BEHAVIORAL ECOLOGY – ORIGINAL RESEARCH

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

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Abstract
Sexual segregation is widely reported among sexually dimorphic species and generally attributed to intraspecific competition. Prey diversity and human activities can reinforce niche segregation by increasing resource heterogeneity. Here, we explored trophic and spatial sexual segregation in the only avian scavenger that exhibits pronounced sexual size dimorphism (up to 50% difference in body mass) and a highly despotic social system, the Andean condor (*Vultur gryphus*). We predicted that larger and dominant males would exclude smaller and subordinate females from high-quality resources, leading to sexual segregation particularly in human-dominated landscapes showing increased prey diversity. We compared resource use between females and males across six sites in Argentina featuring a range of prey diversity via stable isotopes analysis of molted feathers ($n = 141$ individuals). We then focused on two sites featuring contrasting levels of prey diversity and quantified assimilated diet via stable isotopes and space use via GPS monitoring ($n = 23$ and 12 tagged individuals). We found no clear differences in isotopic niche space, individual variation in isotopic signature, or assimilated diet between females and males. However, there were differences in foraging locations between sexes, with females apparently using areas of fewer food resources more frequently than males. Local conditions defined the dynamics of fine-scale sexual differences in foraging sites; yet, unpredictable and ephemeral carrion resources likely prevent segregation by sexes at the landscape scale. Our study highlights complex dynamics of sexual segregation in vultures and the relevancy of analyses under multiple spatial–temporal scales to explore segregation in social species.

Keywords Molted feathers · Movement ecology · Social foraging · Stable isotopes · Vulture

Introduction

Competition is a central mechanism shaping the natural history of species and community assemblages, and driving evolutionary change (MacArthur 1958). Given that

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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 composed of individuals that are either specialists or broad generalists (Bolnick et al. 2003). Such strategies to limit individual similarity often delineate according to sex and age groups (Shoener 1986). Sexual segregation in resource use, in particular, is a common mode by which vertebrates minimize intraspecific competition, especially by species showing pronounced sexual dimorphism (De Lisle and Rowe 2015).

Sexual segregation across avian species has received a great deal of attention due to the conspicuous sexual dimorphism that characterize many species of birds (Catry et al. 2005). Dietary and spatial segregation between sexes is widespread, and have been explained via two main, competing hypotheses. 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 behavior (Catry et al. 2016). Alternatively, the social dominance hypothesis suggests that sexual segregation arises from the despotic exclusion of subordinate individuals from favored resources (Catry et al. 2005). Such social dominance in dimorphic species is often mediated via sexual selection, e.g., male–male competition in American redstart (*Setophaga ruticilla*) results in larger and dominant males that force 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 (Bennett et al. 2019).

Although 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 can be mediated by competitive interactions for diverse resources, and this can change according to environmental context (Jones and Post 2016). Increasing resource diversity and environmental heterogeneity generally increases resource differentiation between conspecifics, and provides opportunities for resource segregation within (Robertson et al. 2015) and among populations (Rosenblatt et al. 2015). Human activities can enhance intraspecific segregation by changing resource diversity and habitat quality. For instance, adult female black bears (*Ursus americanus*) rely more heavily on human-derived foods than adult males (Kirby et al. 2016). Human activities can yet have the opposite effect by homogenizing and increasing the availability of food resources. Habitat fragmentation, for example, reduces prey diversity, and thus, trophic niche size of aquatic top predators (Layman

et al. 2007). It is difficult to predict how anthropogenic activities will alter resource use of populations, especially between sexes.

Andean condors (*Vultur gryphus*) are highly mobile, obligate scavengers that feed opportunistically over a broad geographic area and a range of ecological conditions (Perrig et al. 2020; Duclos et al. 2020). While most vultures show moderate reversed sexual dimorphism, Andean condor males can 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 (Ferguson-Lee and Christie 2001; Alarcón et al. 2017). This pronounced sexual dimorphism is associated with strong sexual despotism: condors feed in well-defined social hierarchies with males displacing females (Wallace and Temple 1987; Marinero et al. 2018) and accessing more food from carcasses (Donázar et al. 1999). Sexual dimorphism also appears to result in temporal partitioning between the sexes since males can have earlier foraging trips to exploit 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 stronger human influence (Donázar et al. 1999). Human-dominated areas are generally regarded as riskier (Speziale et al. 2008) and associated with anthropogenic sources of mortality (Pauli et al. 2018; Plaza and Lambertucci 2019). Thus, sex-based despotism has been linked to higher physiological costs (Gangoso et al. 2016) and mortality rates among female condors resulting in a pronounced male-skewed adult sex ratio (Lambertucci et al. 2012). While social hierarchy and temporal partitioning have 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 free-range domestic ungulates 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 space and diet across a range of environmental conditions. We hypothesized that the degree of segregation between Andean condor females and males would be a function of local prey diversity. Since anthropogenic activities increased prey diversity for condors at our study sites (e.g., introducing exotic herbivores; Fig. 1), we predicted that larger human footprint would provide greater opportunities for condor sexual segregation. Specifically, we predicted that the niche breadth of the population

Fig. 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 84 km buffers surrounding each study site. Prey diversity was estimated via pellet content analyses conducted for this and previous studies (see supplementary material S1). We do not have information on condor diet in Córdoba or Quijadas
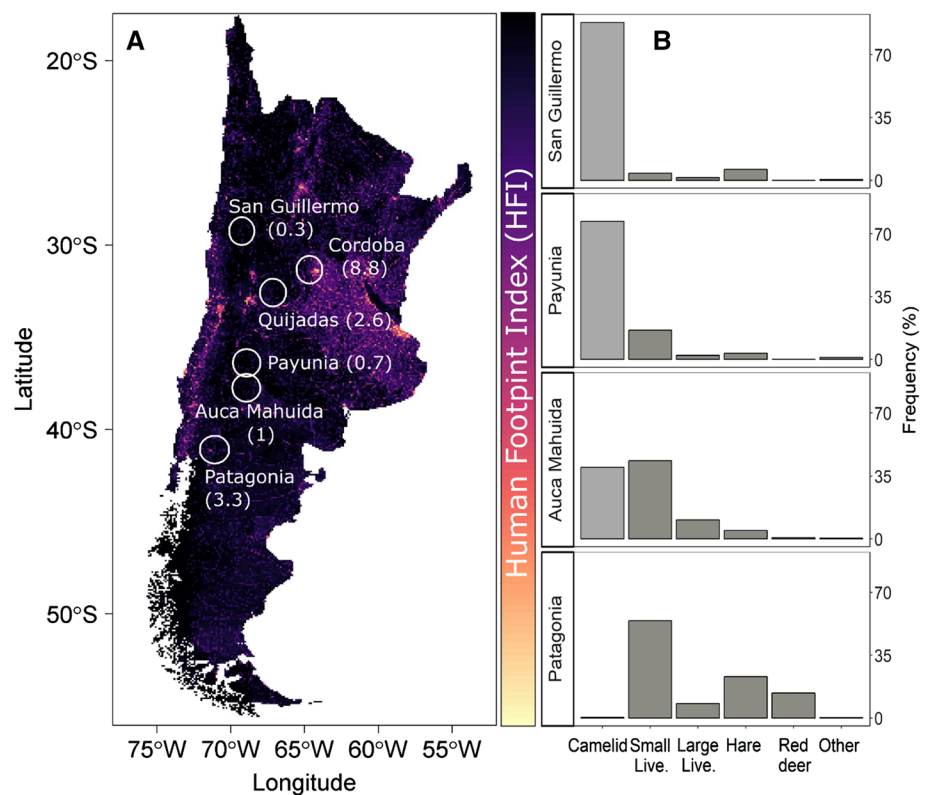
as well as trophic and spatial niche differentiation between sexes would increase with increasing human footprint. We also predicted that females, the subordinate sex, would forage in areas with higher human footprint than males across seasons. To test these predictions, we focused on adult condors —whose smaller home ranges compared to immatures anchors them to local conditions (Padró et al. 2019; Guido et al. 2020)— and analyzed dietary and spatial sexual segregation while foraging across six sites in Argentina that range from near-pristine to human-dominated.

Methods

General approach

We characterized Andean condor diet at six study sites via pellet content analysis (supplementary material S1) or published information (Lambertucci et al. 2009; Perrig et al. 2017). We then analyzed $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios of individually identified and aged, molted feathers to compare sexual segregation in diet across these sites. Lastly, we focused on two sites on opposing ends of human footprint and prey diversity to compare assimilated biomass via stable isotope analysis and spatial segregation via GPS locations of tracked birds. We evaluated foraging locations of females and males during warm and cold seasons to explore if the

putative reduced foraging opportunities in the cold period would increase competition and niche segregation between the sexes.

Study areas

Our study area encompasses four semiarid landscapes in the Puna, Monte, Chaco, and Patagonia regions of central-western Argentina (between 30°–44° S Latitude and 71°–67° W Longitude), under a range of human footprint and prey diversity (Fig. 1). Within the Puna region, we sampled in San Guillermo National Park (hereafter "San Guillermo"; 166 km²), located within one of the most pristine landscapes of South America. This area sustains large populations of native camelids (vicuñas *Vicugna vicugna* and guanacos *Lama guanicoe*), which provide an important food resource for condors, with rangelands to the east of the park (Perrig et al. 2017). In the Monte region, we sampled in two provincial reserves, Payunia (6641 km²) and Auca Mahuida (770 km²), that support large guanaco populations and are grazed by livestock at low densities (Palacios et al. 2012; Schroeder et al. 2014), both of which support Andean condors (Table S1). In the central Mountains of the Chaco region, we sampled in Sierra de las Quijadas National Park (hereafter "Quijadas"; 735 km²) and the Córdoba mountains (Fig. 1), where extensive ranching has functionally replaced native herbivores with livestock (Díaz et al. 1994). In northwestern

Patagonia (hereafter "Patagonia"), Rio Negro province, we sampled the largest population of Andean condors (Padró et al. 2018) sustained through free-ranging livestock (mostly sheep *Ovis aries* and cow *Bos taurus*) and exotic game species (red deer *Cervus elaphus* and hares *Lepus europaeus*) that have largely replaced native camelids (Lambertucci et al. 2009). Herein, Patagonia and San Guillermo serve as two areas representing opposing conditions: Patagonia features relatively high human influence and high prey diversity while 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) identified by plumage coloration (Perrig et al. 2019). We focused our analyses on adults that are anchored to their nesting locations and have annually stable and smaller home ranges compared to immatures (Padró et al. 2019; Guido et al. 2020). We conducted DNA fingerprinting of all feathers at 13 microsatellites loci (2–15 polymorphic alleles per loci) and performed molecular sexing via amplification of the sex chromosome-linked CHD gene (see Padró et al. 2018 for details). We used mass spectrometry to analyze $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios from ~5 cm of the distal extreme of 141 flight feathers of individual birds (Perrig et al. 2017). Specifically, we sampled 20 females and 22 males from Patagonia, 21 and 12 from San Guillermo, 7 and 11 from Córdoba, 7 and 10 from Payunia and Auca Mahuida, and 6 and 8 from Quijadas. For 41 flight feathers from 4 of our study sites, 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. 2009). The isotopic composition of feathers reflect diet during molt (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, when adults are likely breeding (Snyder et al. 1987; Zuberogoitia et al. 2018) and, thus, maintain relatively small foraging areas. We estimated measurement precision by analyzing ~20% of the feathers in duplicate and found little differences between replicates for both $\delta^{13}C$ (difference = 0.03‰) and $\delta^{15}N$ (difference = 0.03‰). We characterized the isotopic signature of the main prey items of Andean condors at our study sites (Fig. S1) by collecting hair opportunistically or via published information from 2 of our 6 study areas (Perrig et al. 2017; Lambertucci et al. 2018).

We compared spatial segregation between Andean condor adult females and males in Patagonia and San Guillermo by tracking 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 (more details in Perrig et al. 2020). We collected one location every hour (22 individuals) or 15 min (13 individuals) according to the GPS device utilized. We used this information to describe locations where the birds were most likely foraging as described in Perrig et al. (2020). Briefly, we defined foraging sites via GPS locations recorded 5–8 h 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.

To explore differences between sexes in space use while foraging, we modeled habitat selection using an availability-use design. We characterized habitat available to condors by generating five times more random absence points than used locations within minimum convex polygons defined by the GPS foraging locations of the individuals tracked in each site. We removed lakes, cities, and the Andean–Patagonian forest as these habitats are not available for foraging by condors (Lambertucci et al. 2018; Perrig et al. 2020). We characterized used and available locations with covariates that could affect condor foraging behavior (Donázar et al. 1999; Speziale et al. 2008; Pérez-García et al. 2017): Human Footprint Index (Venter et al. 2016), elevation (from a Digital Elevation Model; Farr et al. 2007), and Dynamic Habitat Index (DHI; based on the normalized difference vegetation index [NDVI]) representing primary productivity (Radeloff et al. 2019). We standardized the resolution of covariates to 1000 m using the raster package (Hijmans 2019) in R (R Core Team 2020).

Data analyses

Regional comparison

We standardized Andean condor isotopic data across study areas based on trophically corrected isotopic signature of prey items per sampling site (Cucherousset and Villéger 2015). We used trophic enrichment factors of 3.1‰ ± 0.1 for $\delta^{15}N$ and 0.4‰ ± 0.4‰ for $\delta^{13}C$ observed for California condors on a controlled feeding trial (Kurle et al. 2013). With the standardized data, we compared isotopic niche size between study sites 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 95% probability 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 modeled via 10,000 samples and 1000 iterations. We compared dietary consistency of females and males 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 as the 95% contour line of Kernel Utilization Distributions of all GPS locations collected using ad hoc reference smoothing parameters, and quantified their home range overlap via the Bhattacharyya Affinity coefficient (BA) implemented in the R package Adehabitat (Calenge 2006). We did not consider one male from San Guillermo that was monitored during less than 1 month. We present the mean and standard deviation of the average overlap by site between females, males, and females to males.

To evaluate whether and to what extent foraging females and males segregate in space, we only considered individuals with > 5 used foraging locations, resulting in a dataset of 11 females and 8 males from Patagonia (2048 used locations), and 3 females and 7 males from San Guillermo (970 used locations). We ran two hierarchical models of habitat selection as Bernoulli processes with standardized and centered environmental predictors at the observation-level (human footprint, elevation, and primary productivity) and with sex as a group-level predictor. Both models included the categorical variable "site" (San Guillermo and Patagonia), and the second model also included "season" (supplementary material S2). We defined a warm season from October to April to include months of higher ungulate mortality from malnutrition, parturition (Donadio et al. 2012; Villagra and Giraudo 2010) and transhumance farming (Parker 2015), and better weather conditions for soaring flight (Shepard and Lambertucci 2013); a cold season from May to September included months of lower foraging opportunities. Models were estimated using Bayesian inference and implemented in JAGS via the R package 'jagsUI' (Plummer 2012). We set t-Student as prior distributions for all the linear coefficients. We ran three chains with 10,000 iterations each discarding the first 5000 as a burn-in. Convergence was evaluated by visual inspection of trace plots and the Gelman–Rubin statistic (Kruschke 2015).

We evaluated differences in assimilated diet of Andean condors in our two focal sites 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: large livestock, small livestock, 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 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 in San Guillermo and 4 individuals in Patagonia). We implemented Bayesian stable isotope mixing models in the R package simmr (Parnell and Inger 2016); models were ran 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: exotic ungulates = 72%, native camelids = 5%, hares = 15%, marine = 8%), and ran a second model with uninformative priors to explore the influence of our developed priors on dietary estimates (Table S2). We report the mean and 95% credible 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. At two sites with relatively high prey diversity, condors showed the lowest and the highest isotopic richness as informed by standard ellipse areas (Fig. S2). The dispersion of condor isotopic values was similar across most sites, and isotopic differences between individuals were slightly larger in sites with intermediate prey diversity (Fig. S2). We detected a positive relationship between HFI and standardized $\delta^{13}C$ of Andean condor feathers across sites ($\beta = 0.03$, $p < 0.001$, $R^2 = 0.2$; Fig. S3).

Female and male Andean condors exhibited similar isotopic niches. For 4 of our 6 study sites, 95% credible intervals showed non-significant differences in isotopic niche overlap of females and males (Fig. 2). At Patagonia, featuring high prey diversity, we found that the isotopic niche of females was nested within the niche of males, with significant differences between isotopic areas, whereas the

Fig. 2 Comparison of male (black) and female (red) Andean condor (*Vultur gryphus*) stable isotope signatures across 6 study sites in Argentina ordered from lower to higher median Human Footprint Index (Venter et al. 2016). **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% credible intervals. We observed large dietary overlap between the sexes across study areas (color figure online)
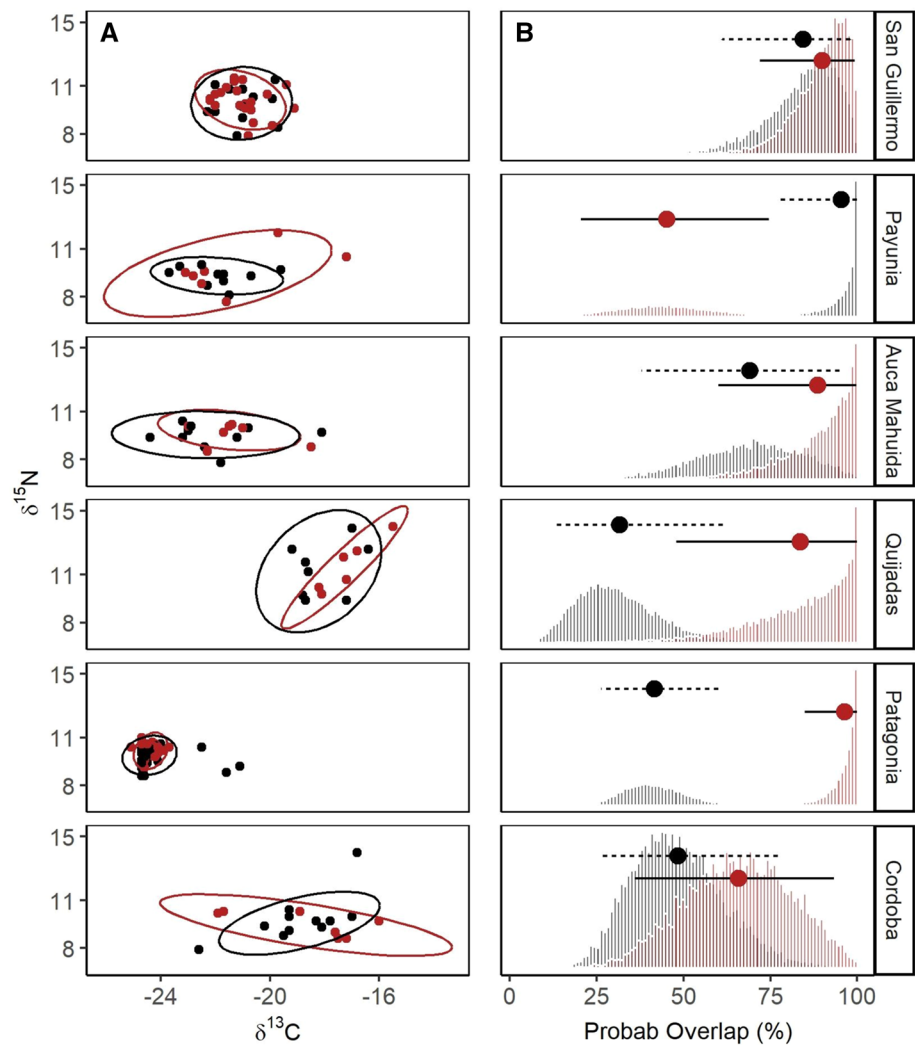
opposite pattern occurred in a site featuring low prey diversity (Payunia; Fig. 2).

Individual variability in isotopic value was similar between sexes (mean [se] δ^{15} $n = 1.1$ [0.1] and 0.9 [0.1]; $\delta^{13}C = 1.1$ [0.2] and 1.4 [0.3] for females and males, respectively; Fig. S4). Indeed, dietary breath —based on isotopic convex hulls— was 0.4 [0.1] and 0.5 [0.1] for females and males, respectively.

Segregation under low and high prey diversity

We found no differences in home range overlap between females and males. The overlap (mean [standard deviation]) between females, males, and females to males in San Guillermo was 0.25 (0.11), 0.44 (0.19) and 0.39 (0.17), respectively, whereas in Patagonia was 0.51 (0.17), 0.50 (0.16), and 0.49 (0.17). In modeling condor habitat selection while foraging, we did not include primary productivity because of a negative correlation with elevation ($r = -0.62$). Our year-round model shows that in Patagonia, females reduced the

use of sites with increasing levels of human footprint more than males, whereas sexes showed a similar and increasing use of areas at higher elevation (Fig. 3). In San Guillermo, differences between females and males were driven by elevation; females used areas of higher elevation than males, and the sexes avoided using areas of increasing human footprint with similar intensity (Fig. 3). Our seasonal model indicates that the year-round pattern remained largely unchanged between seasons in San Guillermo, whereas in Patagonia the year-round pattern changed during the cold season, when females and males used areas with similar footprint (Fig. 3, Fig. S5).

Proportional dietary estimates from stable isotope analysis revealed that at the site with low prey diversity (San Guillermo), Andean condors consumed mostly native camelids and small proportions of large and small livestock. In contrast, at the site representing high prey diversity (Patagonia), most assimilated biomass came from exotic ungulates with small contributions of hares, camelids, and trivial use of marine remains (Fig. 4, Table S2). At the site representing
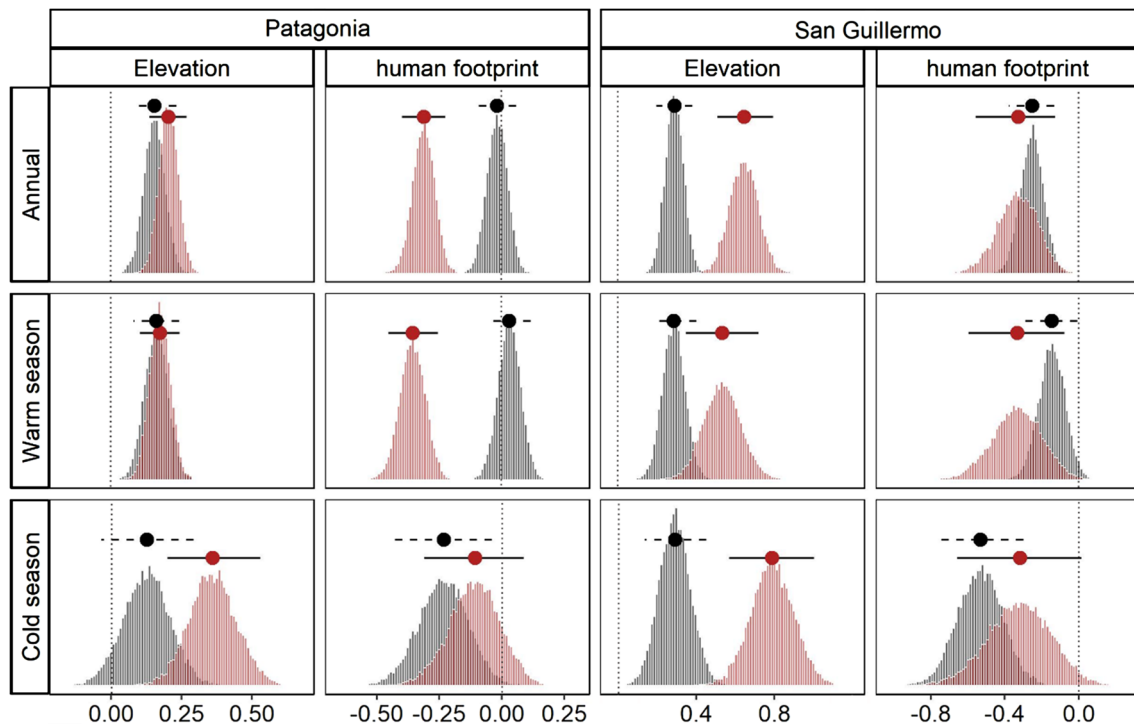
Fig. 3 Posterior probabilities (distributions and 95% credible intervals) of spatial segregation by male (black) and female (red) Andean condors (*Vultur gryphus*) in Patagonia (*n* = 19) and San Guillermo (*n* = 10) during cold (May–September) and warm seasons (October–April). Hierarchical models were estimated using Bayesian inference implemented in JAGS. We found that in Patagonia, females avoided areas with increasing human footprint to a larger extent than males. In San Guillermo, females used higher elevation than males thorough the year (color figure online)

low prey diversity, females consumed slightly less percentage of camelids than males (73 [95% credible interval; 60–85] versus 81 [60–99]), and slightly more large livestock (24 [11–35] and 15 [0.1–33]) but similar percentages of small livestock (3 [0.1–12] and 4 [0.1–18]). At the high prey diversity site, females consumed slightly more exotic ungulates (71 [40–90] and 58 [18–85]), and hares (12 [2–32] and 9 [2–25]) than males, yet less camelids (13 [0.2–48] and 20 [0.2–68]) and marine remains (4 [0.5–9] and 12 [7, 17]). Credible 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 (Table S2).

Discussion

Contrary to our predictions, our results indicate that social dominance had a limited effect on sexual partitioning of space and food resources between adult Andean condors. We observed a slight change in the isotopic signature of condors with increasing human footprint (see also Duclos et al. 2020). Yet, we found no clear evidence on the influence of prey diversity in their 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 study sites, and similar dietary proportions between the sexes under high and low prey diversity. These results suggest similar assimilated diet of Andean condor females and males over the time period when feathers were growing (likely ~ 4 months over the summer; Zuberogoitia et al. 2018), and are congruent with the lack of sexual segregation observed at the home range level. However, we found some evidence of sexual segregation in foraging locations mediated by landscape characteristics and resource availability. Our results, then, indicate that females and males use resources similarly at the landscape scale and that sexual segregation in Andean condors may occur at fine spatial and temporal scales.

Female and male Andean condors used slightly different foraging locations. At our site with high prey diversity, Patagonia, males fed in areas of similar characteristics year-long whereas females in the warm season (when resources are abundant and competition for carrion likely decreases) avoided areas with high levels of human footprint to a greater extent than males. Condors in Patagonia relied almost completely on human-derived carrion resources (Lambertucci et al. 2009), thus, females in the warm season might feed
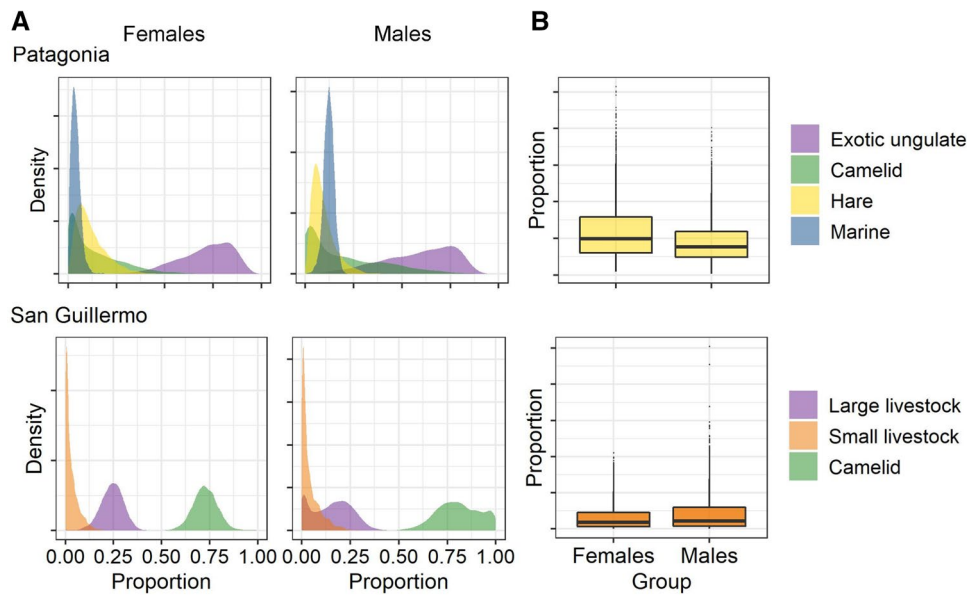
Fig. 4 Comparison of proportional dietary estimates of female and male adult Andean condors (*Vultur gryphus*) in Patagonia and San Guillermo (Argentina) estimated via stable isotope mixing models. **a** Proportional contribution of prey items to the diet of Andean condors. Exotic ungulates in Patagonia include livestock (mostly sheep [*Ovis aries*] and cow [*Bos taurus*]*)* and red deer (*Cervus elaphus*), while in San Guillermo large livestock is represented by cows and small livestock by goats (*Capra aegagrus*). **b** Comparison between female and male estimated consumption of hares (*Lepus europaeus*) in Patagonia and small ungulate in San Guillermo, as examples between all prey categories considered. We found no clear differences in assimilated biomass of Andean condor adult females and males in these two areas

in areas of lower footprint poor in availability or quality of carcasses. At our site with low prey diversity, San Guillermo, females fed at higher elevation than males year-long yet using areas of similar human footprint. Although this result is based on a small sample size (only three females were tracked in San Guillermo), females here might also use foraging areas of lower quality than males as condors feed mostly in farmlands at lower elevations (Perrig et al. 2020). Our stable isotope analysis would not detect very subtle differences in foraging locations or dietary patterns, and studies accounting for prey availability and human impacts at smaller scales are needed to understand the local differences observed.

There is ample evidence that individual size differences lead to a well-defined hierarchical social structure where Andean condor adult males outcompete females and younger individuals (Wallace and Temple 1987; Donázar et al. 1999; Marinero et al. 2018). This social dominance has been related to higher mortality rates in females causing a male-skewed sex ratio with age (Lambertucci et al. 2012). Our results, though, do not support that behavioral asymmetries lead adult females to descend more frequently in places with higher human footprint. This finding contrasts with Donázar et al. (1999), who detected more adult females than males feeding at lower elevation and closer to human settlements during spring in northern Patagonia. The incongruence

between studies could arise from differences in spatial–temporal scales of analyses. Further, we captured the distribution of anthropogenic impacts via the human footprint, an index that integrates human density and an array of land uses (Venter et al. 2016) and can obscure fine-scale, spatial differences in human threats. While parental investment can be similar between sexes or higher for males (Ferguson-Lee and Christie 2001; Lambertucci and Mastrantuoni 2008), asymmetric physiological costs of reproduction and genetic factors could be lowering the lifespan of females, regardless of social behavior (Xirocostas et al. 2020). The cause of Andean condor male-biased adult sex ratio requires timely investigation for the effective conservation of this endangered scavenger (Lambertucci et al. 2012).

Despite the similarity found in assimilated diet between the sexes, male condors generally possessed, albeit only slightly, larger isotopic niches than females. This suggests that males feed in a broader range of habitats and upon a larger diversity of prey. Our finding is congruent with the fact that males can travel longer maximum daily distances and possess larger home ranges than females (Gangoso et al. 2016). The broader niches of male condors —both in space and diet— could be related to their dominant status (Marinero et al. 2018) and to their larger wing load favoring the exploitation of good soaring conditions (Shepard and Lambertucci 2013). Body size differences between the sexes

also appears to result in partially asynchronized activities since males show earlier daily routines than females (< 2 h; Alarcón et al. 2017). Such diel temporal partitioning could limit intraspecific competition, particularly when acting in synergy with fine-scale spatial segregation. Similarly, larger isotopic niche of immature condors compared to adults has been attributed to their lower dominance ranking forcing them to exploit suboptimal prey items (Duclos et al. 2020). Our results, however, indicate very similar dietary proportions between the sexes under high and low prey diversity. It is worth noting that we detected a high, negative correlation between posterior probabilities of dietary proportions (Fig. S6) and used broad prey categories in isotopic mixing models. Along with a lack of species- and sex-specific discrimination factors, this could limit our capacity to detect small dietary differences between the sexes (Wolf et al. 2009). Regardless, partial temporal segregation and slight sexual differences in isotopic niche and foraging locations does not necessarily represent considerable differences in diet or space use among adult females and males.

Andean condors are the only vultures that exhibit pronounced sexual dimorphism (Ferguson-Lee and Christie 2001). Yet, we found similar space and food resource use between condor sexes at the landscape scale, which align with previous studies (Speziale et al. 2008). The unpredictable, scattered, and ephemeral nature of carrion might limit potential differentiation of vultures at meso-habitat scales despite strong dimorphism. 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). Vultures can also exchange social information to enhance detection of carrion, probably linking space use and foraging decisions between individuals (Gil et al. 2018). Therefore, sporadic foraging opportunities likely prevent trophic and spatial resource partitioning among Andean condors at the meso-habitat scale. Our results, then, highlight that sexual segregation can be undermined by resource predictability and distribution despite strong dimorphism and social dominance.

Anthropogenic changes in the spatial–temporal distribution of carrion affect competitive interactions between avian scavengers (Moreno-Opo et al. 2015). For example, sexual segregation can be enhanced by foraging areas that provide human-derived, predictable carrion resources (van Overveld et al. 2018). In contrast, Andean condor reliance on anthropogenic food in central Chile (from landfills and corn-fed livestock) decreases isotopic niche partitioning between age classes, exposing the population to sources of mortality (Duclos et al. 2020; Ballejo et al. 2021). We did not find strong evidence of condor reliance on anthropogenic resources across our study sites since condor isotopic signature was not notably enriched in $\delta^{13}C$ compared

to free-ranging prey items (Fig. S1). Further, pellet content analyses conducted for this and previous studies in Argentina show no evidence of condors foraging at landfills (Perrig et al. 2017; Ballejo et al. 2021). These differences between countries are likely due to a scarcity of native prey and free-ranging livestock in central Chile (Duclos et al. 2020) compared to our study sites in Argentina (Lambertucci et al. 2009, 2018), although research on carrion availability is missing throughout condors' range. Further, the broad foraging patterns of condors (Perrig et al. 2020) and our large-scale approach could be weakening our capacity to detect the effects of environmental context on condor niche partitioning. Since condors faced major changes in their food resources (Lambertucci et al. 2018), a temporal rather than spatial comparison of condor sexual segregation could reveal the mechanism behind the patterns we detected.

Pronounced sexual size dimorphism is typically associated with resource segregation, yet a growing body of literature shows that this is not a universal or direct relationship (Baylis et al. 2016). Misestimated differences in resource use between the sexes can bias our understanding of the effects of sexual segregation on population dynamics (Bennett et al. 2019). Most social species that exhibit sexual dimorphism show partially divergent patterns of resource use which, as a cause or consequence, reduce the high intraspecific competition associated with gregarious life-styles (Bison et al. 2015). Vultures exploit carrion resources under high competition, and yet we found subtle and fine-scale sexual segregation, and large overlap in resource use by a highly dimorphic species. Our results, then, illustrate the limited effect that sexual size dimorphism may have over resource partitioning and the need for studies at multiple spatial–temporal scales to explore sexual segregation.

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Code availability Sample code has been provided in the supplementary material S2.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval Permits were provided by the Argentinean Environmental ministry under CITES permit No. 15US94907A/9, University of Wisconsin-Madison (IACUC A005219), by the Argentine National Park Administration, and Provinces of Córdoba, Mendoza, Neuquén, and Rio Negro.

Availability of data and material Stable isotope ratios of Andean condor molted feathers and prey items can be accessed at Figshare, https://doi.org/10.6084/m9.figshare.14374151. Telemetry data is available from the authors on reasonable request.

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