisons among coefficients (i.e. standardized effect sizes; Harrison et al., 2018).

Statistical analyses

We compared each condor use location for roosting and foraging, and path for flying, to its matching available set using point and path resource selection functions, respectively. We analyzed our matched case-control design using Poisson models with mixed effects following Muff et al. (2019). To ensure robust estimates of variance, we only considered individuals with > 5 used locations or paths (Harrison et al., 2018). For each behavior, we developed a global model that incorporated all standardized, non-correlated landscape covariates as fixed effects, and as random slopes representing population and individual-level responses, respectively. Global models for each behavior were simplified by eliminating random slopes with small variances (<0.1), which we deemed too small to reflect significant differences in selection among individuals. Models were fitted using the *glmmTMB* package in R (version 2.3; Brooks et al. 2017).

The suitability of the final models was evaluated using k-fold cross validation, an out-of-sample technique that assesses how well the model predicts new data. Specifically, we used five folds cross-validation with 100 repetitions as explained by Fortin et al. (2009). The population-level responses to changes in each landscape predictor were evaluated graphically by first calculating how Andean condors altered their probability of use as the predictor changed in availability, while averaging over the range of values of all other covariates in the model (following methods outline in section 5.1, (Avgar et al., 2017). We then averaged these estimates using the gam function of *mgcv* R package (version 1.8-24; Wood et al. 2016) with smoothing factors < 5 aimed at reducing over-parameterization. We evaluated individual variation in the responses to landscape covariates by plotting each individual response (i.e. standardized effect size for each individual calculated by adding the individual random slope to the fixed effect) against the mean availability experienced by each individual to the predictor in question for that behavior.

Spatial prioritization

To map Andean condor habitat suitability for each behavior (roosting, foraging and flying), we extrapolated the fixed selection coefficient of the final model plus the mean of the individual coefficients within each region. We compared the correlation between the three models via Spearman rank correlation using the *raster* package in R. We used these models of relative probability of use to inform a spatial conservation prioritization analysis done using the Zonation software (Lehtomäki and Moilanen, 2013). We used the core-area marginal loss rule to remove grid cells with features (i.e., spatial predictions of probability of use for roosting, foraging and flying) weighted equally (Moilanen et al., 2005). We compared the results of this model to existing protected areas larger than 100 km^2 (area assigned by UNEP-WCMC) under IUCN management categories I and II (representing reserves strictly implemented), and to all reserves under IUCN categories (I-VI) and Biosphere Reserves (IUCN and UNEP-WCMC, 2016).

Results

Satellite tracking

We collected 228,259 GPS locations for 35 individuals that we filtered to our behavioral states: 4915 roosting locations across 34 individuals (3185 and 1730 from Cuyo and Patagonia, respectively), 1903 foraging locations across 29 individuals (820 and 1083), and 1216 paths from 31 birds (951 and 265) available for analyses (Appendix, table S2).

Relative probability of use

Our out-of-sample evaluation indicated high predictive performance of the models developed. For foraging, our model had correlation (mean [sd]) values of 0.97 (0.02) for observed and -0.01 (0.37) for random locations, for roosting 0.99 (0.01) and 0.04 (0.31), and for flying 0.97 (0.02) and 0.03 (0.32). Important covariates for Andean condor relative roosting probability were altitude and roughness; for foraging vegetation seasonality, grassland and shrubland cover, and surface temperature; and for flying vegetation productivity, grassland and shrubland cover, and surface temperature (Table 1).

Topography

We found a positive relationship between altitude and the probability of Andean Condors foraging, roosting and flying (Fig. 2). Specifically, most birds selected higher altitudes while flying, and while foraging and roosting in Patagonia but not in Cuyo (Fig. 3). We excluded slope from all models because it was highly correlated with surface roughness. Andean condors showed higher probability of flying and roosting, and lower probability of foraging as roughness increased (Fig. 2). Further, individuals selected consistently for roughness when flying and foraging but showed inter-individual variation in their selection while roosting. In particular, condors showed a stronger relative selection towards roughness when roosting in Cuyo than in Patagonia (Fig. 3).

Vegetation productivity

When foraging and roosting, the probability of use of areas decreased with increasing levels of vegetation productivity, and was slightly steady when flying (Fig. 2). We removed the random slope for productivity while foraging and flying due to insignificant (< 0.1) individual variances (Fig. 3). For roosting, we found areas of lower productivity in Cuyo than Patagonia, and inter-individual variability in selection coefficients within the first region (Fig. 3). We did not model vegetation seasonality while flying due to negative correlation with shrublands. In areas with increasing vegetation seasonality, condors showed a lower probability of foraging and roosting (Fig. 2), with individuals being relatively consistent in their response (Fig. 3).

Habitat type

We excluded non-vegetated areas from all models due to high correlation with altitude. Condors' relative probability of foraging and roosting was steady as the cover of grasslands increased in the landscape whereas the probability of condors flying slightly increased (Fig. 2). Andean condors showed higher availability (conditional around used locations, herein availability) and slightly more positive selection of grasslands while roosting and flying in Patagonia than in Cuyo (Fig. 3), while individual differences were minimal while foraging (variance < 0.1, Fig. 3). In areas with high shrubland cover, the probability of condors foraging slightly increased while the probability of roosting and flying decreased (Fig. 2). Between regions, Andean condors showed a stronger selection for shrublands while flying and foraging in Patagonia than in Cuyo (Fig. 3).

Soaring conditions

Andean condors showed higher probability of roosting and flying, and decreasing probability of foraging in windy areas (Fig. 2), with only slight differences in individual responses while flying (Fig. 3). We excluded surface temperature from our analysis of roosting due to high correlation with altitude. Andean condors showed reduced probability of flying and foraging in areas with high surface temperature (Fig. 2). Condors in Cuyo experienced a wider range of surface temperatures than in Patagonia although we only found notable regional differences in their selection while flying (Fig. 3). In particular, birds in Patagonia selected against, and birds in Cuyo for, areas of high surface temperature while flying (Fig. 3).

Human influence

Andean condors showed higher probability of roosting, foraging, and flying further from urban areas (Fig. 2). However, birds showed little or slightly negative selection to the variable, especially in Patagonia where condors flew and roosted closer to urban areas compared to most birds in Cuyo (Fig. 3). Additionally, Andean condors showed higher probability of foraging further, and of flying and roosting at intermediate, distances from highways (Fig. 2). Specifically, most individuals selected to roost far from highways, and condors in Cuyo selected to forage and fly further from highways than most birds in Patagonia (Fig. 3). Finally, the probability of condors roosting, foraging and flying decreased in areas with high human footprint (Fig. 2). In particular, availability (< 20%) and selection of areas with high human footprint was slightly higher in Patagonia than in Cuyo (Fig. 3).

Spatial prioritization

We found spatial differences in habitat suitability for roosting, foraging and flying behaviors (Fig. 4). The correlation between the spatial predictions of the foraging and roosting models was <0.1, foraging and flying 0.3 and roosting and flying 0.5. We found highest priority areas for Andean condor conservation – where there is overlapping areas of importance for roosting, foraging and flying –along the Andes in Cuyo and concentrated in the eastern side of Patagonia (Fig. 4). Performance curves of the zonation model indicated that conservation actions in the identified priority areas would be most effective for the protection of sites of higher probability of use for roosting than foraging or flying (Appendix, Fig. A2). We also found that most protected areas are not located in areas of high conservation priority (Fig. 4). From the resulting prioritization map, 30% of cells had a rank value higher than 0.7, of which 7 % overlapped with currently protected areas under IUCN categories I and II, and 13% overlapped with all reserves considered. Additionally, 18 of the 88 protected areas analyzed had an average rank value > 0.7, indicating that they are located in areas of relative importance for Andean condors.

Discussion

There is an increasing tendency towards a mechanistic understanding of individual animals during different behavioral states, but a lack of integration of behavior-specific information into areas of spatial priorities (Frans et al., 2018). We found regional and behavioral differences in Andean condor habitat selection that resulted in distinct maps of probability of use for roosting, foraging and flying. Specifically, maps of roosting and flying had the greatest similarity, probably because mountainous areas provide both cliffs and good flying conditions. Areas of high probability for feeding, on the other hand, occurred at lower elevations and mostly on farmlands. Further, the ensemble spatial prioritization map showed an important mismatch between priority areas for Andean condor conservation and currently protected areas. Our results, then, reinforce the need of behavior-specific analyses of habitat selection for vulture conservation planning (Elia et al., 2015), and indicate opportunities for their integration via spatial prioritization approaches to maximize management efforts.

Habitat selection

We found that condors selected environmental covariates differently during foraging, flying and roosting as expected based on general knowledge of condor ecology. For example, our results indicate that condors select against rugged landscapes to forage, yet select these areas for roosting and flight. Importantly, behavioral state revealed regional differences in habitat selection. Condors showed stronger selection towards altitude while roosting in Patagonia than in Cuyo, whereas regional differences were less important while foraging or flying. This can be explained by high altitudes in Cuyo (>3000 m) associated with inclement weather conditions for roosting, while in Patagonia most roosts and nests are located in mountainous areas of <3000 m contiguous to lowlands (Lambertucci and Ruggiero, 2013). Contrary to our expectations, though, individual selection towards many environmental covariates was largely consistent between behaviors despite regional differences in availability.

Regional differences in Andean condor habitat selection did not fully capture individual differences. We observed individual variability in habitat selection for most environmental covariates, and differences among individuals inhabiting the same region in both selection coefficients and mean habitat availability. These individual differences in habitat selection can result from internal (e.g. sex, breeding season) or external factors (e.g. intra and inter-specific interactions; García-Jiménez et al., 2018). In Patagonia – where foraging, and breeding and roosting areas are spatially segregated – individual condors showed high variability in selection coefficients for surface temperature while flying, and for altitude while roosting. This might be due to their nests being located at different distances from foraging grounds (Lambertucci et al., 2018), which may result in sex-specific fitness differences between birds (Gangoso et al., 2016). Such individuality can be particularly important for vultures due to their social nature: vultures exchange information of foraging opportunities within mixed-age groups while flying and at communal roosts (Harel et al. 2017). Thus, individual differences in habitat selection could lead to maladaptive behaviors (Lambertucci et al., 2018). While it was not the focus of our work, futures studies should seek to understand causes and consequences of individuality in habitat selection of Andean condors.

Limitations

Our models of habitat selection were derived from macro-scale environmental characteristics because fine-scale data are rarely available. Thus, our results do not account for site-specific effects that impact Andean condor habitat selection, like geomorphological characteristics of cliffs (Lambertucci and Ruggiero, 2013), and presence of meadows (Pérez-García et al., 2018). Notably, carrion availability is challenging to model at this large, and static, scale of analysis since it is determined by the abundance of wild and domestic ungulates along with their mortality rate, which may vary in response to environmental conditions, management practices, competitors and accessibility (Santangeli et al., 2018). We used vegetation productivity and seasonality as proxies for carrion availability and predictability. Thus, local variations in ungulate density are probably masked in our analyses by differences in vegetation productivity between habitat types (i.e., forest versus grasslands). Likewise, spatial distribution of uplift potential remains unavailable in open source products at significant spatial resolutions (Scacco et al., 2019). As information becomes available, studies should improve the resolution of our spatial prioritization model.

Multi-scale approaches of species-habitat modelling have been shown to substantially improve the realism and predictive power of habitat selection models (McGarigal et al., 2016). Thus, future studies should explore scale dependency in habitat selection between Andean condors' behavioral states and environmental contexts. On the other hand, inferences of behavior from path geometry could make more specific distinctions of behavior and resource selection than our categorical approach, e.g. by differentiating commuting versus foraging flight (Alarcón and Lambertucci, 2018). These methods are challenging to apply to large telemetry datasets over broad geographic regions, and with data of low temporal resolution (we collected 1 location per hour for most individuals); yet, they might exploit the behavioral information inherent in individual movement data more fully (Gurarie et al., 2016). Thus, we recommend caution in interpreting our results, and our maps should serve as starting points within an adaptive framework for transboundary conservation planning.

Conservation implications

Our spatial prioritization model integrates areas of relevancy for condor roosting, foraging and flying activities, thus targeting the long-term preservation of the species at a relevant spatial scale. However, environmental contaminants are the most serious threat to avian scavengers, including Andean condors (Plaza et al. 2019). Thus, while condors are highly susceptible to human disturbance while roosting and to shooting while flying (Lambertucci, 2007), conservation actions should first focus on areas identified as having high probability of use for foraging. These areas occurred mostly in lowlands and had the lowest representation in currently protected areas, supporting previous findings based on movement patterns of the species (Lambertucci et al., 2014).

We ignored whether anthropogenic impacts to Andean condor populations are spatially variable. Monadjem et al. (2018) showed opposite demographic trends between white-backed vultures (*Gyps africanus*) inhabiting two adjacent areas with different survival rates due to risk of illegal poisoning. Our study area might not be exempt to regional differences in condor survival, as two of the 12 birds tracked in Cuyo were found dead and other two GPS tags unexpectedly stopped transmitting, whereas no mortality events were registered for condors tracked in Patagonia. We believe that a key next step for the protection of Andean condors is to understand how threats distribute in space to improve the activity-specific models we developed.

We found that a few reserves are already located in areas of high priority for Andean condors, and thus should have an active role in protecting the species. Primarily, these reserves should protect populations of wild ungulates and their predators to provide reliable sources of carrion (Cortés-avizanda et al., 2015; Perrig et al., 2017). Additionally, they should minimize human disturbance around potential foraging, roosting and nesting locations (Herrmann et al. 2010). Our model also allows the assessment of areas for potential protection. Indeed, focusing spatial prioritization on iconic, umbrella and threatened species, as the Andean condor, can efficiently guide national initiatives for the conservation of biodiversity (Runge et al., 2019). This is especially relevant for South American countries that are far from reaching international commitments on land protection (Baldi et al., 2018).

Protected areas alone will not efficiently conserve mobile species (Margalida et al., 2016). An immediate challenge is to ensure healthy ecosystems within unprotected farmlands via targeting actions in the priority areas identified, such as northeast Patagonia and delimitated areas around the Andes in Cuyo. These measures should involve educational programs (Cailly Arnulphi et al., 2017), improved agro-grazing practices, and landscape planning of human development (e.g., wind farms) conducted in a transboundary manner (Botha et al., 2017), and be guided by evidence-based data as the model developed herein.

Although mostly used in multi-species analyses (e.g. Santangeli et al. 2019), spatial prioritization approaches represent an important tool for species conservation planning at broad landscapes. Here, we used this approach in an integrative analysis that identifies areas of importance for Andean condor conservation through 30% of the species' distributional range. International efforts should seek to add and combine information on condor habitat selection to extend and improve our model. The success of preserving mobile species in anthropogenic landscapes relies on making efficient use of conservation resources, especially in developing countries. We hope our work will help to guide efforts for transboundary management of Andean condors in South America (Lambertucci et al., 2014), and wide ranging and mobile species elsewhere.

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Table 1. Standardized selection coefficients (mean[standard error]) reflecting responses to landscape covariates within the home range of Andean condors tracked in Cuyo and Patagonia regions of South America during roosting, foraging and flying behaviors. Models were mixed-effects Poisson process under a matched case-control design.

	Roosting	Foraging	Flying
Altitude	**1.23 (0.38)**	0.36 (0.33)	0.59 (0.51)
Roughness	**1.50 (0.10)**	0.09 (0.11)	0.54 (0.10)
Veg. productivity	-0.11 (0.19)	0.03 (0.05)	**0.95 (0.11)**
Veg. seasonality	-0.29 (0.09)	**-0.64 (0.13)**	
Grasslands	0.29 (0.07)	**0.52 (0.04)**	**0.71 (0.14)**
Shrublands	0.35 (0.09)	**0.64 (0.09)**	**1.03 (0.22)**
Wind power	0.04 (0.02)	0.05 (0.03)	0.02 (0.10)
Surface Temp.		**-1.00 (0.22)**	**-1.71 (0.47)**
Distance to buildup	-0.47 (0.12)	0.15 (0.04)	-0.23 (0.13)
Distance to highways	0.17 (0.09)	-0.07 (0.11)	-0.07 (0.12)
Human Footprint	-0.02 (0.09)	-0.09 (0.04)	0.10 (0.10)

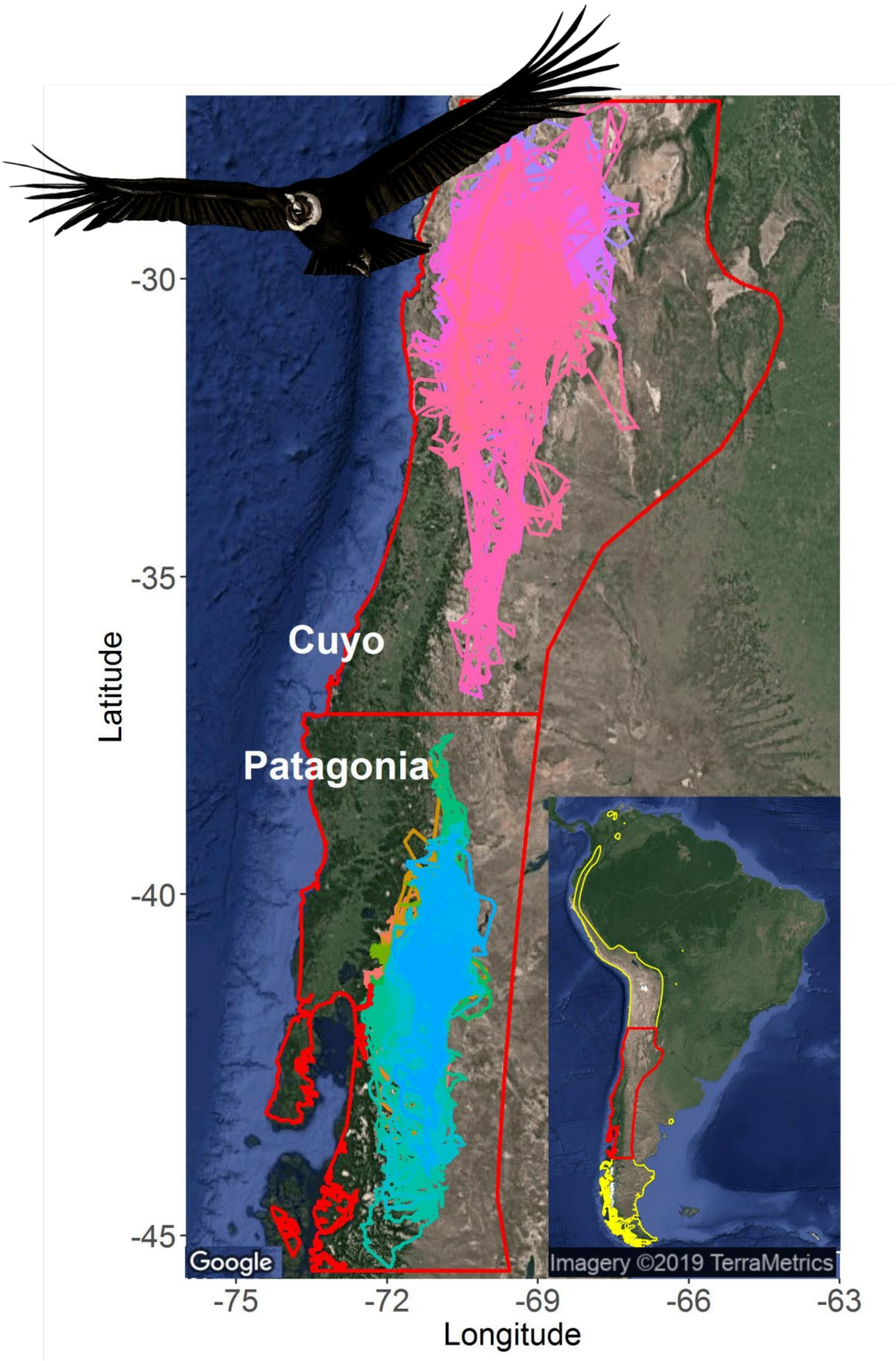

Figure 1. Map of study area in South America showing the movement pattern of adult Andean condors analyzed within our two study regions, Cuyo in the north and Patagonia in the south. Different colors represent movements for different individuals. Yellow line indicate Andean condor distributional range, and red line our study area.

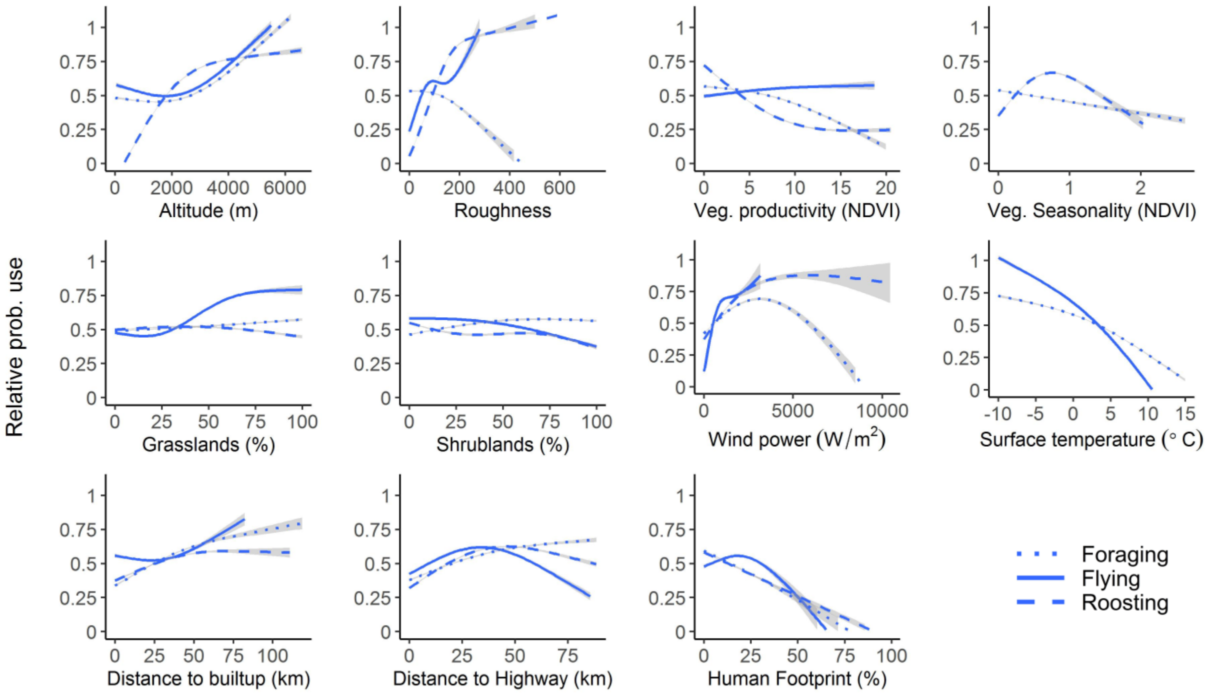

Figure 2. Estimated relative probability of use by Andean condors during roosting (dashed), flying (solid), and foraging (dotted) behaviors for each landscape covariate while keeping other covariates at their observed values. Results are from mixed-effects Poisson process models under a matched case-control design. Lines are missing when the predictor was not in the behavior model due to correlation with other covariates.

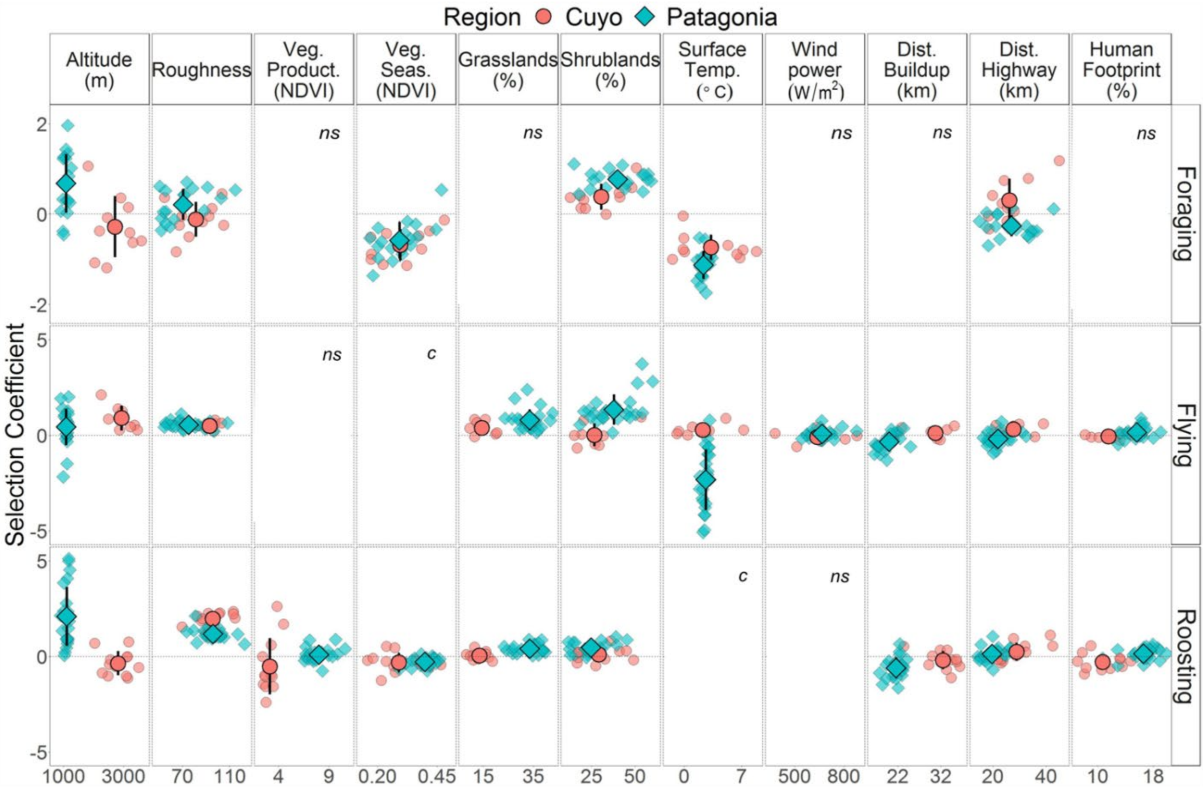

Figure 3. Individual responses to landscape covariates in models assessing habitat selection within the home range of Andean condors during foraging, roosting, and flying in the Cuyo and Patagonia regions of South America. Results are from mixed-effects Poisson process models under a matched case-control design. Positive values represent selection for, and negative values selection against each predictor. Points with black outlines represent regional means, with lines representing corresponding standard deviations. Panels labeled with *C* indicate covariates that were not included due to > 0.7 correlation with other model covariates. Panels labeled with *ns* did not include random slopes for that predictor in the final model due to insignificant individual variance (< 0.1). Note that foraging covariates are displayed on a different y-scale compared to those for flying and roosting.

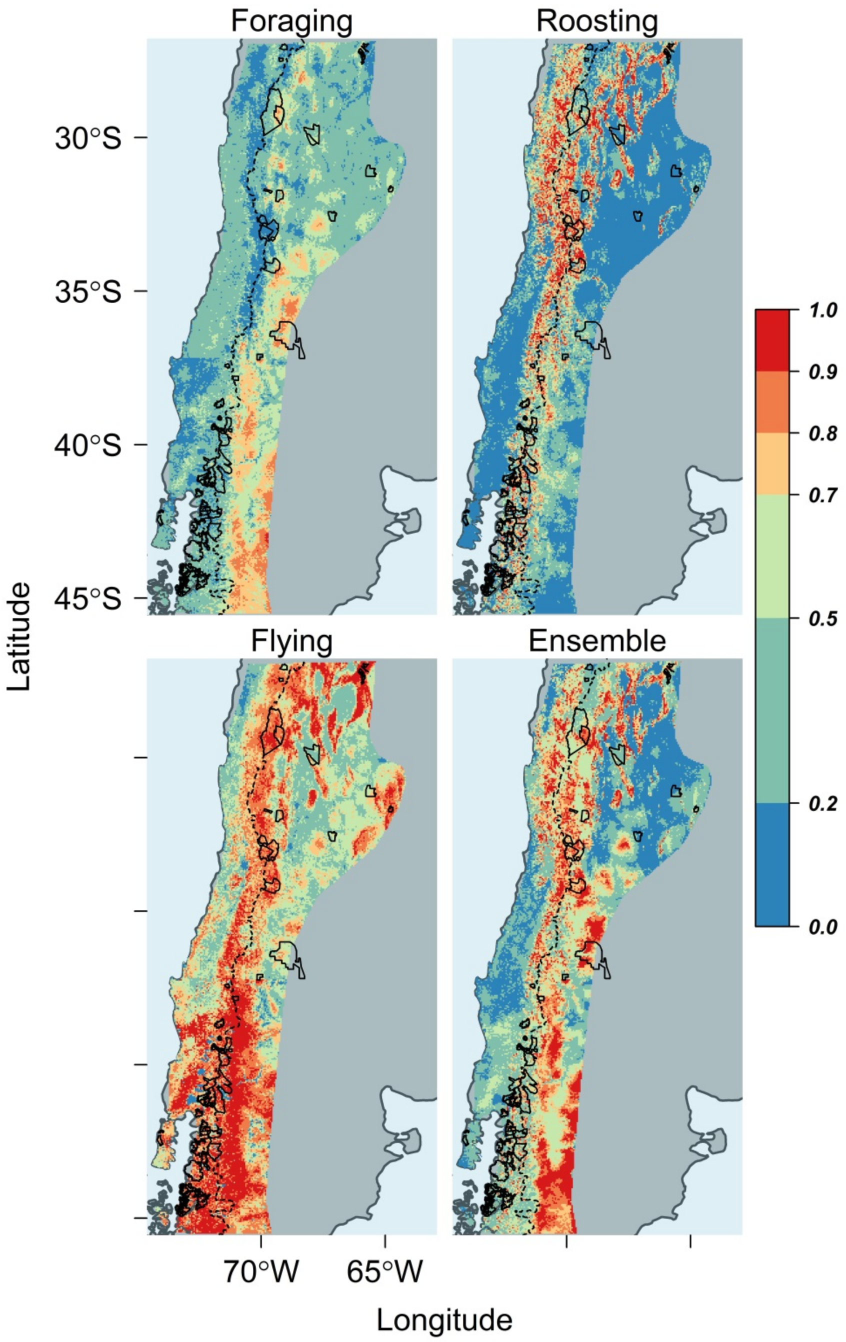

Figure 4. Estimated predictions of relative habitat use by Andean condors in southern South America while foraging, roosting, and flying. Bottom, right panel represent results for the spatial prioritization model using Zonation based on combined spatial predictions of relative use during foraging, roosting, and flying behaviors. The black lines represent the contour of protected areas under IUCN category I-II (IUCN and UNEP-WCMC 2016), whereas the dashed line represents the international boundary between Argentina and Chile.

Supplementary material

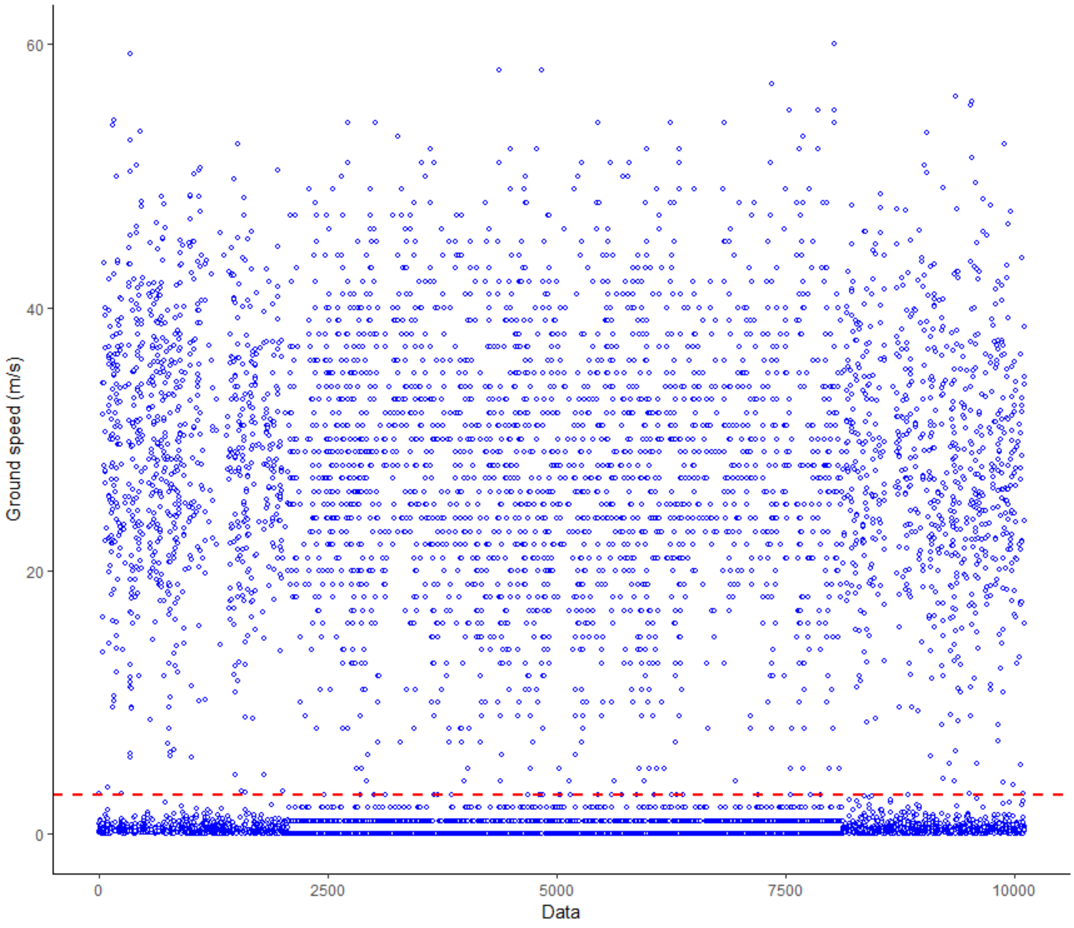

Figure S1. Ground speed for a subset of each tracking locations obtained. The red line at 3m/s indicates the threshold used to split the dataset on Andean condor flying behavior.

Table S1. Remote-sensed environmental variables used as landscape covariates of habitat suitability models for Andean condors in southern South America.

Category	Name	Definition	Accessed	Spatial resolution
Topography	Elevation	Digital elevation model (DEM) for each cell	Shutter Radar Topographic Mission (Farr et al., 2007)	90m
	Slope	Rate of elevation change among 8 surrounding cells in degrees.	Developed from DEM	
	Roughness	Mean absolute differences in elevation between the values of a cell and the mean value of its 8 surrounding cells.	Developed from DEM	
Vegetation productivity and seasonality	Cumulative, minimum, and variation DHI	Annual cumulative, minimum and coefficient of variation in productivity based on NDVI for the year 2015	http://silvis.forest.wisc.edu/data (Radeloff et al., 2019)	1 km
Vegetation	Grassland (%)	Dominated by herbaceous annuals	https://earthdata.nasa.gov/	500m

characteristics			MODIS product	
	Shrublands (%)	Dominated by woody perennials (1-2 m height) or 10-30% tree cover (> 2m height).	(Friedl and Sulla-Menashe, 2015)	
	Non-vegetated (%)	At least 60% of cover is barren or permanent snow and ice.		
Soaring conditions	Surface Temperature	Climatology of annual mean land surface temperature derived by Boher et al. (2012).	http://icdc.cen.uni-hamburg.de/1/daten/land/modis-lst-annualcycle.html	1km
	Wind power density (W/m^2)	Wind power potential from atmospheric re-analysis data and high-resolution topographic features developed by the Wind Energy Department of the Technical University of Denmark in partnership with the World Bank (data provided by Vortex, with funding provided by the Energy Sector Management Assistance Program).	Global Wind Atlas v2.2 accessed at http://globalwindatlas.info	1km
Human	Distance to	Euclidean distance (km) from areas with at	MODIS	500m

influence	buildup areas	least 30% of impervious surface based on MODIS land cover data.	(Friedl and Sulla-Menashe, 2015)	
	Distance to roads	Euclidean distance (km) from roads from Chile and Argentina countries.	Instituto Geográfico Nacional, Argentina (www.ign.gob.ar) Infraestructura de Datos Espaciales, chile (https://www.ide.cl/)	1km
	Human Footprint Index (%)	Index developed by the Wildlife Conservation Society (WCS) and the Center for International Earth Science Information Network (CIESIN) for the year 2005 from nine global data layers considering population density, human land use and infrastructure (built-up areas, nighttime lights, land use and land cover) and human access (coastlines, roads, railroads and navigable rivers).	http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic (Sanderson et al., 2002)	1km

Table S2. GPS tracking data collected from 35 adult Andean condors tagged in Argentina, including capture region within Argentina as defined by this study (region), the operating period of each tag (start-end), Total (N) and thinned (thinned) dataset analyzed after defining roosting, foraging and flying paths (tracks) for each monitored individual.

				Roosting		Foraging		Tracks			
Individual	Region	Start	End	N	Thinned	N	Thinned	N	Thinned	MeanL	MaxL
9033	Patagonia	1/24/2013	2/26/2013	58	15	4	3	24	17	8	13
9041	Patagonia	1/16/2013	10/18/2017	62	8	292	46	213	75	7	14
9066	Patagonia	1/16/2013	12/3/2013	301	40	26	11	58	26	6	10
73425	Patagonia	11/4/2010	11/11/2012	49	12	20	15	86	24	5	10
73427	Patagonia	10/24/2010	1/20/2015	202	59	48	34	217	74	4	8
74584	Patagonia	10/24/2010	2/19/2013	294	29	29	16	206	20	4	8
74586	Patagonia	10/24/2010	6/12/2014	204	36	20	14	239	40	5	11
74587	Patagonia	10/30/2010	5/17/2011	53	3	7	4	48	10	4	9
74588	Patagonia	10/24/2010	10/7/2012	91	20	8	6	117	16	5	8
74589	Patagonia	10/24/2010	8/9/2013	178	48	37	25	142	38	4	8
74699	Patagonia	11/2/2010	10/3/2011	186	22	6	4	73	34	4	9

74700	Patagonia	10/30/2010	12/16/2011	97	14	12	7	124	26	5	9
74755	Patagonia	11/2/2010	7/11/2011	117	20	12	11	61	20	5	8
32204783	Patagonia	12/4/2011	9/7/2016	1013	26	299	47	594	67	7	15
32205053	Patagonia	12/4/2011	3/9/2014	336	34	86	39	189	6	6	13
32205160	Patagonia	12/6/2011	10/30/2016	786	72	404	95	557	79	7	15
32205194	Patagonia	12/6/2011	2/5/2016	267	59	506	84	189	106	7	12
32205319	Patagonia	12/6/2011	11/26/2016	365	22	116	31	346	51	8	17
32205426	Patagonia	11/30/2011	2/15/2013	103	27	483	75	219	94	7	15
32205632	Patagonia	12/4/2011	11/24/2016	913	29	81	29	523	51	7	16
32206010	Patagonia	12/4/2011	4/3/2014	60	11	23	14	151	37	8	15
32218700	Patagonia	12/6/2011	12/1/2016	1617	82	239	63	458	91	7	13
32219252	Patagonia	11/30/2011	3/25/2014	155	18	74	20	166	45	7	11
120508	Cuyo	12/9/2014	7/29/2015	96	14	4	4				
127779	Cuyo	12/9/2014	6/10/2016	1015	84	47	18	125	44	4	10
146613	Cuyo	11/21/2015	10/29/2018	1413	271	344	172	283	160	4	10
146614	Cuyo	4/2/2015	8/15/2015	198	43	23	14	51	30	5	9

146614_B	Cuyo	2/13/2017	10/27/2018	711	164	103	66	180	109	4	9
146615	Cuyo	2/13/2017	11/12/2017	345	41	31	14	57	27	4	7
146616	Cuyo	11/21/2015	1/18/2017	515	83	44	25	51	33	4	7
146617	Cuyo	11/21/2015	2/19/2018	695	139	171	82	195	95	5	11
147019	Cuyo	4/3/2015	1/13/2017	531	88	38	24	113	66	5	10
147020	Cuyo	4/4/2015	10/26/2018	1011	322	273	185	200	158	4	9
147021	Cuyo	2/13/2017	10/2/2018	673	138	142	87	216	124	5	10
74589_B	Cuyo	12/10/2014	12/29/2014	31	14	3	3	5	4	6	9

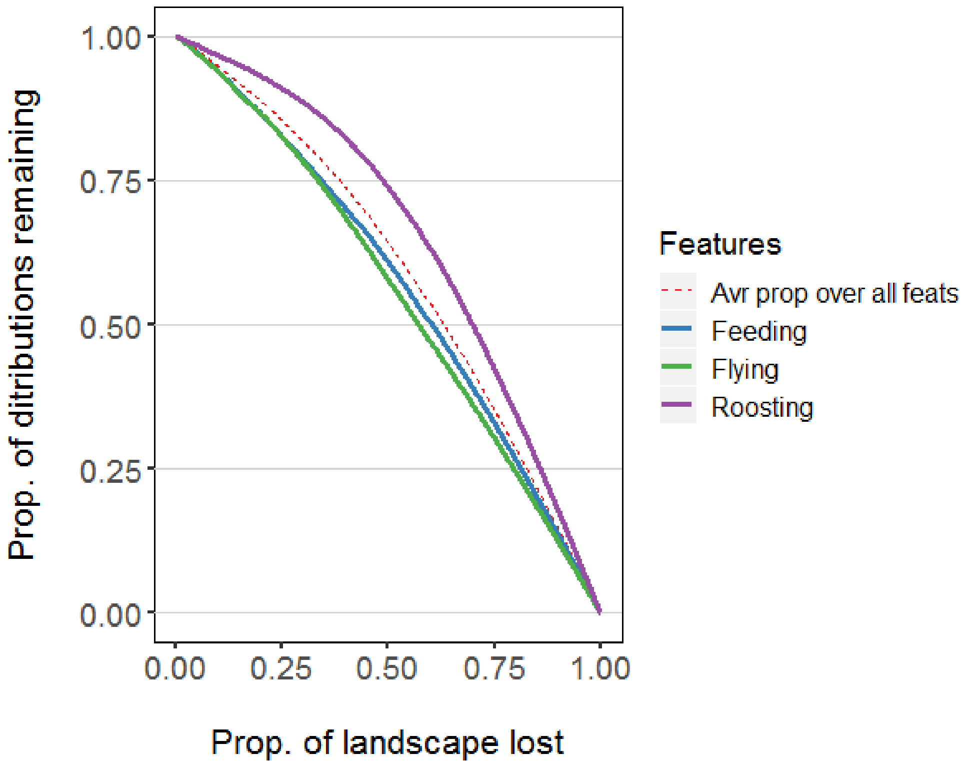

Figure S2. Results from Zonation model showing mean proportion of the areas with higher probability of use remaining in the landscape as a function of proportion of geographic area under conservation.

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Limited sexual segregation in a dimorphic avian scavenger, the Andean condor

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Abstract

Sexual segregation is widely reported among vertebrates and generally attributed to intraspecific competition. In sexually dimorphic species, larger individuals generally exclude smaller ones from resources leading to niche segregation. Prey diversity and human activities can reinforce niche segregation by increasing resource heterogeneity. Herein, we explored sexual differentiation in an avian scavenger that exhibits pronounced sexual-size dimorphism (up to 50% difference) and a highly despotic social system, the Andean condor (*Vultur gryphus*). We compared resource use between females and males across 6 discrete sites featuring a range of prey diversity via the analysis of stable isotopes. We focused on two sites that featured extremes in prey diversity: Patagonia (high diversity) and San Guillermo (low diversity), and quantified assimilated diet via stable isotopes and space use via GPS monitoring (n = 35). We found no differences in isotopic niche space or trophic segregation between sexes at any location, nor did we detect differences of individual variation between females and males. At Patagonia and San Guillermo, we observed no sex-based differences in either space use or assimilated diet. We observed equivalent home range overlap between females, males, and females to males, and the sexes used similar landscape features (low altitude and human footprint) in feeding locations. Further, large ungulates was the most important diet item for both sexes at both sites, which matched prey availability, and assimilated diet overlapped between sexes in both locations. We believe that the social foraging habits of vultures centered on information transfer to exploit unpredictable carcasses, prevents sexual differentiation in Andean condors despite divergent phenotypes and social dominance. Our results suggest that sexual segregation is largely determined by predictability of trophic resources, even for social species under strong intraspecific competition.

Keywords

Argentina, Habitat segregation, Molted feathers, Social foraging, Stable isotopes, *Vultur gryphus*.

Introduction

Competition is a central mechanism driving the natural history of species, community assemblages, and evolutionary change (MacArthur 1958). Given that competition is particularly strong between phenotypically similar individuals, intraspecific competition can have a disproportionate effect on shaping strategies around resource acquisition (Svanbäck and Bolnick 2007). Indeed, intraspecific competition can result in populations comprised of individuals that are either targeted specialists or broad generalists (Bolnick et al. 2003). Such strategies to limit individual similarity often fall according to sex and age groups (Shoener 1986). Sexual segregation, in particular, is a common mode by which vertebrates minimize intraspecific competition, especially by species showing pronounced sexual dimorphism (Shine 1989, De Lisle and Rowe 2015).

Sexual segregation has been well-studied across avian species (Catry et al. 2005). Ecologists have explored differences between sexes especially in regards to the conspicuous sexual dimorphism that characterize many species of birds (Andersson 1994, McDonald et al. 2005). Dietary and spatial segregation between sexes is widespread, and have been explained via two main competing hypotheses (Catry et al. 2005). The ecological specialization hypothesis posits that males and females exploit different resources because of sex-specific habitat preferences (Cleasby et al. 2015), physiological and anatomical differences (Catry et al. 2014), or breeding role specializations (Catry et al. 2016). The social dominance hypothesis alternatively suggests that sexual segregation arises from the despotic exclusion of subordinate individuals from favored areas (Catry et al. 2005). Such social dominance is often mediated via sexual dimorphism; male-male competition and sexual selection conveys advantages to larger males, and often forces smaller and subordinate females into habitats of lower quality (Marra 2000). Regardless of the underlying mechanism, sexual segregation can expose the sexes to different quality of resources, predation, diseases and human impacts, and drive population dynamics (Rubin and Bleich 2005, Bennett et al. 2019).

While sexual segregation has been widely reported among birds, how it varies with environmental conditions remains poorly explored (Mancini et al. 2013). It is well-known that intra-population variation in resource use is largely mediated by competitive interactions for diverse resources, and this can change according to environmental context (Jones and Post 2016). Increasing resource diversity generally increases resource differentiation between conspecifics (Layman et al. 2015), and provide opportunities for resource segregation within (Robertson et al. 2015) and among (Rosenblatt et al. 2015) populations. Human activities can enhance intraspecific segregation by increasing resource diversity and affecting habitat quality (Kirby et al. 2016). Yet, how anthropogenic impacts alter resource use, especially between sexes, remains understudied (Moss et al. 2016).

Andean condors are highly mobile obligate scavengers that feed opportunistically over a broad geographic area and a range of ecological conditions (Perrig et al. *in review*). Condors exhibit strong sexual dimorphism – males weigh up to 50% more than females (11-15 kg vs. 8-11 kg) and possess sexual ornamentation including a large comb and neck wattle (Houston 2001, Alarcón et al. 2017). This sexual dimorphism is associated with strong sexual despotism: condors feed and roost socially in well-defined group hierarchies with males dominating females (Donázar & Feijóo 2002, Donázar *et al.* 1999). Sexual dimorphism also appears to result in temporal partitioning between the sexes since males have earlier routines than females to forage under optimal soaring conditions (Alarcón et al. 2017). Given the social hierarchy and temporal partitioning, foraging locations might differ between the sexes (Donázar et al. 1999, Alarcón et al. 2017) with females, in particular juveniles, being displaced to lower quality habitats; notably, sites featuring strong human influence (Donázar et al. 1999). Human-dominated areas are generally regarded as riskier (Speziale et al. 2008) and associated to anthropogenic sources of mortality (Pauli et al. 2018, Plaza et al. 2019). Thus, sex-based despotism has been linked to higher physiological costs (Gangoso et al. 2016) and mortality rates among female condors (Lambertucci et al. 2012). While social hierarchy and temporal partitioning has been clearly documented, no previous study has directly quantified the degree to which males and females overlap in space and whether they exhibit dietary segregation (but see Perrig et al. 2017).

In the southern Andes, within the core of the Andean Condor contemporary distribution, a spectrum of human footprint exists. These conditions range from pristine landscapes where native camelids represent the main food resource for condors, to human-dominated ones where an array of domestic and exotic game species sustain condors (Fig. 1). This relationship between human footprint and local prey diversity provides an opportunity to test if male and female condors partition both habitat and diet across a range of environmental conditions (Fig. 1). To test for differences in Andean condor sexual segregation as a function of resource diversity, we analyzed dietary and spatial segregation among adult females and males across six sites that range from near-pristine to human-dominated. We analyzed stable isotopes of individually identified, molted feathers to compare dietary sexual segregation across these six areas. We then focused on two sites on the extreme ends of human footprint and prey diversity to compare assimilated biomass, and spatial and habitat segregation via GPS locations of tracked birds. We hypothesized that sexual segregation between adult Andean condors would be a function of local prey diversity. Specifically, we predicted trophic and spatial niche differentiation between sexes, greater variation in isotopic niche of males than females, and wider population niche breath and larger sexual differences where human footprint is higher and has increased prey diversity.

We also predicted that females, the subordinate sex, would forage in areas with higher human footprint than males.

Methods

Study areas

Our study area encompasses semiarid landscapes of central-western Argentina (between 30-44° S Latitude and 71-67° W Longitude; see supplementary material for details), under a range of human influence and prey diversity (Fig. 1). Within the high Andes, we sampled in San Guillermo National Park (hereafter “San Guillermo”; 166 km^2), located within one of the most pristine landscapes of South America (Haene et al. 2001). This area sustains large populations of native camelids (vicuñas *Vicugna vicugna* and guanacos *Lama guanicoe*), which provide an important food resource for condors (Perrig et al. 2017), with rangelands to the east of the park (Wurstten et al. 2013). In the northern Patagonian steppe, two provincial reserves, Payunia (6660 Km^2) and Auca Mahuida (770 Km^2), support large guanaco populations (Palacios et al. 2012, Schroeder et al. 2014) and are grazed by livestock at low densities (Rivas et al. 2015). In the Pampas Mountains of central Argentina, extensive ranching has functionally replaced native herbivores (Díaz et al. 1994, Cingolani et al. 2008); our sampling occurred in Sierra de las Quijadas National Park (hereafter “Quijadas”; 735 Km^2) and Cordoba mountains (Fig. 1). Northwestern Patagonia (hereafter “Patagonia”) sustains the largest population of Andean condors (Lambertucci 2010, Padró et al. 2018) through free-ranging livestock (mostly sheep *Ovis aris* and cattle *Bos taurus*) and exotic game species (red deer *Cervus elaphus* and hares *Lepus europaeus*) that have replaced native camelids (Lambertucci et al. 2009). Herein, Patagonia and San Guillermo serve as two areas representing opposing conditions: Patagonia features high human influence and prey diversity; San Guillermo features low human influence and low prey diversity (Fig. 1).

Data collection and processing

From roosting sites and feeding locations, we sampled Andean condor molted flight feathers of adult birds (> 6 years old; Wallace and Temple 1987) identified by plumage coloration (Perrig et al., 2019). We conducted DNA fingerprinting of all feathers via multi-locus genotyping and molecular sexing (see Padró et al. 2018 for details). We analyzed $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios from ~5 cm of the distal extreme of 141 feathers of individual birds (table S2) through mass spectrometry (Pauli et al. 2009, Perrig et al. 2017). For 41 flight feathers from 4 of our study sites (table S2), we additionally sampled two intermediate and a bottom section of each sample to analyze trophic consistency as a proxy to evenness on diet over time (Jaeger et al. 2010). The isotopic composition of feathers reflects diet during moult (Bearhop et al. 2002); although molt chronologies are unavailable for Andean condors, primary feather replacement in large birds generally occur over 4 months during summer (Zuberogoitia et al., 2016, Snyder et al. 1987). We estimated measurement precision by analyzing ~20% of the feathers in duplicate and found little differences between replicates for both $\delta^{13}C$ ($\overline{x}$ difference = 0.03‰) and $\delta^{15}N$ ($\overline{x}$ difference = 0.03‰). We characterized the isotopic signature of the main prey items of Andean condors at our 6 study locations by collecting hair opportunistically (table S3) or via published information (Perrig et al. 2017, Lambertucci et al. 2018).

We compared spatial segregation between Andean condor adult females and males in Patagonia and San Guillermo via GPS-tagged Andean condors. We tracked 4 females and 8 adult males during 2015-2017 in San Guillermo, and 13 females and 10 adult males during 2011-2013 in Patagonia (see details in Perrig et al. *in review*). We used this information to describe locations where the birds where most likely foraging as described in Perrig et al. *in review*. Briefly, we defined foraging sites via GPS locations recorded 5-8 hours after sunrise with zero velocity, away from roosting locations (i.e. found outside a 5 km-buffer surrounding roosts) and located in non-forested areas.

We explored differences between sexes in space use while foraging by analyzing the number of locations of individual birds in each 500 m cell grid encompassing our study area. We characterized each grid cell with at least 1 GPS location with three environmental covariates: Human Footprint Index (Venter et al. 2016), altitude (from a Digital Elevation Model; Farr et al., 2007), and Dynamic Habitat Index (DHI) based on the normalized difference vegetation index (NDVI) for the year 2015 (Radeloff et al. 2019).

Data analyses

Regional comparison

We performed all statistical analyses in R 3.6.1 (R Core Team). We standarized Andean condor isotopic data across study locations based on trophically-corrected isotopic signature of prey items per sampling site (Cucherousset and Villéger 2015, Gil et al., 2016). We used trophic enrichment factors of 3.1‰ ± 0.1 for δ^{15}N and 0.4‰ ± 0.4‰ for δ^{13}C observed for Californian condors on a controlled feeding trial (Kurle et al. 2013). With the standarized data, we compared isotopic niche size between study locations estimating standard ellipse areas with sample size correction (SEAc) in the R package *SIBER* (Jackson et al. 2011). To compare the spread of Andean condor isotopic data, we calculated isotopic dispersion (in relation to the center of isotopic convex hull) and uniqueness (similarity of individuals) within sites (Cucherousset and Villéger 2015). We bootstrapped diversity metrics to correct for group differences in sample sizes and create associated confidence intervals using the R package *boot* (Canty and Ripley 2019).

To compare the isotopic niche of females and males across study areas, we calculated the probability ($\alpha = 0.95$) that a female occurs within the niche region of males, and a male in the niche region of females, with the R package *nicheRover* (Swanson et al. 2015). Estimates were modelled via 10,000 samples and 1000 iterations. We also estimated similarity and nestedness based on isotopic convex hull of each sex (Cucherousset and Villéger 2015). We compared dietary consistency by calculating for each bird with repeated measurements minimum convex hull area using the R package *SIBER* (Jackson et al. 2011) and difference in range of $\delta^{13}C$ and $\delta^{15}N$.

Segregation under low and high prey diversity

We estimated home ranges of GPS-tracked individuals via Autocorrelated-Kernel Density Estimators (AKDE) and quantified their home range overlap using the biased-corrected Bhattacharyya coefficient (BC) implemented in the R package *ctmm* (Calabrese et al. 2016, Winner et al. 2018). We did not consider one male from San Guillermo and one female from Patagonia that were not monitored long enough to show range residency (Winner et al. 2018). We present the mean and standard deviation of the average overlap by site between females, males, and females to males.

To explore differences in space use between females and males while foraging, we used generalized linear mixed models. Specifically, we modelled number of foraging locations in each grid cell as a function of sex, region, human footprint and altitude, with individuals as a random effect. To ensure a robust estimate of variance, we only considered individuals with > 5 used locations (Harrison et al. 2018), resulting in 909 locations of 11 females and 8 males from Patagonia, and 756 locations of 3 females and 7 males from San Guillermo. We evaluated collinearity between explanatory variables using Pearson correlation coefficient ($|r| < 0.7$), and standardized variables to zero mean and unit variance to allow direct comparisons among coefficients (Harrison et al., 2018). Models were fit with a truncated poisson distribution and logit link using the R package *glmmTMB* (Brooks et al. 2017). We compared 15 candidate models based on Akaike Information Criteria (AIC) using the R package *AICcmodavg* (Mazerolle 2019), and considered models with $\Delta AIC < 2$ as competitive.

We evaluated differences in Andean condor assimilated diet betweeen our two focal areas via Bayesian mixing models. We employed Multivariate Analysis of Variance (MANOVA) to evaluate differences in isotopic signature of condor potential prey items per site ($\alpha < 0.05$) a priori. For San Guillermo, we considered 3 isotopically distinct and biologically meaningful prey groups: exotic-large ungulate, exotic-small ungulate, and camelids (Perrig et al. 2017). For Patagonia, we identified 3 isotopically distinct prey groups: native camelids (guanacos, n = 7), exotic-small prey (hares = 17), and exotic-large ungulates (including red deer [n=11], sheep [n=5], cow [n=7], and horse [n=4]). We also incorporated marine prey (n=4) in the mixing space of Patagonia since previous studies suggest a small contribution of marine remains in Andean condor diet within that area (Lambertucci et al. 2018). We evaluated the mixing space through simulated mixing polygons (Smith et al. 2013), and eliminated samples with <5% probability that a combination of those food sources could explain their isotopic signature (3 individuals for San Guillermo and 4 individuals for Patagonia). We implemented Bayesian stable isotope mixing models in the R package *simmr* (Parnell et al., 2010); models were run with 10,000 iterations and 4 chains. We estimated proportional contributions for females and males using informative priors from pellet content analyses (San Guillermo: camelids = 94%, small livestock = 4.2%, and large livestock = 1.8%; Patagonia: large ungulate= 72%, native = 0.5%, hares = 15%, marine = 0.8%), and also ran a second model with uninformative priors to explore the influence of our developed priors on dietary estimates (table S7). We report the mean and 95% crediblility interval to statistically summarize the marginal posterior distribution calculated by all models.

Results

Regional comparison

Andean condors differed in isotopic niche space across study sites but exhibited no clear patterns in relation to prey diversity. Of the three sites with higher prey diversity, one showed the smallest and two the largest standard ellipse areas (Fig. S1). We found that isotopic dispersion was similar across sites except for one location featuring high prey diversity, where it was significantly smaller. Isotopic uniqueness was slightly larger in sites with intermediate prey diversity (Fig. S1). We detected a positive relationship between HFI and standardized δ^{13}C of Andean condor feathers across locations ($\beta = 0.03$, $p < 0.001$, $R^2 = 0.2$; fig. S2).

Female and male Andean condors exhibited similar isotopic niches. Isotopic nestedness between sexes was large across study areas (range 55-93%), with lower values (60% and 55%) occurring in locations of high prey diversity (table S5). We found that similarity in convex hulls was largest in the site with the lowest prey diversity (70%) yet similar across the remaining areas (47-14%; table S5). For 4 of our 6 study locations, the probability of a male occuring within the isotopic niche of females did not differ to the probability of a female being within the isotopic niche of males (Fig. 2). In Patagonia, featuring high prey diversity, we found greater probability of a female occuring within the niche of males than a male overlapping the niche of females, whereas the opposite pattern occurred in a site featuring low prey diversity (Payunia; Fig. 2).

Individual variability was similar between females and males (mean[se] δ^{15}N = 1.1[0.1] and 0.9[0.1]; δ^{13}C = 1.1[0.2] and 1.4[0.3] for females and males, respectively). We found no differences in the area of individual convex hulls between females and males (0.4[0.1] and 0.5[0.1]) or clear differences on individual variability between sites (Fig. S3).

Segregation under low and high prey diversity

We found no differences in home range overlap between females and males (Fig. 3). The overlap (mean[standard deviation]) between females, males and females to males in San Guillermo was 0.31 (0.13), 0.48 (0.19), 0.45 (0.19), respectively, whereas in Patagonia was 0.47 (0.18), 0.49 (0.18), 0.47 (0.19). In modelling habitat use while foraging, we did not include dynamic habitat index because of a negative correlation with altitude (*corr* = -0.75). The most supported model included the variables footprint and altitude, both with negative relationships with condor use (table 1). Three other competitive models also included the variables region and sex, although 95% confidence intervals of both beta coefficients overlapped zero. Notably, when accounting for sex only the model was not competitive and ranked below the null (table S6).

Proportional dietary estimates revealed that at the site with low prey diversity, Andean condors consumed mosly native camelids and small proportions of large and small livestock; in contrast, at the site representing high prey diversity, most assimilated biomass came from exotic ungulates with small contributions of hares, camelids, and trivial use of marine remains (table S7). At the site representing low prey diversity, females consumed slightly less percentage of camelids than males (73 versus 81%), and slightly more large livestock (24 and 15%) but similar percentages of small livestock (3 and 4%). At the high prey diveristy site, females consumed slightly more exotic ungulates (71% and 58%), and hares (12 and 9%) than males, yet less camelids (13 and 20%) and marine remains (4 and 12%). Credibility intervals (95%) of these dietary proportions by study area overlapped between the sexes for all prey items but marine, which represented a negligible food resource for the species.

Discussion

We found no evidence of significant sexual segregation by Andean condors, even across a range of prey diversity. In particular, we observed no differences between sexes at the level of the home range or in foraging locations. Our results are in concordance with previous studies showing that female and male condors forage in the same areas (Lambertucci et al. 2014), travel similar mean daily distances (Gangoso et al. 2016), and feed upon carcasses in similar densities (Speziale et al. 2008). These findings, however, run in contrast to Donazar et al. (1999), who detected more adult males than adult females feeding in mountainous areas closer to nesting grounds during spring, whereas no sexual differences were found in summer. This observed spatial segregation, though, could be confounded by a higher abundance of adult males than females (Lambertucci et al. 2012) increasing the probability of observing more males (Conradt 2005). Nonetheless, seasonal patterns of sexual segregation do exist among sexually dimorphic birds (Phillips et al. 2004), and condors appear to change their space use seasonally (Sarno et al. 2000). While future work should explore temporal differences in resource partitioning between Andean condors, we found no evidence of sexual segregation among adults at meso- to micro-habitat scales or trophic resources.

Our results indicate that social dominance does not mediate sexual resource partitioning between adult condors. We observed a slight increase of $\delta^{13}C$ in condor feathers with increasing human footprint but no clear patterns in isotopic geometry. More importantly, we found similar short-term dietary consistency between sexes, a nested pattern in the isotopic signature of males and females across locations, and similar dietary proportions between the sexes under high and low prey diversity. Like other vultures, male and female condors exhibit parity in investment to reproduction and extended parental care (Lambertucci and Mastrantuoni 2008). Further, vultures forage in mixed age and sex-groups and exchange social information (e.g., vulture “kettles” circling fresh carrion) to enhance detection of carrion on the landscape (Cortés-Avizanda et al. 2014). Such information transfer undoubtedly links space use and foraging decisions between individuals (Gil et al. 2018). The fact that carrion is spatiotemporally unpredictable might also limit potential differentiation between dimorphic sexes. Indeed, a lack of sexual segregation in dimorphic seabirds in the tropics compared to polar or temperate regions has been linked to unpredictable foraging grounds (Mancini et al. 2013). Not only is carrion unpredictable and sparsely distributed, but it is also ephemeral. Therefore, sporadic foraging opportunities and reliance on social information might prevent partitioning of resources between the sexes despite the pronounced sexual dimorphism and marked social hierarchy. It is worth noting, though, that we detected high negative correlation between posterior probabilities of dietary proportions (Fig. S2) and used broad prey categories in isotopic mixing models. This along with lack of species- and sex-specific discrimination factors could limit our capacity to detect dietary differences between the sexes (Wolf et al. 2009). However, we are confident on our conclusions since multiple lines of evidence suggested limited sexual segregation between adult Andean condors.

Despite the similarity in resource use between the sexes, male condors generally possessed slightly larger isotopic niches than females. This suggests that males may feed in a broader range of habitats and upon a larger diversity of prey. This finding appears to be congruent with the fact that males can travel longer maximum daily distances and possess larger home ranges than females (Gangoso et al. 2016). It is likely that broader niches – both in space and diet – of male condors are ultimately due to their larger wing load favoring the exploitation of good soaring conditions (Shepard and Lambertucci 2013). Body size differences between the sexes also appear to result in partially asynchronized activities: males show earlier daily routines than females (< 2 hours) thus arriving first to carcasses (Carrete et al. 2010, Alarcón et al. 2017). Our results, though, indicate that partial temporal segregation and slight differences in isotopic niche between male and female Andean condors does not represent significant differences in diet or habitat use among adults.

Andean condors are the only New World vultures that exhibit pronounced sexual dimorphism (Houston 2001). Given the similarity between sexes in parental investment (Lambertucci and Mastrantuoni 2008) and current resource use, sexual selection might be the most parsimonious explanation for males being up to 50% heavier than females (Andersson

1994). Regardless of the mechanism underlying sexual dimorphism, there is ample evidence that size differences lead to a well-defined hierarchical social structure were Andean condor adult males outcompete females and younger individuals (Marinero et al. 2018). Our results, though, do not support that behavioral asymmetries lead adult females to utilize significantly more carcasses in places with high human disturbance, which has been discussed as a cause of higher stress (Gangoso et al. 2016) and mortality rates in females than males (Lambertucci et al. 2012). This is relevant given that the species is characterized by an increasingly male-skewed sex ratio with age (Lambertucci et al. 2012). Sexual dominance could still be acting over juvenile females, the most subordinate group (Wallace and Temple 1987, Donázar et al. 1999, Donázar and Feijóo 2002). Notably, though, there is no evidence of spatial segregation between immature females and males (Donázar et al. 1999, Speziale et al. 2008). Further, dispersal is led by immature males (Padró et al. 2019) which could counterbalance mortality of subordinate immature females (Lucas et al. 1994). The causes for the higher mortality of females and potential fitness consequences of social despotism require timely investigation for the development of effective conservation actions (Lambertucci et al. 2012).

Pronounced sexual size dimorphism is typically associated with sexual segregation, yet a growing body of literature shows that this is not a universal or direct relationship. Strongly dimorphic species can show no sexual segregation (Mancini et al. 2013), monomorphic species can segregate in habitat and diet (Senior et al. 2005), and populations can partition resources differently according to their availability (Baylis et al. 2016). Altogether, these examples expose the multifactorial nature of sexual segregation (Ruckstuhl 2007). Many social species that exhibit sexual dimorphism show partially divergent patterns of resource use which, as a cause or consequence, reduce the high intra-specific competition associated with gregarious life-styles (Bison et al. 2015). For avian scavengers, though, reliance on social information to find and exploit unpredictable and ephemeral carrion resources likely prevents sexual segregation despite divergent phenotypes and marked social hierarchies. Our results thus highlight that the effects of social dominance and dimorphism on sexual segregation are undermined by resource predictability and distribution (Mancini et al. 2013).

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Table 1. Standarized coefficent estimates (mean [95% confidence interval]) of top-ranked mixed effects models (ΔAIC <2) of Andean condor space use while foraging in two study areas, Patagonia and San Guillermo. ΔAIC is the difference between model AIC and lowest AIC between candidate models; Wi represents Akaike model weight.

Model	Altitude	Footprint	Region	Sex	AIC	ΔAIC	Wi
1	-0.17 [-0.32, -0.03]	-0.11 [-0.17, -0.05]	__	__	4146.27	0	0.29
2	-0.15 [-0.29, 0.00]	-0.11 [-0.17, -0.05]	0.49 [-0.16, 1.15]	__	4146.38	0.11	0.28
3	-0.17 [-0.31, -0.03]	-0.11 [-0.17, -0.05]	__	-0.24 [-0.89, 0.40]	4147.73	1.46	0.14
4	-0.15 [-0.29, 0.00]	-0.11 [-0.17, -0.05]	0.46 [-0.23, 1.14]	-0.12 [-0.74, 0.50]	4148.23	1.96	0.11

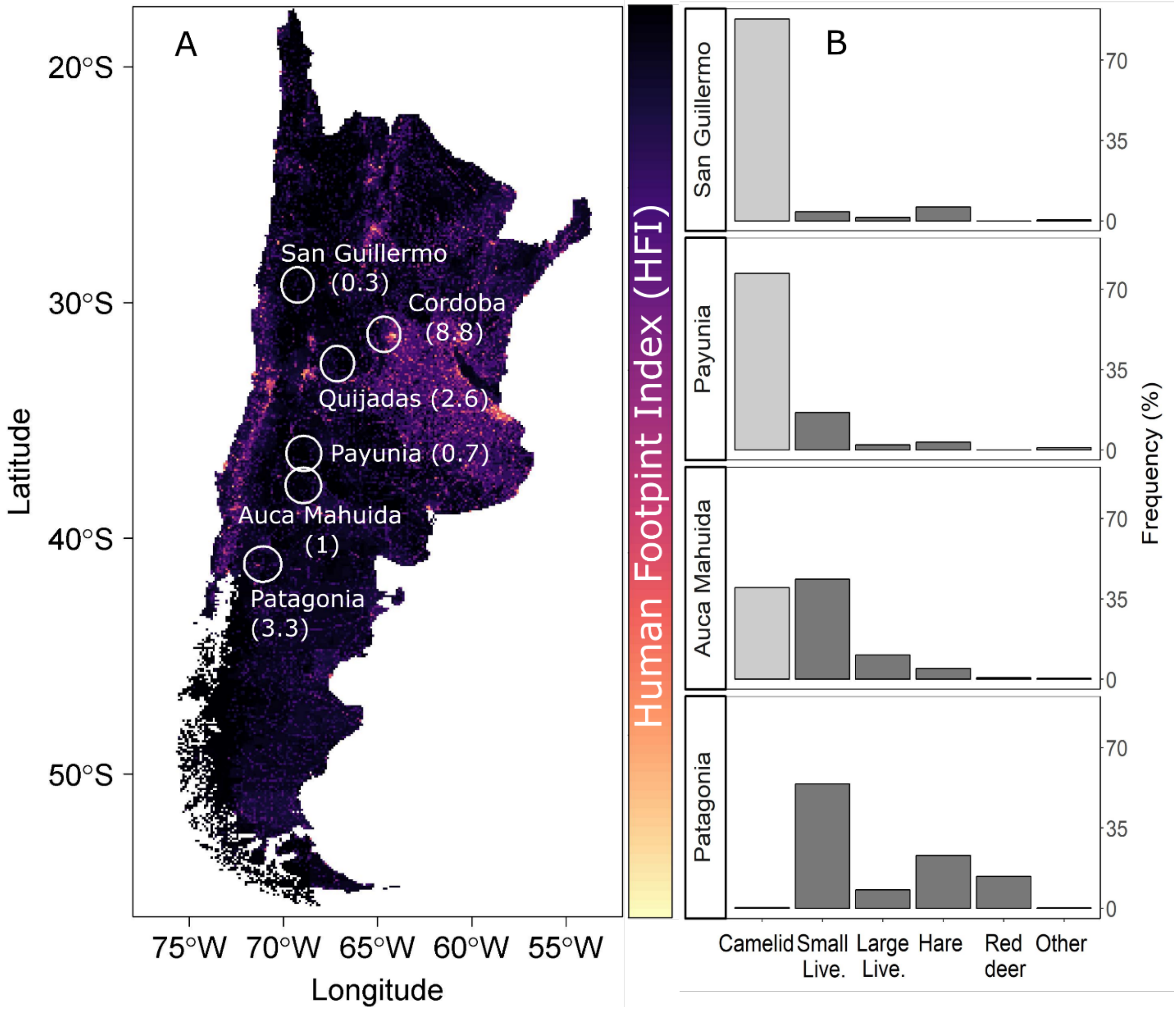

Figure 1. Location of 6 study sites in Argentina across a gradient of (A) Human Footprint Index (HFI; Venter et al. 2016), and (B) Andean condor prey diversity comprising native (light grey) and exotic (dark grey) prey. Numbers in parenthesis indicate median HFI in a buffer area of 84 km radius surrounding each study area. Prey diversity was estimated via pellet content analyses conducted for this study (see supplementary information) or previously (San Guillermo [Perrig et al. 2017]; Patagonia [Ballejo et al., 2017]). We do not have information on condor diet in Cordoba or Qujadas.

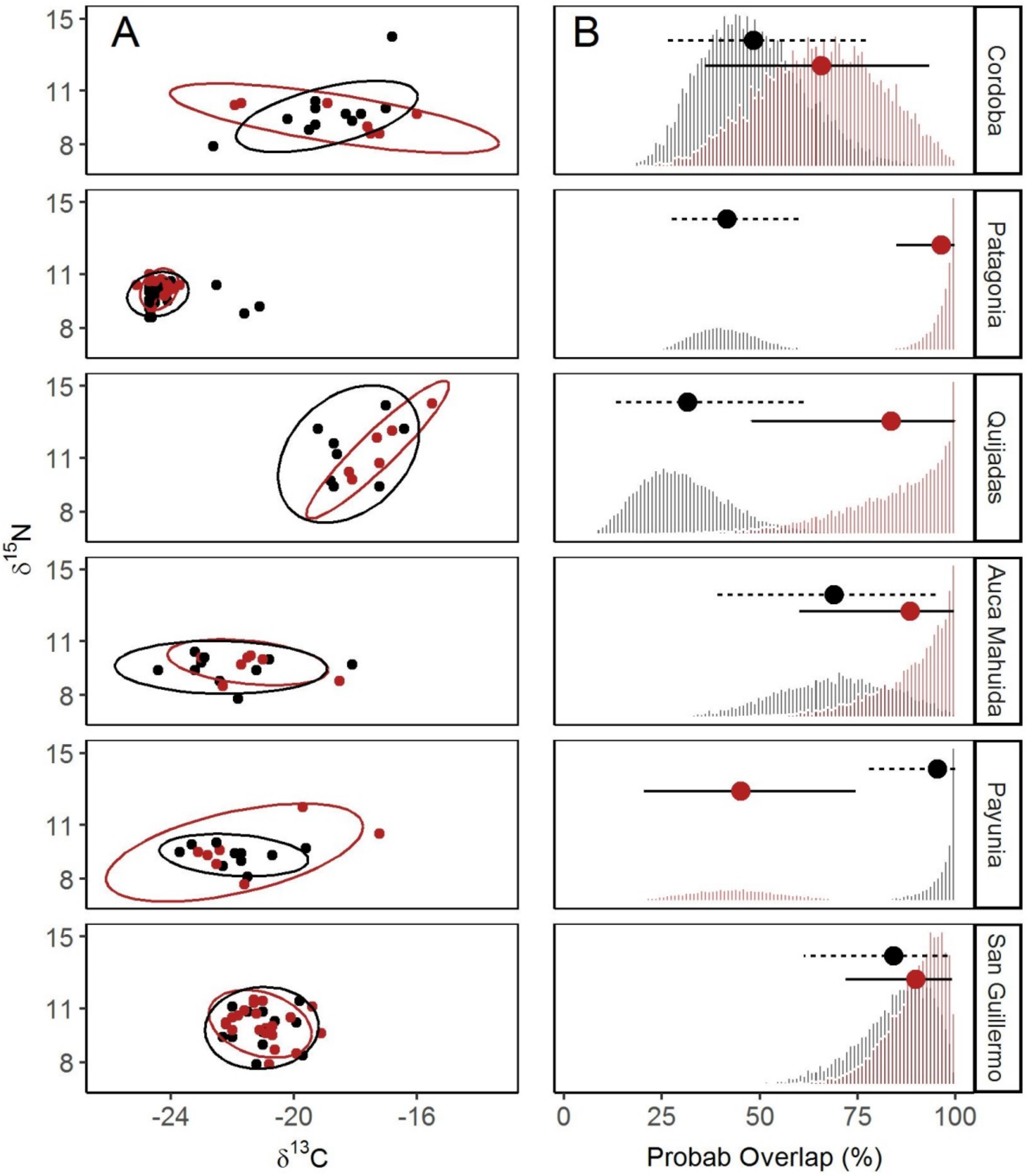

Figure 2. Comparison of male (black) and female (red) Andean condor (*Vultur gryphus*) stable isotope signatures across 6 study locations in Argentina. (A) Isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of individual birds (dots) and standard ellipses by sex. (B) Probability distribution of females occurring within the isotopic niche of males, and males occurring within the isotopic niche of females, with associated 95% credibility intervals. We observed large dietary overlap between the sexes across study areas.

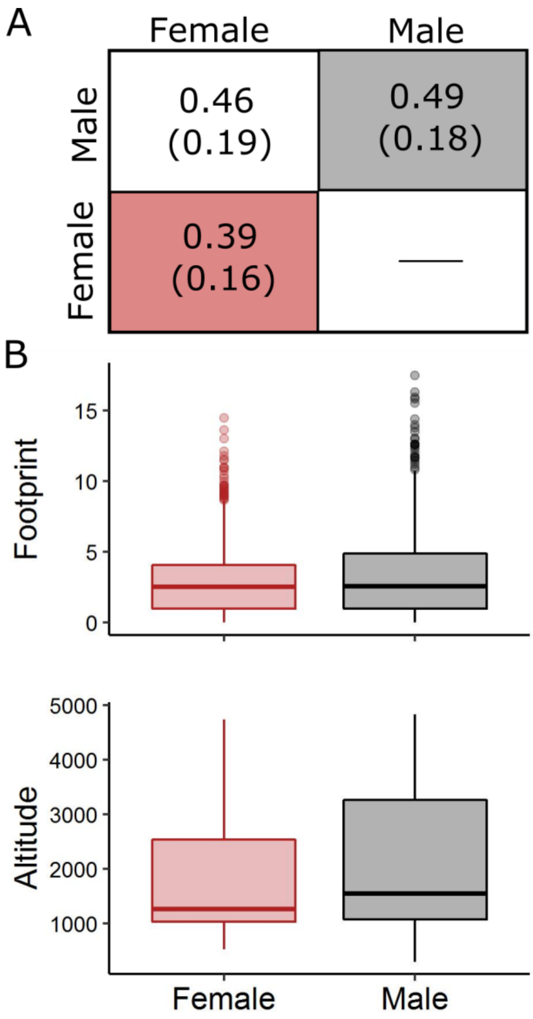

Figure 3. Analyses of spatial segregation by female (red) and male (black) Andean condors (*Vultur gryphus*) in Patagonia (n = 23) and San Guillermo (n = 12), Argentina. (A) Mean (sd) value of pairwise home range overlap between sexes estimated with Bhattacharyya Coefficient (0 no overlap - 1 complete overlap) computed from Autocorrelated Kernel Density Estimator of individual home ranges. (B) Human Footprint Index and altitude estimated via Geographic Information Systems at GPS-derived foraging locations of females and males. These results show no differences in space or foraging habitat use by Andean condor sexes.

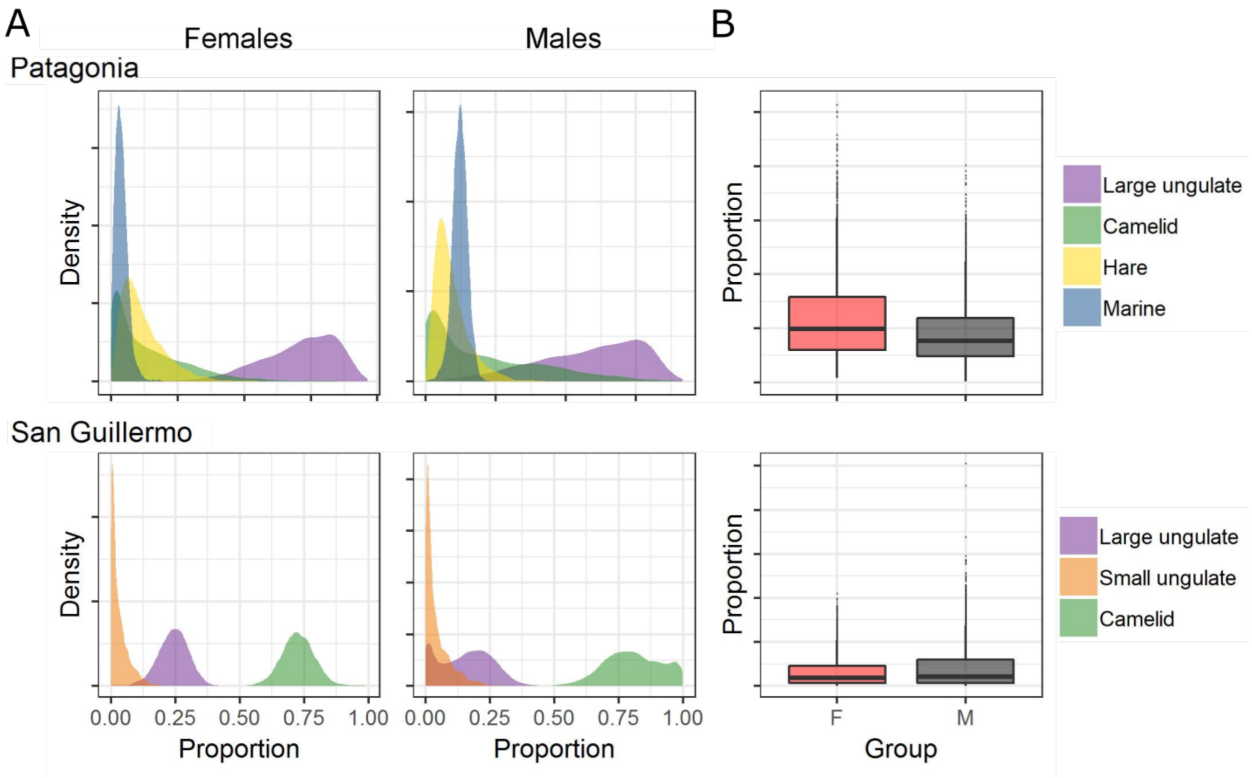

Figure 4. Comparison of proportional dietary estimates of female and male adult Andean condors (*Vultur gryphus*) in Patagonia and San Guillermo (Argentina) estimated via stable isotope mixing models. (A) Proportional contribution of prey items to the diet of Andean condors. Large ungulates in Patagonia include livestock (mostly sheep [*Ovis aris*] *and cow* [*Bos taurus*]*)* and red deer (*Cervus elaphus*), while in San Guillermo large ungulate is represented by cows and small ungulate by goats (*Capra aegagrus*). (B) Comparison between female (red) and male (grey) estimated consumption of hares in Patagonia and small ungulate in San Guillermo. We found no significant differences in assimilated biomass of Andean condor adult females and males in these two area

Supplementary material

Characterization of study areas

Pellet content analyses

We collected pellets at roosting sites in La Payunia and Auca Mahuida Reserves. In the laboratory, pellets were oven-dried at 55°C for 48 hours, weighed, covered with water and broken up in a Petri dish. Bird feathers and large mammal remains were identified microscopically via feather and guard hair morphology (Chehébar and Martín 1989). A minimum of five samples were analyzed from each pellet, grouping species into camelid (vicugnas *Vicugna vicugna* and guanacos *Lama guanicoe*), large (cow *Bos taurus*/horse *Equus sp.*) and small (goat *Capra aegagrus* /sheep *Ovis aries*) livestock, hares *Lapues europaeus*, red deer *Cervus elaphus*, and other infrequent prey items (e.g. *Lycalopex sp.*, *Sus scrofa*, *Lagidium viscacia*). Results are presented as (1) percentage of occurrence (number of times a prey species occurred divided by the total number of prey items in all pellets), and (2) percentage volume of each prey item, estimated visually.

We compared condor diet in La Payunia and Auca Mahuida (table 1) with previosuly published diet analyses via pellet content in San Guillermo (Perrig et al. 2017) and Patagonia (Ballejo et al. 2017). Unfortunately, given the remoteness of roosting sites, we were unable to collect condor pellets in Cordoba or Quijadas. For each available site, we estimated diet diversity via Shannon index using the R package *vegan* (Oksanen et al. 2019). We found a positive relationship between diet diversity and mean human footprint at each study location (Patagonia: 1.19; Auca Mahuida: 1.17, La Payunia: 0.75; San Guillermo: 0.50).

GIS-derived environmental conditions

We characterized environmental variables across our study areas (table S2) in a 84 km buffer radius around the center of our collection sites. This radio represents the median distance (median[sd]; 93.5[66.5] km) travelled by Andean condors tagged in San Guillermo and Patagonia estimated from daily trajectories. Specifically, we considered daily trajectories on summer and spring seasons (October to April) with a minimum of 9 GPS locations collected at 1 hour intervals across 11 individuals tracked in San Guillermo (1243 trajectories) and 23 individuals tracked in Patagonia (1226 trajectories). The resulting buffer area (22167 km^2) represents ~70% of the median 95% minimum convex polygon (31974[63429] km^2) of all individuals tracked during summer (October to April) for more than a year (10 individuals in Patagonia and 7 in San Guillermo). Within this buffer, we estimated the median value of Human Footprint Index (Venter et al., 2016; spatial resolution ~1km), Ranching intensity (Gilbert et al., 2018; ~10km), Altitude (Jarvis et al., 2008; ~90 m), Dinamic Habitat Index based on NDVI (Radeloff et al., 2019; ~ 1km resolution), and temperature and rainfall (Fick and Hijmans, 2017l. 2017; ~1 km; table S2).

Table S1. Condor diet in Auca Mahuida and La Payunia reserves (Argentina) estimated via pellet content analyses, and presented as (1) number of times a prey species occurred divided by the total number of prey items in all pellets (%F), (2) number of times a prey species occurred divided by total number of pellets (%O), and (3) percentage volume of each prey item, estimated visually (%V).

	Prey	Camelids	Goat/Sheep	Cow/Horse	Hare	Red deer	Other	Total Prey	Total Pellets
Auca Mahuida	%F	40	44	11	5	1	0.4	273	212
	%O	51	56	14	6	1	0.5	-	-
	%V	65(31)	77(23)	55(31)	10(11)	5(0)	5(0)	-	-
Payunia	%F	77	16	2	3	-	1	178	152
	%O	90	19	3	4	-	1	-	-
	%V	71(24)	56(29)	26(19)	29(20)	-	37(46)	-	-

Table S2. Median environmental variables obtained from Geographic Information Systems (GIS) within a buffer area of 84 km radius from approximated sampling locations in our 6 study areas.

Site	Human Footprint	Ranching Intensity	Altitude	Cumulative DHI	Temp.	Rainfall
San Guillermo	0.3	23	3678	1.8	4	127
Payunia	0.7	1230	1395	4.0	11	311
Auca Mahuida	1.0	788	718	4.2	13	211
Quijadas	2.6	2128	527	6.9	19	356
Patagonia	3.3	1406	1125	5.5	7	738
Cordoba	8.8	10801	746	11	16	701

Table S3. Summary of stable isotope signature (mean [sd]) and sample size of Andean condor individually identified, molted feathers collected across six study areas in Central Argentina.

Site	Sex	N	δ13C	δ15N	N repeated measures
Auca Mahuida	F	7	-21.34 (1.4)	9.63 (0.7)	5
Auca Mahuida	M	10	-22.10 (1.8)	9.48 (0.7)	4
Cordoba	F	7	-18.69 (2.3)	9.53 (0.8)	-
Cordoba	M	11	-18.93 (1.6)	9.85 (1.5)	-
Patagonia	F	20	-24.40 (0.3)	10.15 (0.5)	7
Patagonia	M	22	-24.10 (1)	9.79 (0.6)	6
Payunia	F	7	-21.33 (2.1)	9.63 (1.3)	2
Payunia	M	10	-21.89 (1.2)	9.30 (0.6)	3
Quijadas	F	6	-17.18 (1)	11.55 (1.6)	-
Quijadas	M	8	-18.08 (1)	11.33 (1.7)	-
San Guillermo	F	21	-20.99 (0.9)	10.10 (0.9)	8
San Guillermo	M	12	-21.00 (0.9)	9.87 (1.1)	6

Table S4. Isotopic values (mean [sd]) of Andean condor main prey items collected at six study areas in Central Argentina. Measurement precision based on ~50% of samples run in duplicate was 0.03‰ and 0.01‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Site	Species	Sample size	δ13C	δ15N
Auca Mahuida	Horse	5	-20.64 (1.7)	3.76 (1)
	Goat	13	-19.23 (2.7)	6.75 (2.7)
	Sheep	5	-23.06 (1.5)	4.1 (0.9)
	Cow	8	-19.06 (3.9)	4.15 (0.7)
	Guanaco	5	-21.82 (0.8)	3.74 (0.6)
Cordoba	Horse	8	-22.84 (1.3)	4.74 (1.6)
	Goat	3	-22.23 (0.3)	10 (0.4)
	Lama	3	-24.57 (0.1)	9.37 (0.1)
	Sheep	14	-22.04 (2.7)	8.81 (2.8)
	Cow	17	-21.25 (4)	5.48 (2.6)
Patagonia	Red deer	6	-24.5 (0.7)	4.28 (1.5)
	Cow	8	-24.94 (0.8)	4.59 (2.1)
	Guanaco	5	-23.76 (0.7)	5.5 (0.7)
Payunia	Horse	8	-20.27 (2.1)	3.55 (0.9)
	Goat	9	-18.38 (2.5)	4.74 (2.1)
	Hare	3	-22.73 (2.4)	2.87 (0.8)
	Sheep	9	-19.47 (3.1)	5.78 (1)
	Cow	11	-14.7 (2.1)	4.83 (1.2)
	Fox	2	-17.25 (0.1)	9 (0.1)
	Guanaco	9	-15.89 (1.6)	4.23 (0.7)

Quijadas	Horse	6	-16.18 (0.9)	7.32 (1.2)
	Goat	16	-20.15 (1.1)	8.82 (1.2)
	Sheep	2	-18.4 (1.4)	7.95 (0.1)
	Cow	5	-15.78 (2.7)	8.74 (1.4)
	Wild boar	2	-19.2 (0.3)	7.1 (0.1)
San Guillermo	Mountain vizcacha	3	-22.83 (0.2)	5.97 (1)

Table S5. Overlap metrics between females and males by study location based on the convex hull area of each sex in a shared isotopic space. Isotopic similarity represents the ratio between the volume shared and the volume of the union of the two convex hulls, whereas isotopic nestedness is the ratio between the volume shared and the volume of the smallest convex hull (Cucherousset and Villéger 2015).

Site	Patagonia	San Guillermo	Auca Mahuida	Payunia	Quijadas	Cordoba
Similarity	0.14	0.7	0.47	0.29	0.2	0.19
Nestedness	0.6	0.83	0.93	0.87	0.82	0.55

Table S6. Comparison among candidate models to explain space use by adult Andean condors in two of our study locations, Patagonia and San Guillermo. Models were truncated-Poisson mixed effects and included individual as a random effect.

Models	K	AIC	ΔAIC	AIC_{Weight}	Cum_{weight}	Log-lik.
count ~ Altitude + Footprint	4	4146.27	0.00	0.29	0.29	-2069.14
count ~ Altitude + Footprint + Region	5	4146.38	0.11	0.28	0.57	-2068.19
count ~ Altitude + Footprint + Sex	5	4147.73	1.46	0.14	0.71	-2068.87
count ~ Altitude + Footprint + Region + Sex	6	4148.23	1.96	0.11	0.82	-2068.12
count ~ Altitude + Footprint + Region + Sex + Footprint*Sex	7	4149.78	3.51	0.05	0.87	-2067.89
count ~ Footprint	3	4149.87	3.59	0.05	0.92	-2071.93
count ~ Footprint + Region + Sex	5	4150.05	3.78	0.04	0.97	-2070.02
count ~ Footprint + Sex	4	4151.06	4.79	0.03	0.99	-2071.53
count ~ Region	3	4156.06	9.79	0.00	0.99	-2075.03
count ~ Altitude	3	4156.90	10.63	0.00	1.00	-2075.45
count ~ 1	2	4157.19	10.92	0.00	1.00	-2076.59
count ~ Region + Sex	4	4157.88	11.60	0.00	1.00	-2074.94

count ~ Altitude + Sex	4	4158.30	12.03	0.00	1.00	-2075.15
count ~ Sex	3	4158.42	12.14	0.00	1.00	-2076.21
count ~ Altitude + Region + Sex	5	4158.66	12.39	0.00	1.00	-2074.33

Table S7. Estimated proportional contribution (mean [95% confidence interval) of prey items to the diet of Andean condor females and males at San Guillermo and Patagonia from informed and uninformed isotopic mixing models.

	Uninformed, no group	Uninformed prior		Informed prior	
	Population level	F	M	F	M
San Guillermo					
Large ungulate	0.28 [0.20, 0.35]	0.26 [0.15, 0.37]	0.23 [0.08, 0.39]	0.24 [0.11, 0.35]	0.15 [0.001, 0.33]
Small ungulate	0.12 [0.04, 0.2]	0.09 [0.02, 0.19]	0.14 [0.03, 0.29]	0.03 [0.001, 0.12]	0.04 [0.001, 0.18]
Camelid	0.60 [0.5, 0.71]	0.64 [0.51, 0.77]	0.63 [0.4, 0.82]	0.73 [0.60, 0.85]	0.81 [0.6, 0.99]
Patagonia					
Large ungulate	0.22 [0.02, 0.58]	0.50 [0.07, 0.85]	0.26 [0.02, 0.66]	0.71 [0.4, 0.9]	0.58 [0.18, 0.85]
Camelid	0.58 [0.19, 0.85]	0.25 [0.03, 0.71]	0.50 [0.09, 0.86]	0.13 [0.002, 0.48]	0.20 [0.002, 0.68]
Hare	0.07 [0.01, 0.21]	0.19 [0.02, 0.52]	0.11 [0.01, 0.34]	0.12 [0.02, 0.32]	0.09 [0.02, 0.25]
Marine	0.01 [0.08, 0.16]	0.05 [0.01, 0.16]	0.12 [0.06, 0.18]	0.04 [0.005, 0.09]	0.12 [0.07, 0.17]

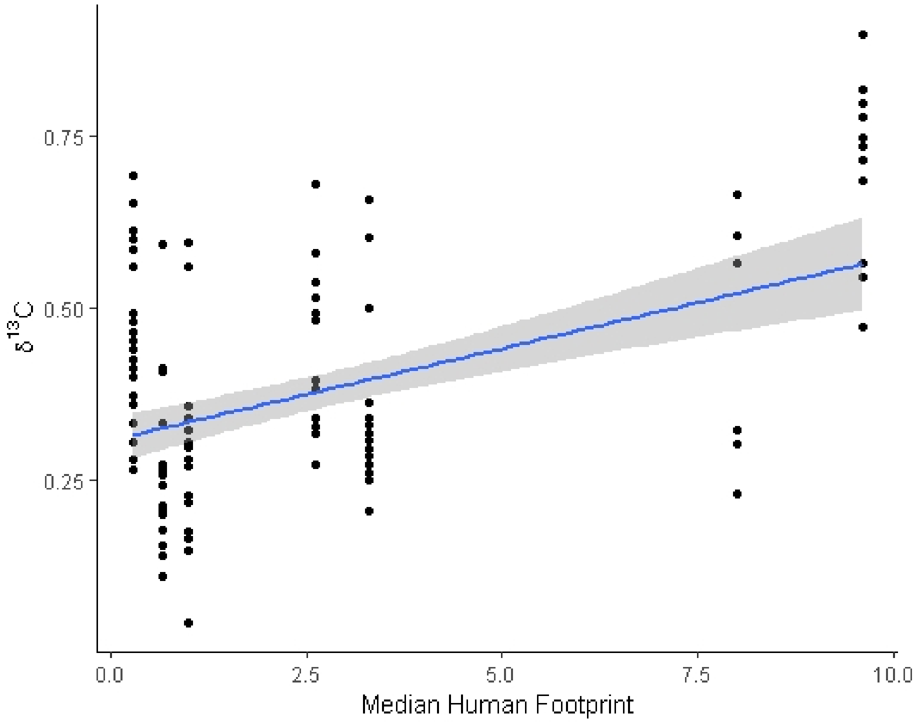

Figure S1. Relationship between standardized δ13C and median Human Footprint Index (Venter et al. 2016) across sampling locations. Here we show 2 sampling sites within Cordoba, which we considered together for remaining analyses.

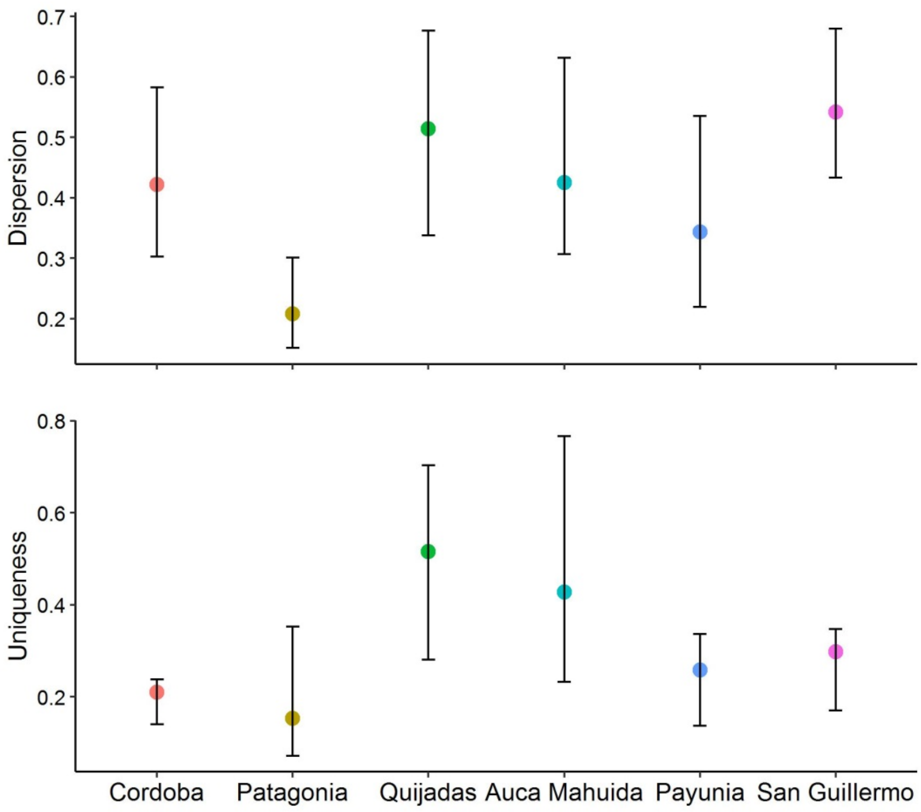

Fig S2. Isotopic diversity metrics by study site ordered from high to low human footprint. Isotopic dispersion is the weighted-mean distance to the center of gravity of the convex hull of all feathers per location, and isotopic uniqueness is the weighted-mean of distances to nearest neighbors in each site-specific isotopic space (Cucherousset and Villéger 2015). Isotopic ellipse area was 0.015 for Patagonia, similar for Payunia, San Guillermo and Auca Mahuida (0.034, 0.039 and 0.038), and larger for Cordoba and Quijadas (0.063 for both sites).

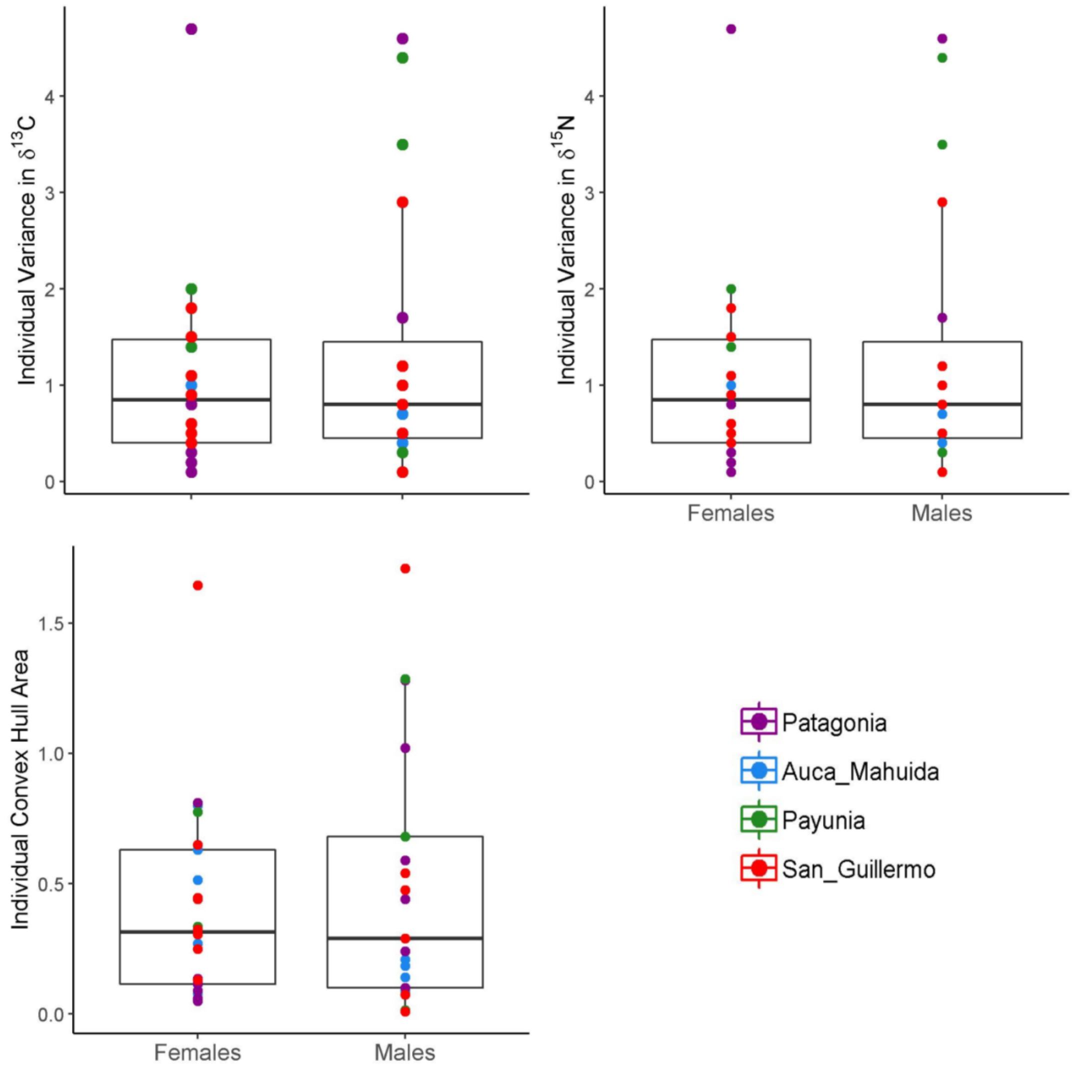

Fig S3. Variance (difference in range) and convex hull area of δ^{13}C and δ^{15}N isotopic signature of individuals with repeated measurements obtained via serially sampling (n = 4) primary feathers. Dots are presented color-coded by sampling location.

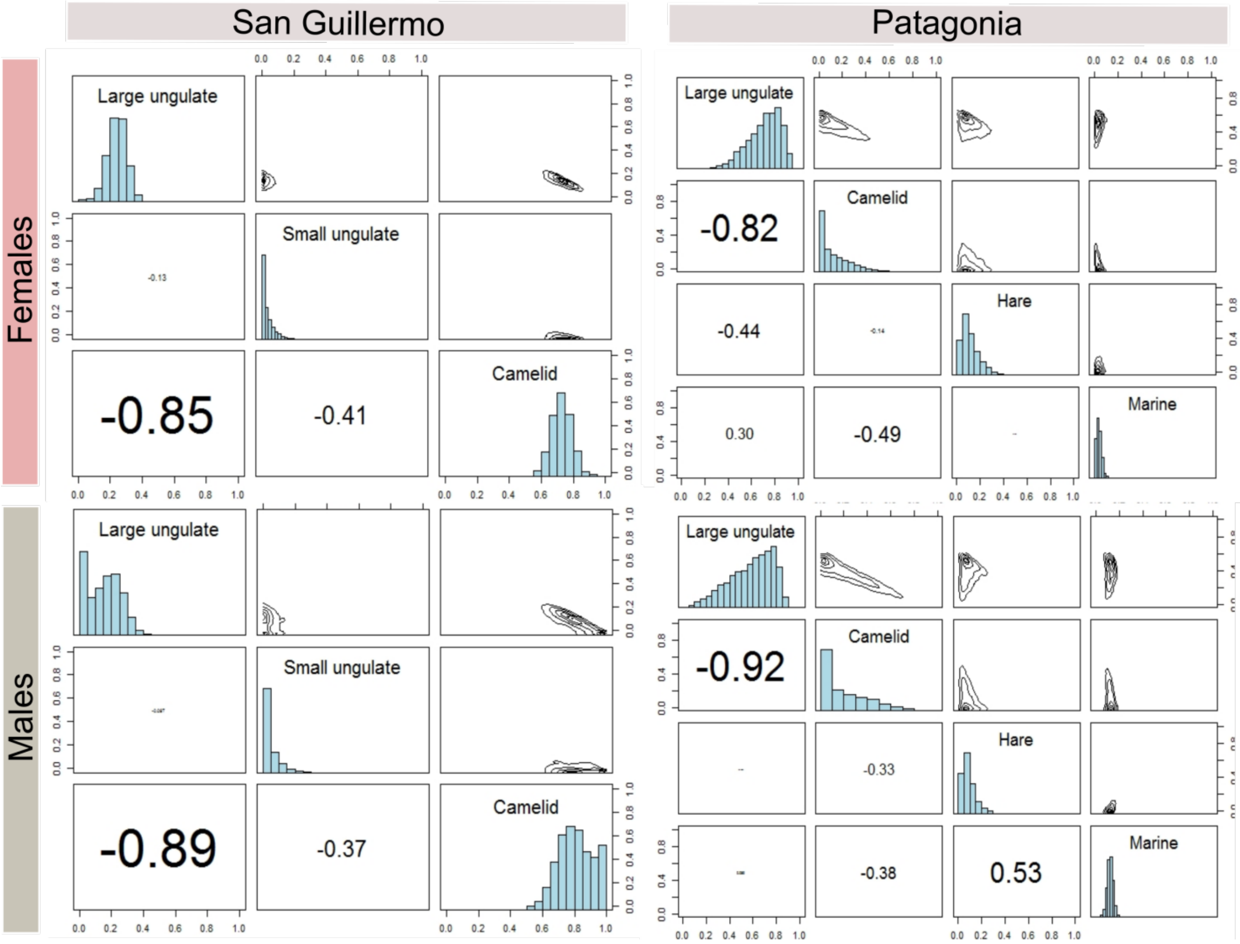

Fig S4. Diagnostic matrix plots illustrating correlations in posterior probabilities of dietary proportions in mixing models conducted for Andean condor females and males in Patagonia and San Guillermo.

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Monitoring vultures in the 21st Century: the need for standardized protocols

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A conservation challenge

Effective conservation relies on robust monitoring programmes to design and evaluate management actions (Nichols and Williams 2006). Large vertebrates with slow life history strategies present a challenge for monitoring given the necessary long-term investment of effort and resources. Furthermore, many of these vertebrates possess expansive habitat requirements, demanding large-scale monitoring approaches (Rudnick et al. 2009). For such species, localized monitoring efforts of limited duration can result in partial or even biased information, and delayed detection of threatened viability and population changes (Ogada et al. 2016). The development of practical, affordable and broadly applicable methods for monitoring vertebrates with slow life history traits remains a challenge for applied ecologists globally.

The use of non-invasive genetic-based techniques, in particular, has enabled the estimation of demographic parameters for many long-lived species that are elusive, wide-ranging or rare. The identification of individuals by their multi-locus genotypes enables a "capture-recapture" framework to estimate vital rates (such as survival and recruitment), and derive population size, growth and viability (Carroll et al. 2018). Rapid development of genetic techniques are making non-invasive monitoring more efficient and financially viable (Carroll et al. 2018). However, a "conservation genetic gap" has emerged between genetic research and its practical application, partially due to lack of access to expertise and funding by conservation managers, particularly in developing countries (Taylor et al. 2017). Despite best efforts to make genetic approaches accessible to wildlife managers, non-invasive genetic monitoring is generally conducted by researchers at academic institutions and rarely used in long-term monitoring programmes (Taylor et al. 2017).

Vultures – avian obligate scavengers – constitute a major conservation challenge for the 21st Century. Sixteen of 23 extant vulture species are currently at-risk of extinction;

vulture declines have been recent and rapid, and many species continue to exhibit range-wide contractions in both abundance and distribution (Ogada et al. 2016). These declines result from the confluence of the guild's intrinsic susceptibility to extinction (e.g., dietary specialization, extensive individual home ranges, slow demography) with anthropogenic impact (Ogada et al. 2012). Because of their strict dependence on ephemeral carrion resources, vultures are particularly vulnerable to dietary toxins such as lead pellets in hunted game, residual pharmeceutical compounds in livestock remains, and intentionally poisoned carcasses. The collapse of most vulture populations has raised awareness of the ecological, economic and cultural services these birds provide (Ogada et al. 2012). Vultures are a stabilizing force on the structure and dynamics of food webs, central in nutrient cycling and exchange, barriers to pests and disease epizootics, agents of carrion and waste disposal, important attractions for eco-tourism and culturally iconic species (Donázar et al. 2016). The recognition that ecological services provided by vultures are generally declining triggered global efforts to preserve them.

Efforts to rescue vulture populations have focused on reintroduction and rehabilitation, and the establishment of food supplementation stations, so-called "vulture restaurants" (Cortés-Avizanda et al. 2016). While many of these programmes have found success, a critical yet currently overlooked aspect of them are the scarcity of coordinated efforts to monitor vulture populations to obtain robust estimates of demographic attributes. Vultures present special challenges in monitoring as they often occur at low densities over expansive areas, breed and roost in sites that are remote and difficult to access, and possess long generation times (Donázar et al., 2016). Although coordinated cases of monitoring programmes exist (e.g., the International Bearded Vulture Monitoring network; http://www.gyp-monitoring.com/), these are limited to only a few localized areas, focused on particular species, and often methodologically inconsistent between programmes (Figure 1).

Standardized monitoring programmes that wildlife managers can implement on the ground, across vultures' ranges and between species would strengthen the management of both highly endangered as well as larger and healthier populations.

Herein, we compared the common techniques used to study vulture populations using Andean condors (*Vultur gryphus*) – a large, widely distributed vulture of conservation concern – as a case study (Figure 2). From this comparison, we identified the use of shed feathers as the most robust method for long-term and large-scale monitoring of avian scavengers across species and political boundaries. Further, we provide an effective, efficient and tested protocol for monitoring Andean condors via shed feathers, and call for its implementation by conservation practitioners at a continental scale.

Vulture monitoring techniques

Capture-based

For many longitudinal studies, mark-resight analyses of marked individuals via rings, wing bands, or bleached feathers are commonly employed (Figure 1). When sufficient sample sizes are obtained, analytical techniques that incorporate detection probability can yield demographic estimates readily comparable across studies (Hurley et al. 2013). Thus, mark-resight has proven effective for closely managed or studied populations –especially when rehabilitated or captive breeding individuals are tagged. However, this approach is difficult to apply over large spatial and temporal scales by managers given their expense, time requirements, and risks associated with capturing and handling wildlife, for both the vultures under study and researchers conducting the work (Rudnick, Katzner, & DeWoody, 2009).

Count-based

Many vulture monitoring programmes currently rely upon field counts of unmarked individuals (visual surveys), including counts at roosting sites, colonies, provisioned carcasses, fix point counts, road counts on vehicle or foot, and monitoring of occupancy of breeding sites (Figure 1). Given that these techniques can be implemented with little training by a large number of observers, they represent a useful approach for studies developed over large temporal and spatial scales, while allowing the involvement of citizen-scientists for outreach and education. Despite being technically simpler than other approaches, these estimates are demanding in time, labour and logistics (Rudnick, Katzner, & DeWoody, 2009). Estimation of sex ratios through this technique is unfeasible for monomorphic species, which include most species of vultures, potentially leading to overestimation of effective population sizes (Lambertucci et al. 2012). Further, estimated population parameters can present important biases due to repeated observations of the same individuals during the survey, inconsistencies of monitoring efforts among sites and times, and spatial-temporal concentration of individuals. For example, abundance estimates based on colonies are biased towards the breeding portion of populations (Rudnick et al. 2008), and age structure of vultures using communal roosts vary with the location and characteristics of perching sites (Lambertucci, Jácome, & Trejo, 2008).

Vulture restaurants – stations where carrion is routinely delivered to vultures – provide a unique opportunity to simultaneously monitor a large number of individuals and species that aggregate to feed despite the presence of observers (Cortés-Avizanda et al. 2016). However, data collected at these sites can be biased towards the most social, dominant, and abundant vulture species, or towards a particular segment within the population (e.g., birds with lower body condition, or some age or sex category). Furthermore, vulture restaurants are inconsistently distributed and are intended to be a short-term management practice to recover a species (Cortés-Avizanda et al. 2016); thus, they represent an unsuitable approach for long-term monitoring programmes of vulture populations.

Feather sampling

Non-invasively collected moulted feathers combined with molecular techniques allows robust estimates of demographic parameters for a variety of rare and elusive species (Rudnick, Katzner, & DeWoody, 2009), yet only a handful studies have used naturally shed feathers to assess vulture populations (Figure 1). Feathers provide a reliable source of high-quality DNA for individual identification and molecular sexing (Rudnick et al. 2005, Bayard de Volo et al. 2008), appropriate for capture-recapture analysis (Kapetanakos, 2014; Rudnick, Katzner, Bragin, & DeWoody, 2008) and estimation of minimum population size and sex ratios (Alcaide et al. 2010). Further, moulted feathers can reveal a population's age structure for species that change plumage coloration while maturing (Alcaide et al. 2010). Since genetic tagging is permanent, in contrast to bleached feathers or wing bands that are temporary, it is a particularly useful method to monitor long-lived species (Rudnick, Katzner, & DeWoody, 2009). When using this technique, important considerations in sampling designs must be made. Firstly, feather collection needs to account for behavioural differences in space use and foraging between individuals of different sex, age and breeding status to obtain a representative sample of the population under study (Katzner, Ivy, Bragin, Milner-Gulland, & DeWoody, 2011; Lambertucci, Jácome, & Trejo, 2008). Additionally, the size of the feather and time since moulting affects DNA yields, with large and freshly moulted feathers being most reliable. Secondly, prescreening of DNA yields and estimations of genotyping errors are required steps to ensure robust results (Bayard de Volo, Reynolds, Douglas, & Antolin, 2008). Further, approaches based on non-invasive sampling of DNA require laboratory analyses, which could be challenging for managers to implement themselves. Yet, molecular techniques continue to be improved for their implementation by personnel with limited training, and a large number of laboratories offer these services (see Supplementary material S2). Even with laboratory services, this approach is more cost effective when compared to live-capturing and marking individuals (Carroll et al. 2018).

Baited camera traps

The use of remote cameras at baited stations can provide data on complete scavenger communities over large scales when standardized protocols are implemented by professional and citizen scientists (Jachowski et al. 2015). Further, single estimates of population densities can be obtained via capture-recapture models of uniquely identifiable individuals (e.g. via moulting patterns or natural marks such as crest shape), or from unmarked birds (Steenweg et al. 2017). This technique requires detailed standardization of camera configuration and station arrangement, and does not retrieve sex structure for monomorphic species. Further, carrion size, location and season can influence the use of baited stations by scavenger communities (Turner et al. 2017). The most time-consuming step associated with this method is photo processing, but an increasing number of tools are available for the efficient management and sharing of camera trap data of large scale studies, and citizen-science web portals can be used for crowdsourcing image analysis (Steenweg et al. 2017). It has been suggested that interconnected remote camera networks will be key for global monitoring of biodiversity in the near future (Steenweg et al. 2017). However, similar to DNA-based non-invasive approaches, this method remains largely unemployed to monitor vulture populations (Figure 1).

Andean condors – a case study

To compare the potential of emerging non-invasive approaches to estimate population parameters for vultures, we applied count-based, baited camera traps and feather sampling approaches to study Andean condors (*Vultur gryphus*) in a pristine area of the high Andes of Argentina, San Guillermo National Park (SGNP), where no previous estimates of condor population size were available. Surveys at communal roosts are commonly used to monitor Andean condors (see Supplementary material S1), but resulted an unfeasible approach for this area, as for many others in condors' distribution, due to the remote location and relatively small size of perching sites. Thus, we tested the efficiency of genetic monitoring of moulted feathers and remote camera traps to estimate Andean condor minimum population size, age and sex ratios.

We monitored via one camera trap eight standardized food patches offered simultaneously in open plains during March-April, 2017. Each station consisted of carrion remains (obtained from a local slaughterhouse), and remained active for 7 days. All stations were used by facultative scavengers present in the area (mountain caracaras *Phalcoboenus megalopterus*, and culpeo foxes *Lycalopex gymnocercus*) while Andean condors used 6 of the 8 stations in groups that ranged from 3-19 birds. Given that condor feeding groups are dynamic, we estimated mean sex and age ratio per station from the ratios registered in camera trap photos that allowed the classification of >70% of the birds present. We identified immature birds (juveniles and sub-adults) by their brownish-gray plumage and adult birds from their black and white plumage; males were identified by the presence of a crest. We found that the structure of the feeding groups differed across stations, with proportion of males ranging from 0 to 80% and proportion of adults from 0 to 93%. Overall, we observed large disparity in the use of standardized baited station by Andean condors. The type of carrion provided and the complexity of the area surrounding each station probably determined their use by condors, given that we had observed more than 60 individuals feeding upon a carcass of a native camelid in the area. Thus, spatial comparisons of demographic parameters obtained with this technique are likely unreliable even with standardized field protocols.

We collected moulted feathers (12-70 cm long) at the base of roosts and condor feeding sites during summer 2013. We extracted DNA from 151 feathers, and successfully genotyped 131 samples at 3-5 species-specific, neutral markers (probability of identity < 0.01; Perrig, Donadio, Middleton, & Pauli, 2017). We identified 89 birds, of which 30% were males (Perrig, Donadio, Middleton, & Pauli, 2017). We aged remiges and rectrices feathers (>19 cm, n = 49) according to coloration: 70% of the samples were black, or black and white, and classified as belonging to adults, whereas 30% brown or grey feathers were classified as belonging to immature birds (Alcaide, Cadahía, Lambertucci, & Negro, 2010, Supplementary material S2). Overall, the use of shed feathers resulted in higher sampling rates than baited camera traps, reducing heterogeneous sampling due to behavioral differences between sex and age classes. We developed 2 multiplex reactions for 6 polymorphic markers (Supplementary material S2) that allow the identification of 99% of 278 feathers genotyped across central Argentina (Padró et al. 2018). We provide a detailed protocol on Andean condor feather sampling in Supplementary material S2. The use of this readily available and affordable protocol (~U$15 per sample) on feathers collected from a variety of sources (e.g. roosting, feeding sites, and rehabilitated or dead individuals) will yield transboundary estimates of Andean condor population demography.

A unified protocol

The precipitous declines of most vultures globally stress the relevance of range-wide and long-term monitoring programmes for vulture conservation (Jachowski, Katzner, Rodrigue, & Ford, 2015). Yet, we found that vulture studies remain restricted to specific regions and species, and mostly brief in temporal scale. While transboundary conservation actions targeted at vulture populations have been established – like the international Multi-species Action Plan to Conserve African-Eurasian Vultures (vultures MsAP) approved in 2017 (Botha et al. 2017) – such agreements are dependent upon demographic parameters to evaluate the achievement of settled conservation goals, though no vulture monitoring protocol is provided. With the understanding that some monitoring techniques are particularly suitable for a species or region, standardized approaches that allow international collaboration and comparison of estimated demographic parameters are necessary for managing species as vagile and long-lived as vultures. We call on scientists and organizations focused on vulture conservation (e.g. Saving Asia’s Vultures form Extinction, [SAVE], VulPro, Hawk Mountain Sanctuary) to promote and use standardized monitoring programmes. As we showed for Andean condors, non-invasive monitoring approaches based on moulted feather sampling provide robust, complete and cost-effective demographic data compared to traditional techniques. Similar species-specific laboratory and sampling protocols should be used to generate profiles of individual birds shared via web repositories. We see this as a promising approach for international collaboration towards continental vulture monitoring programmes.

Genetic analysis of shed feathers have been thoroughly tested, repeatedly validated (Rudnick, Katzner, & DeWoody, 2009), and previously shown to outperform traditional monitoring approaches (Katzner, Ivy, Bragin, Milner-Gulland, & DeWoody, 2011), but remain rarely used by practitioners for the estimation of demographic parameters. Indeed, shed feathers have been successfully used to monitor birds via “mark-recapture” modeling (Kapetanakos, 2014; Olah, Heinsohn, Brightsmith, & Peakall, 2017; Rudnick, Katzner, Bragin, & DeWoody, 2008) or via turnover rates of occupied territories (Rudnick, Katzner, Bragin, Rhodes, & DeWoody, 2005; Selås, Kleven, & Steen, 2017). These studies generally require a large number of feathers to obtain a representative sample of the population, or sufficient recapture rates, and laboratory and analytical methods to control for genotyping errors (Kapetanakos, 2014; Rudnick, Katzner, Bragin, & DeWoody, 2008). Simple non-invasive protocols, though, yield standardized and robust results, with affordable field efforts and laboratory cost. Thus, we encourage continued efforts to increase the accessibility of non-invasive genetic techniques beyond primary research, and for practitioners to adopt these approaches for monitoring large and long-lived birds.

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Data accessibility

Data available via the Dryad Digital Repository http://doi.org/10.5061/dryad.gd1t410 (Perrig, Lambertucci, Donadio, Padró, & Pauli, 2019).

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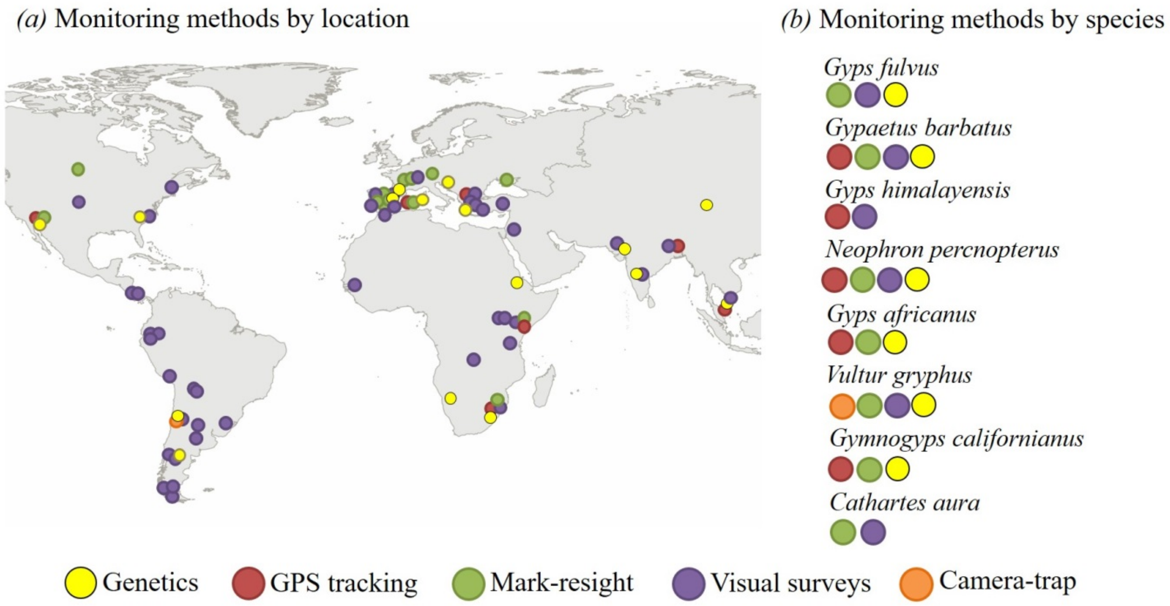

Figure 1. Non-exhaustive review of methods used to study vulture populations (a) globally (b) by representative vulture species. See Supplementary material S1 for references.

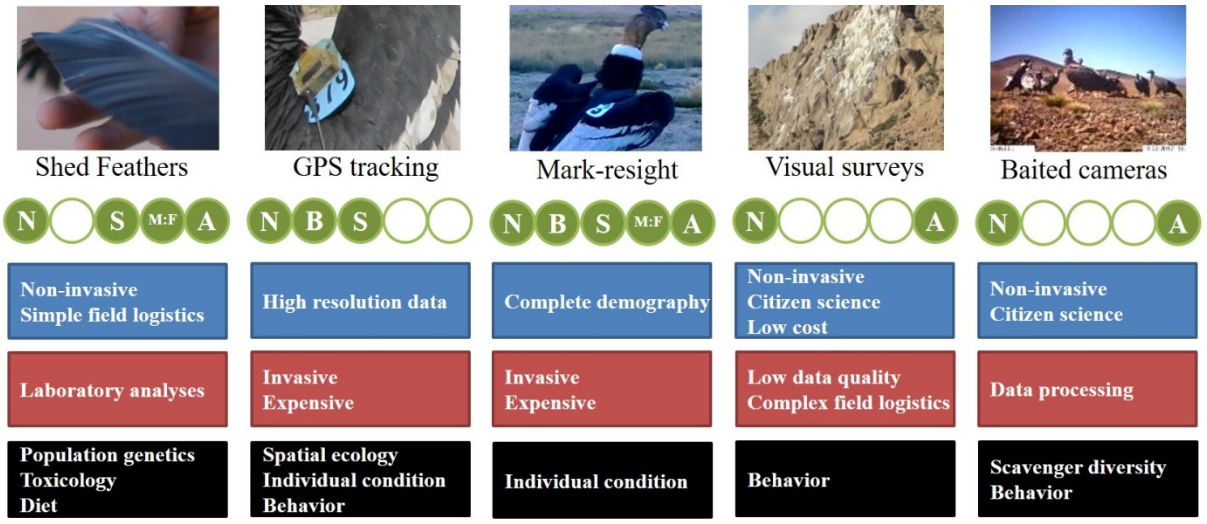

Figure 2. Comparison of sampling techniques used to monitor vulture populations based on data products [green; population size [N], proportion adult females breeding [B], survival rate [S], sex ratio [M:F], and age ratio [A]), advantages (blue), disadvantages (red), and additional data generated (black)].

Supplementary material S1

Table S1. Some examples of approaches used to obtain demographic data on vulture populations across the globe.

Technique	*Species*	Location	Reference
Visual counts	*Aegypius monachus*	Europe	(Fernández-Bellon *et al.* 2016)
Visual counts	Complete guild	Africa	(Pomeroy *et al.* 2015); (Pomeroy *et al.* 2011)
Visual counts	Complete guild	Africa	(Virani *et al.* 2011)
Visual count; GPS tracking	Complete guild	Asia	(Clements *et al.* 2013)
Visual counts	Complete guild	Europe	(Poirazidis 2017)
Mark-resight	*Neophron percnopterus*	Europe	(Sanz-Aguilar *et al.* 2017)
Mark-resight; GPS tracking	*Neophron percnopterus*	Europe	(Sanz-Aguilar, De Pablo & Donázar 2015)
Mark-resight	*Neophron percnopterus*	Europe	(Lieury *et al.* 2015)
Visual counts	*Neophron percnopterus*	Eurasia	(Bilgecan, Tavares & Bilgin 2017)
Visual counts	*Neophron percnopterus*	Europe	(Oppel *et al.* 2017)
Visual counts	*Neophron percnopterus*	Europe	(Tauler *et al.* 2015)
Visual surveys	*Neophron percnopterus*	Europe	(Cortés-Avizanda *et al.* 2015)
GPS tracking	*Neophron percnopterus*	Europe	(Oppel *et al.* 2015)
Visual counts	*Neophron percnopterus*	Europe	(Dobrev *et al.* 2016)

Visual counts	*Gypaetus barbatus*	Europe	(Milanesi *et al.* 2015)
GPS tracking	*Gypaetus barbatus*	Africa	(Reid *et al.* 2015)
Mark-resight	*Gypaetus barbatus*	Europe	(Schaub *et al.* 2009)
Mark-resight	*Gypaetus barbatus*	Europe	(Oro *et al.* 2008)
Visual counts; Mark-resight	*Gypaetus barbatus*	Europe	(Margalida, Colomer & Oro 2014)
Mark-resight	*Gyps africanus*	Africa	(Monadjem *et al.* 2018)
Visual counts; Genetics	*Gyps bengalensis and Gyps indicus*	Asia	(Arshad, Chaudhary & Wink 2009)
Visual counts	*Gyps bengalensis*	Asia	(Thakur 2015)
Visual counts	*Gyps coprotheres*	Africa	(Schabo *et al.* 2017)
Mark-resight	*Gyps fulvus*	Europe	(Chantepie *et al.* 2016)
Visual counts	*Gyps fulvus*	Middle East	(Freund *et al.* 2017)
Visual counts	*Gyps fulvus*	Europe	(Van Beest *et al.* 2008)
GPS tracking	*Gyps himalayensis*	Eurasia	(Sherub *et al.* 2017)
Visual counts	*Gyps himalayensis*	Africa	(Paudel *et al.* 2016)
Visual counts	*Gyps ruepelli*	Africa	(Virani *et al.* 2012)
Visual counts	*Trigonoceps occipitalis*	Africa	(Murn *et al.* 2016)
Visual counts	*Trigonoceps occipitalis*	Asia	(Murn *et al.* 2015)
Visual counts	All guild	Africa	(Virani *et al.* 2011)
Visual counts	*Trigonoceps occipialis, Torgos tracheliotos, Gyps africanus*	Africa	(Murn & Botha 2016)
Visual counts	*Vultur gryphus*	South America	(Ríos-uzeda & Wallace 2007)

Genetics	*Vultur gryphus*	South America	(Alcaide *et al.* 2010)
Visual counts	*Vultur gryphus*	South America	(Sarno, Franklin & Prexl 2000)
Visual counts	*Vultur gryphus*	South America	(Lambertucci, Jácome & Trejo 2008)
Visual counts	*Vultur gryphus*	South America	(Lambertucci 2010)
Visual counts	*Vultur gryphus*	South America	(Kusch 2004)
Visual counts	*Vultur gryphus*	South America	(Donázar & Feijóo 2002)
Visual counts	*Vultur gryphus*	South America	(Koenen 2000)
Visual counts - camera trap	*Vultur gryphus*	South America	(Cailly, Ortiz & Borghi 2013)
Visual counts	*Vultur gryphus*	South America	(Martínez, Naoki & Vedia-Kennedy 2010)
Visual counts	*Vultur gryphus*	South America	(Herrmann, Costina & Costina 2010)
Visual counts	*Vultur gryphus*	South America	(Naveda-Rodríguez *et al.* 2016)
Baited cameras	*Vultur gryphus*	South America	(Escobar-Gimpel *et al.* 2015)
Visual counts	*Vultur gryphus*	South America	(Astudillo *et al.* 2011)
Visual counts	*Vultur gryphus*	South America	(Méndez *et al.* 2015)
Genetics	*Vultur gryphus*	South America	(Perrig *et al.* 2017)
Genetics	*Vultur gryphus*	South America	(Padró *et al.* 2018)
VHF tracking, Mark-resight	*Gymnogyps californianus*	North America	(Kelly *et al.* 2015)

Mark-resight	*Cathartes aura*	North America	(Houston *et al.* 2007)
Visual counts	*Cathartes aura*	South America	(Zilio, Verrastro & Borges-Martins 2014)
Mark-resight	*Gymnogyps californianus*	North America	(Bakker *et al.* 2017)
Visual counts	*Cathartes aura, Coragyps atratus*	North America	(Avery 2004)
Visual counts, Genetics	*Coragyps atratus*	North America	(Blackwell *et al.* 2007)
Visual counts, Genetics	*Coragyps atratus*	North America	(Parker, Waite & Decker 1995)
Visual surveys	*Cathartes aura*	Central America	(Porras-Peñaranda, Robichaud & Branch 2004)
Visual surveys	*Cathartes aura, Coragyps atratus*	South America	(Goldstein & Hibbitts 2004)
Genetics	*Gyps bengalensis*	Asia	(Johnson *et al.* 2008)
Genetics	*Gypaetus barbatus*	Europe	(García *et al.* 2012)
Genetics	*Gyps fulvus*	Europe	(Mereu *et al.* 2017)
Genetics	*Gyps barbatus*	Africa	(Krüger *et al.* 2014)
Genetics	*Neophron percnopterus*	Europe	(Agudo *et al.* 2011)
Genetics	*Gyps bengalensis, Gyps africanus, Gyps indicus and Gyps fulvus*	NA	(Arshad *et al.* 2009)
Genetics	*Aegypius monachus*	Asia and	(Poulakakis *et al.* 2008)

		Europe	
Genetics	*Gyps fulvus*	Europe	(Le Gouar *et al.* 2008)
Genetics	*Gypaetus barbatus*	Europe, Asia, Africa	(Godoy *et al.* 2004)
Genetics	*Gyps bengalensis, Gyps tenuirostris, Sarcogyps calvus*	NA	(Kapetanakos, Lovette & Katzner 2014)

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Supplementary material S2

Andean condor molted feather sampling to obtain demographic parameters

Feather collection and DNA extraction

We collected molted feathers from Andean condors in feeding and active roosting sites (Padró, Lambertucci, Perrig, & Pauli, 2018; Perrig, Donadio, Middleton, & Pauli, 2017). Data on Cathartidae molt patterns are few (Chandler, Pyle, Flannery, Long, & Howell, 2010), and no molt information is available for Andean condors. However, molt pattern in California condors indicates that condors' primary molt occurs in a two-year cycle, with the replacement of feathers occurring in a ~4 months interval during summer (Snyder, Johnson, & Clendenen, 1987). Feathers in good condition (i.e., recently molted and undamaged) were stored in envelopes at room temperature for their analysis. DNA was extracted from the 1 cm basal tip of the calamus and from the superior umbilicus (Horváth, Martínez-Cruz, Negro, Kalmar, & Godoy, 2005); for large feathers we only used the superior umbilicus. We followed a standard DNA extraction protocol (QIAamp DNA micro Quit, QIAGEN, Valencia, California). We quantified DNA yield using a NanoDrop, or Qbit when yield was <30 ng μl^{-1}, and evaluated DNA quality from the 260/280 absorbance ratio of each sample using a NanoDrop (ratio 1.8 is indicative of "pure" DNA; Thermo Fisher Scientific 2008). As expected from previous research (Vili et al., 2013), we found no relation between feathers length and the quantity or quality of DNA obtained (Fig. S1). However, we highlight the importance of using remiges and rectrices in good condition for more precise aging of the individual (see below).

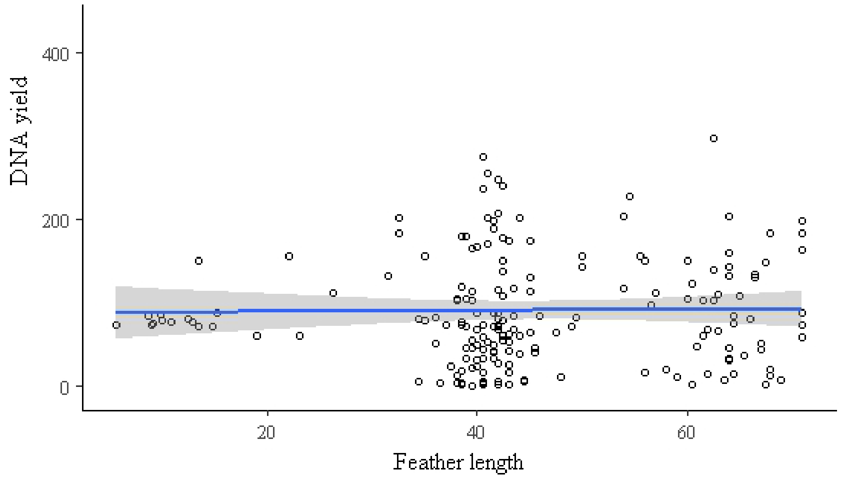

Figure S1. DNA yield and purity extracted from Andean condor molted feathers estimated using a spectrophotometer in relation to feather length (cm).

Individual identification

Analysis of 300 feathers collected across Argentina (Padró, Lambertucci, Perrig, & Pauli, 2018) indicates that genotypes at the 6 most polymorphic markers allows the discrimination of >99% of individuals with high confidence (Figure S2). We designed 2 multiplex reactions of 3 markers each for the identification of individuals, and tested them in 38 individual birds.

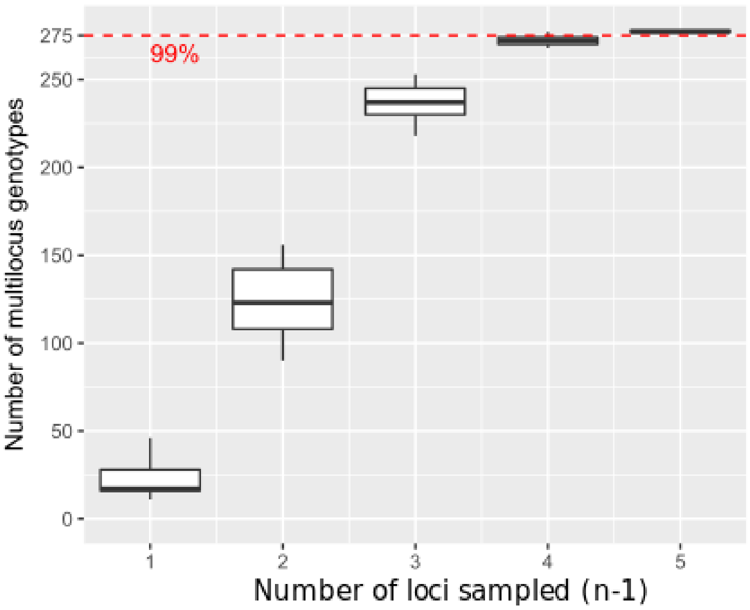

Figure S2. Genotype accumulation curve and information for the 6 most polymorphic markers

Multiplex PCRs were performed in a final volume of 10µl with individual mixes containing 0.6 µL template DNA, 1x PCR buffer, 10.0mM dNTP, 5U/ µl Taq (HotStarTaq DNA Polymerase, Qiagen Cat No./ID 206143), 0.5µM fluorescently-labelled forward and reverse primers grouped as indicated in Table S2. PCR profiles consisted on (Q) a 15 min denaturation step at 95 °C, 10 touch-down cycles of 30 s at 94 °C, 90 s at 62.5 °C decreasing 0.5 °C per cycle, 1 min at 72 °C, and 25 final cycles of 30 s at 94 °C, 90 s at 56 °C and 1 min at 72 °C, with a final 10 min step at 72 °C; (R) 15 min denaturation step at 95 °C, 35 cycles of 30 s at 94 °C, 90 s at 56 °C and 1 min at 72 °C, with a final 10 min step at 72 °C. Amplified PCR products were scored via fluorescent DNA fragment analysis on ABI 3730xl DNA analyzer (Applied Biosystems) and analyzed with GeneMapper v5 software (Applied Biosystems).

Table S2. Number of alleles (k), heterozygosity observed (HObs) and expected (HExp), polymorphic information content (PIC), allele size, fluorescent used and multiplex protocol (see text for details) for 6 markers developed for Andean condors at two multiplex reactions.

Primer	Primer sequence (5'-3')	Motif	k	HObs	HExp	PIC	Size	Color	Multiplex
Vg021	F: AAAGACTGAGTTTCTTCATTTCCC	AAAC(40)	4	0.68	0.7	0.64	237-284	HEX	Q
	R: CATCCAGGTCACAGCTTTCC								
Vg001	F: AAACCACAACAGAGGGAGACG	ATGG(56)	7	0.722	0.743	0.69	239-275	FAM	Q
	R: AGCCGAACAGAGGTAAGGGC								
Vg009	F: CGGGTAGAGTGTTAAGGTGTGG	TTCC(44)	6	0.702	0.741	0.69	286-325	NED	Q
	GACGTCAGAAGCAACACATGG								
Vg015	F: TGAAGAATTACCAAGAAAGTTTGCC	ATCT(40)	6	0.741	0.735	0.65	207-241	FAM	R
	R: CGATGAAATACTTGGGCCTAGC								
Vg005	F: GACAGGTCATAAATCTCAAATCCC	TTCC(44)	9	00.714	0.751	0.71	230-279	NED	R
	R: TCCATCCACTGTCTCTCACC								
Vg007	F: GGTGCCGCCTGTCTCTCC	ACTG(44)	15	0.741	0.735	0.71	273-357	HEX	R
	R: GGCAGAGAAGCGCATTAGCC								

Molecular sexing

Molecular sexing was accomplished by amplification of sex-chromosome-link CHD genes through the universal primers P2 and P8 following (Griffiths, Double, Orr, & Dawson, 1998). PCR product needs to be differentially cut using the restriction enzyme HaeIII (Promega) to allow fragment separation by electrophoresis on 3% agarose gels (males, ZZ; females ZW; Griffiths, Double, Orr, & Dawson, 1998). For this last step, individual mixes containing template DNA 2 µl, enzyme 10x buffer 2µl, acetylated BSA (10 µg/µl) 0.2µl, water 15.3µl. and restriction enzyme (10u/µl) 0.5µl were incubated at 37ºC for 4 hours. See Padró, Lambertucci, Perrig, & Pauli (2018) for results.

Age determination

Andean condor age classes can be inferred from feather coloration: plumage of immature birds (juveniles and subadults, up to 5-6 years old) transition from dark brown to brownish gray until becoming completely black with white coverts on the upper wing when turning into adults (>6 years old; Figure S3) (Alcaide, Cadahía, Lambertucci, & Negro, 2010). To test the reliability of feather color classification, we evaluated inter-observer agreement on age discrimination of molted feathers. The determination of age category of 76 molted feathers by 3 independent experts resulted in 90% agreement. Thus, we recommend agreement by at least two trained observers before a feather is aged based on its color, and applying a strict rule of thumb: classify feathers as black, or black and white, as belonging to adults versus brown or grey to immature birds (Figure S3). It is also critical the use of recently molted remiges and rectrices feathers to improve reliability on classification since smaller feathers are more difficult to differentiate.

Figure S3. Andean condor shed feathers categorized as belonging to an immature individual (a) and adult (b).

Available laboratory resources in South America

The molecular methods presented above are routine services that many genetic laboratories can provide across the globe. Herein we provide a non-exhaustive list of potential laboratories that could provide genotyping services in South America. We call for the identification of main laboratories to conduct these analyses by region to reduce costs of producing fluorescently labeled primers.

http://www.ege.fcen.uba.ar/servicios/secuenciador/

http://tecnologiagenomica.org/?page_id=29

https://inta.gob.ar/documentos/formularios-del-servicio-secuenciacion-de-acidos-nucleicos-adn-por-electroforesis-capilar

http://www.cerela.org.ar/docs/servicioDeSecuenciacion.pdf

https://www.macrogenlatam.com.ar/servicios.html

http://www.indear.com/servicios/

https://www.uco.es/servicios/scai/impresos/GEN/G-GEN-01%20Guia%20de%20Usuario%20de%20Genomica%20rev%201.pdf

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