

Exploring the size of Andean condor foraging groups along an altitudinal and latitudinal gradient in the Tropical Andes: Ecological and conservation implications

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Abstract

Patterns of variation in the size of vulture foraging groups, and their ecological causes and consequences, remain little explored despite strong links with the carrion recycling service that this key functional group provides. We documented the group size-frequency pattern of Andean condors *Vultur gryphus* gathered to feed on 42 equine carcasses experimentally placed in Bolivia, between 2012 and 2019, along an elevation range of 1,300–4,500 m asl. Based on the location (altitude and latitude) of the foraging groups, we examined the relationship between their size and species' population parameters (size and trend), habitat conditions, and livestock carcass availability and predictability. Condors utilized a high frequency (93%) of carcasses forming groups that ranged from 1 to 80 individuals (mean = 25, median = 18) and shaped a “lazy-J curve” typical pattern of size-frequency distribution whereby few groups (5, 12%) were large (> 55 individuals) and most (21, 50%) were relatively small (<19 individuals). Group size related to altitude in that most larger groups formed at lower sites (below c. 3,000 m asl), likely following an altitudinal gradient whereby larger groups are more likely to form around larger carcasses (i.e., cattle), which are more likely to occur at lower elevations. Regardless of population size, group size could be an adaptive response of condors via local enhancement for improving individual scavenging efficiency. Many information gaps on this topic still exist, thus we provide a set of questions to address them, especially amidst the unrestricted impacts of human activities that condition vulture survival globally.

Key words: cóndor andino, fusion–fission dynamics, group size, scavenger, social foraging, vultures.

Animal congregations are impressive phenomena of nature. Animals congregate when this is more beneficial than being solitary despite the possible costs (e.g., competition for resources, disease transmission, increase of predation risk or injuries inflicted by other congregated animals), and one of the reasons why they do so is to increase individual fitness through optimal foraging (i.e., social foraging) (Krause and Ruxton 2002; Ward and Webster 2016). Foraging individuals tend to aggregate until mean fitness in the group equals the fitness of individuals isolated (Sibly 1983; Kramer 1985), and to maximize individual fitness of the group members, social species adjust group size in response to a wide range of factors (e.g., behavioral, environmental, anthropogenic) (Caraco and Wolf 1975; Krause and Ruxton 2002; Ward and Webster 2016). While there are widely studied social foragers, such as baboons, elephants or wolves, foraging in groups is not restricted to particular taxa (e.g., vertebrates and invertebrates do so) or guilds (e.g., carnivores, herbivores and

necrophagous do so) (Krause and Ruxton 2002; Ward and Webster 2016).

Vultures, remarkable for being the only vertebrate obligate scavengers, have evolved social foraging as a strategy for exploiting unpredictable resources, and their readily recognizable feeding gatherings constitute ideal scenarios to study and understand the ecology of this behavior; indeed, of the 23 vulture species, 13 (56.5%) are known to be conspicuous social foragers (Houston 2001; Bildstein 2022). Social foraging in vultures is intrinsically linked to feeding group size (Cortés-Avizanda et al. 2014). For example, the larger the carrion biomass, the higher the probability that a large aggregation of vultures will occur (Bosè and Sarrazin 2007; Bosè et al. 2012; Baruzzi et al. 2022). Similarly, the more predictable a food source is, the more predictable will be how and when vulture groups gather around it (Deygout et al. 2010; Buechler et al. 2022). Furthermore, the size of vulture foraging groups can vary in space and time, depending on vulture species and their adaptability to carrion availability dynamics,

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which can be influenced both by natural (e.g., habitat characteristics) and anthropogenic factors (e.g., dumpsite management regimes) (Wilbur et al. 1974; Hille et al. 2016; van Overveld et al. 2020a).

Vultures' group foraging behavior has double-edged implications because it makes them more susceptible to mass mortality events as the recurrent aggregation of many vultures to feed means that even a few poisoned baits, usually placed by people to kill animals perceived as vermin, have the potential to decimate entire populations (Méndez et al. 2021; Baruzzi et al. 2022). As a result, and with 18 (78%) species in this group that are declining or have considerably small populations, vultures are also remarkable for being the most threatened group of birds globally (BirdLife International 2022). Hence, with fewer and fewer vultures, finding foraging groups as large as they may have been in the past could be regarded as increasingly rare or less likely (Houston 2001; Koenig 2006; Jackson et al. 2008; Bildstein 2022), a fact which would affect their scavenging efficiency via weakening facilitation interactions, as well as the maintaining of the ecosystem service of carrion removal that they provide as a functional group (Jackson et al. 2008; Baruzzi et al. 2022).

The Andean Condor *Vultur gryphus*—the largest and most threatened Neotropical vulture (BirdLife International 2022)—is a social forager whose aggregations around carcasses have a long history in the specialized literature, from the writings of early naturalists visiting South America (e.g., Orton 1871; Chapman 1917) to present works (e.g., Cailly-Arnulphi et al. 2013; Escobar Gimpel et al. 2015). However, apart from anecdotal observations, there is no quantification of the variation in size of these foraging groups nor an assessment of the ecological causes and consequences of it. Here, we report foraging events of the Andean Condor at 51 single carcasses in the eastern Bolivian Andes between 2012 and 2019, describe the observed pattern of condor foraging group size frequency distribution, and test the following hypotheses that interrelate the size of condor foraging groups with the species' population size and trend, and conditions of carcass availability and predictability: (1) Since Andean Condor populations are declining (BirdLife International 2022), the size of the species' foraging groups might also show a declining trend over time. (2) Since the Andean Condor population size decreases from south to north (BirdLife International 2022), then its foraging group sizes might follow a similar pattern. (3) Given that carcass biomass is known to be directly proportional to foraging vultures' group size (Houston 1988; Kendall et al. 2012), that cattle are the source of the largest and most abundant carcasses potentially available in Bolivia, and that in this country the abundance of this type of livestock increases as altitude decreases (Ministerio de Desarrollo Rural y Tierras 2012; Instituto Nacional de Estadística 2015), then, larger condor foraging groups could be more likely to form at elevations where larger carcasses are more likely to be found. Finally, we highlight how knowledge on feeding group sizes may serve as baseline for future research on key ecological, behavioral, and evolutionary mechanisms and implications associated with the variation in the size of foraging groups in the Andean condor, and potentially in other vulture species.

Materials and Methods

Field procedures

As part of our studies on the population status and movement ecology of the Andean Condor in Bolivia, over the course of

2012, 2014, 2018, and 2019, we placed and monitored 51 ethically sourced carcasses (23 donkeys and 22 horses of c. 200 kg each, 3 goats and 2 sheep of c. 40 kg each, and 1 alpaca of c. 50 kg; ethically sourced from local abattoirs or farmers) across an area encompassing approximately 570 longitudinal and 800 latitudinal km (roughly 33% of the species' distribution range in Bolivia and c. 4% of its global range; BirdLife International 2022), with an altitude range of 1,300–4,500 m asl, and imitating as much as possible the conditions in which carcasses could appear naturally (Méndez et al. 2015, 2019) (Supplementary Figure S1, Supplementary Table S1). All carcasses were located in comparable sites, characterized by offering equivalent displacement and visibility conditions for observers, being rather undisturbed open spots within a mountainous or hilly relief, non-forested and close to cliffs or rocky outcrops, equally detectable and accessible to condors, and distributed over several ecoregions (Méndez et al. 2015, 2019).

Data collection

Carcass sites were georeferenced using a hand-held Global Positioning System. Carcasses were monitored via direct observation, aided by photography and filming, by at least two observers stationed at hides 20–100 m from the carcass, from dawn to dusk (07:00–19:00 h, local time), from the moment they were placed until they were totally consumed (i.e., only skin and bones remained), which occurred over the course of 1–6 days for each carcass. Condors visiting carcasses (i.e., individuals that were in the vicinity of a carcass, perched or flying, and unequivocally showed that they had detected it) were routinely counted every ten minutes in order to have consistent condor counts across carcasses. Thereby, for each carcass, we defined the Andean Condor foraging group size as the maximum number of condors recorded simultaneously at the carcass site, this is, the number of condors we were certain were attracted to that particular carcass throughout the monitoring days.

Data analysis

We tested the hypotheses raised by fitting 3 generalized linear models with negative binomial distribution, each to examine the relationship between the size of Andean Condor foraging groups and one of the following predictors: (1) the period when the carcass was placed (2 levels: years 2012 and 2014, and years 2018 and 2019), which accounted for the species population trend (BirdLife International 2022); (2) carcass site perpendicular distance to the equator, which accounted for the species population size with respect to latitude (BirdLife International 2022); and (3) altitude at carcass site. This third predictor was used as a proxy for two linked factors that could not be measured due to logistical constraints; first for ecoregional characteristics, as there is a good amount of biological and ecological information that demonstrates that in our study area, as altitude decreases, localities get warmer, drier, more biodiverse, and have denser/taller vegetation (Ibisch and Mérida 2003); second for cattle carcass availability and predictability, as the official agricultural information available in Bolivia (Ministerio de Desarrollo Rural y Tierras 2012; Instituto Nacional de Estadística 2015), superimposed on the range of distribution of the condor in this country (Ministerio de Medio Ambiente y Agua 2020), indicates that there is an altitudinal gradient in cattle raising there, whereby most of the cattle are found in the lowest elevations (i.e., the

Chaco, Inter-Andean valleys and Boliviano-Tucumano ecoregions), from where their numbers diminish as one ascends, until they reach their minimum at the highest elevations (i.e., the Puna ecoregion). Carcass site altitude and carcass site perpendicular distance to the equator did not correlate with each other (Pearson correlation, $r = -0.252$, $df = 40$, $P = 0.107$).

For model fitting, we only considered the data obtained at the equine carcasses that were visited by condors ($n = 42$); first to avoid bias from the smaller carcasses visited (sheep, alpaca) which were too few ($n = 3$) to attempt analyzing the effect of carcass size (Supplementary Table S1), second because zero (i.e., no visiting condors) is not a group size, as well as being a number that can be considered informative regarding the condors' decision to visit a place or not, but not regarding their decision to aggregate or not. For each model, we assessed the effect size of the predictor using Cohen's f^2 (i.e., the ratio of the model's coefficient of determination value to this value subtracted from 1) whose magnitude determined the effect size as non-significant ($f^2 < 0.02$), small ($0.02 \leq f^2 < 0.15$), medium ($0.15 \leq f^2 < 0.35$), or large ($f^2 \geq 0.35$) (Cohen 1988). Computations were performed in RStudio version 2.3.4

(RStudio Team 2020), and R packages “MASS” (Venables and Ripley 2002) and “MuMIn” (Barton 2022) were used. Variables were deemed significant at $P < 0.05$.

Results

Condors visited 45 of the 51 monitored carcasses; 42 (93%) out of 45 equine carcasses and 3 out of 6 from the other species (Supplementary Table S1). Across the 42 equine carcasses that were visited by condors, the size of their foraging groups ranged from 1 to 80, with a mean \pm SD of 25 ± 21 individuals (median = 18), and followed a “lazy-J curve” pattern in which as the size of the groups became larger, they also became less frequent (Figure 1). In the period 2012 and 2014 ($n = 37$ carcasses), the mean \pm SD size of foraging groups was 24 ± 19 (median = 19, range = 1–72), slightly lower than in the period 2018 and 2019 ($n = 5$ carcasses), when it was 28 ± 35 , (median = 6, range = 1–80), without reaching statistical significance ($P = 0.712$) nor a significant effect size for period ($f^2 = 0.014$) (Figure 2, Tables 1 and 2). There was not a clear pattern of foraging group size in relation to latitude

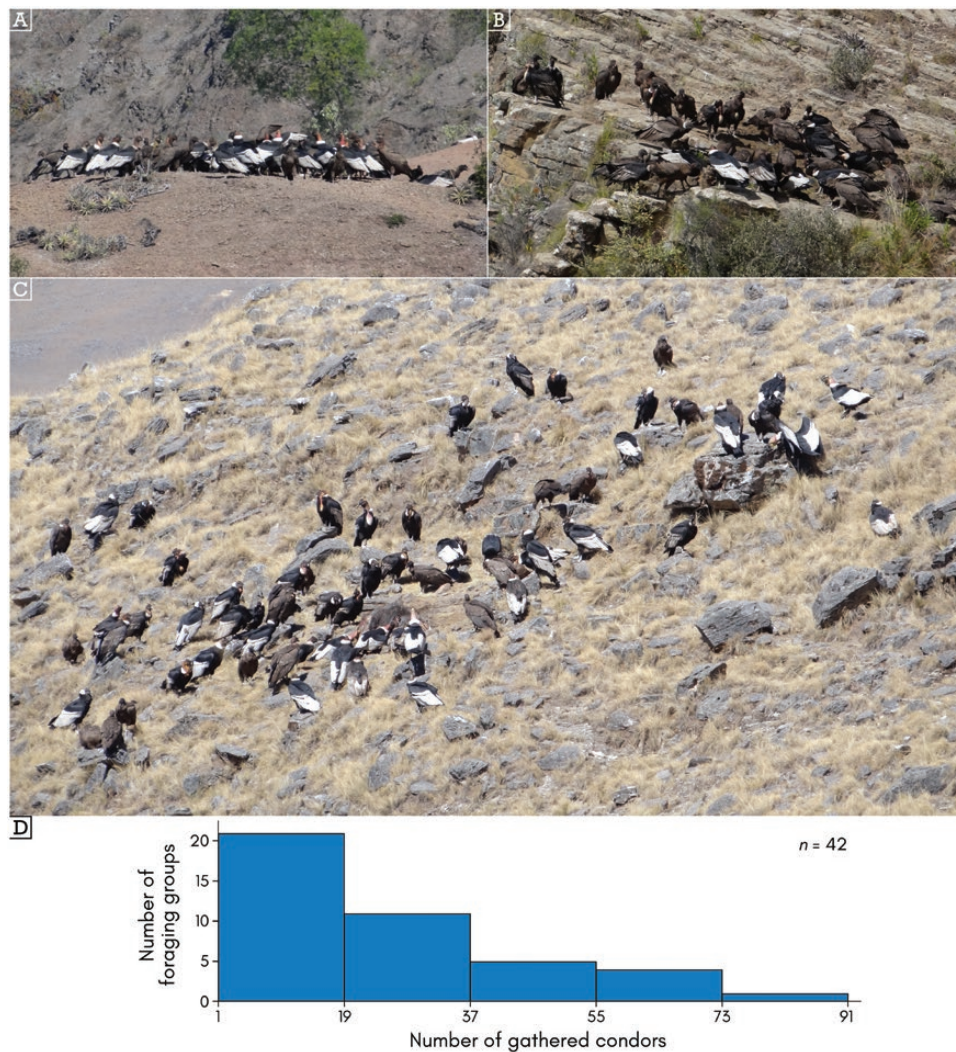


Figure 1. Example photographs of tens of Andean condors gathered around single equine carcasses in the eastern Bolivian Andes; remarkable sightings that prompted our exploration of the size of Andean Condor feeding aggregations: (A) June 2, 2012; (B) July 27, 2012; (C) August 20, 2012. (D) The size and frequency of Andean Condor aggregations around single carcasses recorded in that region between 2012 and 2019 (See Supplementary Table S1 for additional data).

($P = 0.462$, $f^2 = 0.003$), insofar as the size of foraging groups at the 4 carcasses placed in the northernmost locations were among the smallest (≤ 12 individuals), but similar group sizes were also observed in carcasses that were placed further south; furthermore, group sizes at carcasses located at equivalent latitudes included both extremes of the size range (Figure 2, Tables 1 and 2). Although group sizes at carcasses located at equivalent elevations included both extremes of the size range, there was a significant tendency toward the

formation of larger groups at lower sites (i.e., below c. 3,000 m) ($P < 0.05$, $f^2 = 0.200$) (Figure 2, Tables 1 and 2).

Discussion

We found that Andean condors utilized a high frequency (93%) of equine carcasses experimentally placed in the field, in which sizes of foraging groups ranged widely (from 1 to 80 condors), and displayed a trend related to altitude (Figures

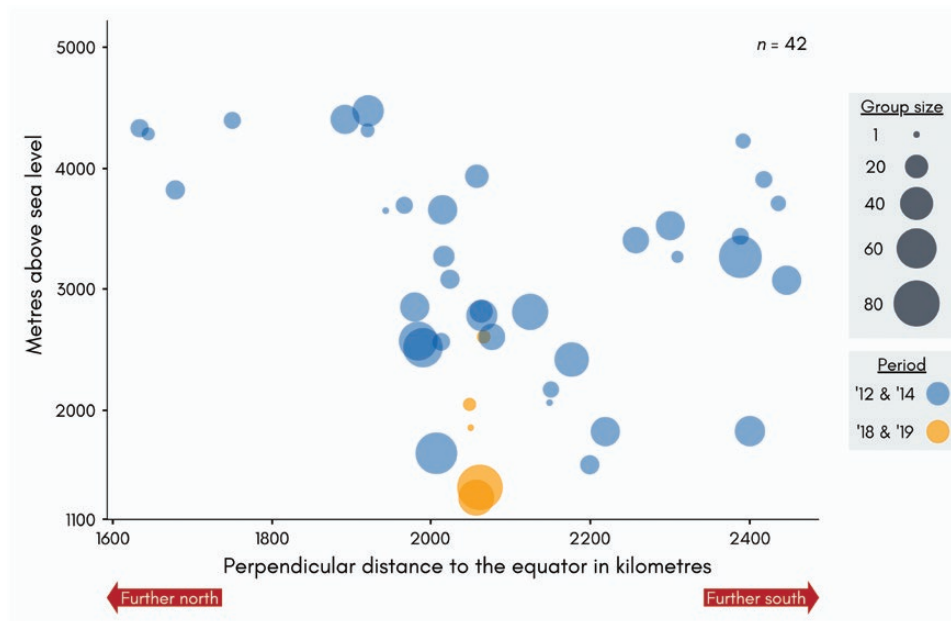


Figure 2. The size of 42 Andean Condor foraging groups observed at single equine carcasses in the eastern Andes of Bolivia; as a function of carcass site perpendicular distance to the equator and altitude, and the period (2012 and 2014, and 2018 and 2019) when the carcass was placed.

Table 1. Summary results of the 3 negative binomial generalized linear models fitted to explain the size of Andean Condor foraging groups at single carcasses in the eastern Andes of Bolivia, Tropical Andes

Model	Predictor	Estimate	SE	z	CI _{0.025} ; CI _{0.975}	P-value
s ~ p	Intercept	3.190	0.146	21.840	2.916; 3.490	0.000
	p	0.156	0.422	0.370	-0.604; 1.076	0.712
s ~ d	Intercept	2.185	1.397	1.565	-1.000; 5.376	0.118
	d	0.000	0.001	0.735	-0.001; 0.002	0.462
s ~ a	Intercept	4.148	0.447	9.278	3.309; 5.053	0.000
	a	0.000	0.000	-2.286	-0.001; 0.000	0.022

Predictors to model the size of Andean Condor foraging groups (s) were: period when carcasses were placed (p); carcass site perpendicular distance to the equator (d); carcass site altitude (a). Upper and lower 95% confidence intervals (CI) are reported. Significant variables at $P < 0.05$ are in bold.

Table 2. Comparative overview of the 3 negative binomial generalized linear models fitted to explain the size of Andean Condor foraging groups at single carcasses in the eastern Andes of Bolivia, Tropical Andes, and effect size of their predictors as given by Cohen's f^2

Model	R^2	df	logLik	AIC _c	Δ AIC _c	W	Predictor's f^2
s ~ a	0.167	3	-174.290	355.212	0.000	0.847	0.200
s ~ d	0.003	3	-176.634	359.900	4.688	0.081	0.003
s ~ p	0.014	3	-176.762	360.157	4.945	0.071	0.014

Predictors to model the size of Andean Condor foraging groups (s) were: period when carcasses were placed (p); carcass site perpendicular distance to the equator (d); carcass site altitude (a). Coefficient of determination (R^2), degrees of freedom (df), log likelihood (logLik), Akaike's information criterion corrected for small sample size (AIC_c), difference in AIC_c (Δ AIC_c), and Akaike weight (W) are presented. Significant effect sizes at $f^2 > 0.02$ are in bold.

1 and 2, Tables 1 and 2). Several environmental conditions that correlate with altitude (topography, weather, vegetation cover, etc.) (Ibisch and Mérida 2003) might explain its effect on the size of condor foraging groups; but since the characterization of those variables at each carcass site was beyond the reach of our study, further investigation is needed on this topic (Figure 3). Nonetheless, we posit that livestock carcass availability and predictability at landscape and ecoregional scales could be two of the most important variables linked with altitude that influence the size of the Andean Condor foraging groups in our study area. First, the diet of the Andean Condor consists mainly of domestic ungulates (Lambertucci et al. 2009, 2018; Duclos et al. 2020; Ministerio de Medio Ambiente y Agua 2020). Second, the recorded altitudinal distribution of foraging group sizes (Figure 2) coincided with

the altitudinal gradient of livestock distribution in that, as expected, the elevations at which most of the largest groups occurred overlapped with the elevations at which a greater abundance of larger carcasses (i.e., cattle) is more likely to be found (Ministerio de Desarrollo Rural y Tierras 2012; Instituto Nacional de Estadística 2015). Thus, just as larger carcasses have the potential to attract greater numbers of condors (Houston 1988; Kendall et al. 2012), areas where this type of carcasses is abundant could concentrate larger numbers of condors (e.g., Pérez-García et al. 2018), potentially leading to the formation of larger group sizes at carcasses. In this regard, a priority objective subsequent to this work will be to estimate the density of foraging condors and its variation as a function of altitude and altitude-dependent factors (e.g., If condors segregate altitudinally to forage, how

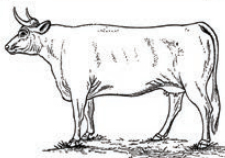
Key questions about the size of Andean Condor foraging groups

About causes

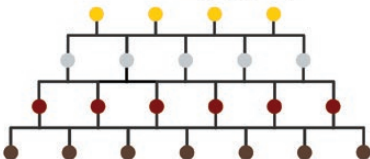
- ▶ What factors – environmental (e.g. weather, seasonality, topography, vegetation cover), anthropogenic (e.g. dogs' presence, urbanization, garbage dumps' existence) – and to what degree, influence the size of Andean Condor foraging groups?



- ▶ How does carcass availability and predictability affect the formation of foraging groups of certain sizes? / To what extent has the introduction of domestic ungulates to South America and the declines of wild animals contributed to changes in carcass availability and predictability?



- ▶ What is the role of Andean Condors' hierarchical dominance behavior in the formation of larger/smaller foraging groups?



- ▶ How does the relationship between the size of foraging groups and carcasses mass and type vary?



- ▶ How do other species of carrion feeders, and predators, affect the size of foraging groups?

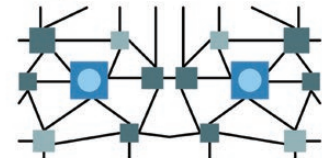


About consequences

- ▶ What is the role of larger/smaller foraging groups in shaping scavenger assemblages and scavenging dynamics?



- ▶ What is the role of larger/smaller foraging groups in determining Andean Condor social behavior (e.g. learning, foraging, courtship, allopreening, roost selection)?



- ▶ What are the advantages/costs of larger/smaller foraging groups for individuals and populations (individual fitness and group survivorship)?



- ▶ In addition to poisoning events, what is the risk of larger foraging groups to other forms of conservation threats (e.g. dog attacks)?



Figure 3. Several non-mutually exclusive variables may be behind and affect the size of feeding aggregations of Andean condors at single carcasses. This set of basic questions highlights research avenues and is aimed at fostering new studies on this topic.

long and in response to what factors do they remain in a certain altitudinal layer?). Since the geographic distribution of carcasses of specific sizes appears as such a relevant factor in our study area, we note that it will be equally important to examine the effect of carcass size itself on condor foraging group size using the most appropriate field designs and sample sizes (Figure 3).

As happens in most of South America, in Bolivia carcass availability and predictability have hardly been assessed, yet the non-random distribution of livestock of different types (e.g., cattle, sheep, goats, equines, and camelids that are raised at given elevations, in particular farming conditions and within distinctive landscapes) throughout the Andean Condor range in the country (Ministerio de Desarrollo Rural y Tierras 2012; Instituto Nacional de Estadística 2015; Ministerio de Medio Ambiente y Agua 2020) guarantees the existence of multifaceted, interesting interactions with the size of condor foraging groups (Figure 3). Overall, carcass availability and predictability (e.g., seasonality, distribution, density) are little-studied topics in the Andes despite being central to carrion ecology (Moleón et al. 2019), whose relationship with the variability of scavengers' foraging groups needs further investigation. For example, what is the relationship between wild mammal abundance (e.g., Wallace et al. 2010), the types of livestock management, and the size of condor foraging groups? How are the spatiotemporal changes in carcasses' size and supply throughout South America (e.g., Steinfeld et al. 2006) related to the variation in the size of condor foraging groups? (Figure 3).

Most of the condor foraging groups we observed (21, 50%) were relatively small (<19 individuals); notwithstanding, some of the larger foraging groups that we observed (>55 individuals; 5 groups, 12%) (Figure 1), accounted for up to 1.2% (80 individuals) of the estimated Andean Condor global population (6,700 individuals; BirdLife International 2022). Importantly, the largest groups we observed at the beginning of our campaigns in 2012 represented a significant fraction—up to 92.3% (72 individuals)—of the only Andean Condor population that had been estimated in Bolivia at that time (78 individuals for the Apolobamba Mountains, northwest of the country; Ríos-Uzeda and Wallace 2007); plus we continued to observe groups of similar sizes until the end of our fieldwork (Supplementary Table S1), even as the global Andean Condor population is considered to have been declining for at least a hundred years (Chapman 1917; McGahan 2011; BirdLife International 2022). Consequently, we expect such large foraging groups to represent a larger proportion of the population nowadays than in the past, even though condor feeding group sizes and their frequency have not been estimated before. Moreover, we did not find evidence for a relationship between size of Andean Condor foraging groups and population size: it did not decrease from south to north (Figure 2, Table 2), as does the size of its populations (BirdLife International 2022), nor between periods 2012 and 2014 and 2018 and 2019 following a declining population trend (BirdLife International 2022) (Figure 2, Tables 1 and 2). Therefore, our results indicate that large Andean Condor feeding concentrations at single carcasses are regardless of population size and indeed can be formed even with limited population sizes, suggesting that formation of large foraging groups seems to be needed to increase scavenging efficiency (Baruzzi et al. 2022).

The gathering of large numbers of condors to feed always involve the well-known risk of mass poisoning (Méndez et al. 2021). As there seems to be a spatial tendency toward the formation of larger groups in certain regions or localities depending on their altitude and associated factors (this study), a concrete Andean Condor conservation measure will be the preparation of mass poisoning risk maps to visualize where it is more likely that its populations may suffer greater losses, and therefore where in situ actions should be prioritized to reduce their vulnerability and eliminate this serious threat (e.g., Mukherjee et al. 2014; Santangeli et al. 2019).

One further issue to be explored is the relationship between foraging group size and their age and sex structure (Méndez et al. 2015, 2019). Foraging groups of particular sizes may indeed have a particular age and sex structure, and thereby estimating the proportion of individuals in the population that are present in these aggregations as well as exploring the sex, age, and individual identity of those occurring in them could help to explain why these occur (e.g., Are there some individuals more likely than others to participate in aggregations of a certain size?) (Figure 3). Since effective social foraging in vultures depends on many individuals sharing information with each other, further investigating condors' communication patterns when forming groups of certain sizes will help to explain such events (e.g., How do avian scavenger aerial networks—for carcass search—function along Andean Condor's distribution range?) (Jackson et al. 2008; Cortés-Avizanda et al. 2014; Silk et al. 2014; Harel et al. 2017; van Overveld et al. 2020b) (Figure 3).

If deliberately foraging in groups of a certain size is an adaptive response of Andean Condors, some fundamental parameters to quantify its benefit are which and how many condors should be part of these groups to be as efficient as possible, and what is the physical, physiological and behavioral states of each of them (Bosè and Sarrazin 2007). In particular, foraging group size is a feature that can be assumed to have an optimal value in terms of fitness for the members of the group (Sibly 1983; Sheppard et al. 2013) within a range of group sizes and functional values (Bosè et al. 2012; Harel et al. 2017). Monitoring group sizes in the Andean condor and identifying size-frequency profiles can be of great ecological and conservation value. For example, identifying group sizes smaller than expected according to carcass biomass and/or recording extremely slow carrion disposal times might indicate dysfunctional condor foraging groups. Remotely and automatically obtained imagery and footage of avian scavengers at carcasses (Mateo-Tomás et al. 2017; Moreno-Opo et al. 2020), and techniques for marking, recognition and tracking of individuals (Bosè and Sarrazin 2007; Bosè et al. 2012; Duriez et al. 2019), have proven instrumental to investigate their foraging behavior in experimental field conditions, and can be applied to further investigate the size of groups of condors feeding on single carcasses in nature.

Beyond spectacular, Andean Condor foraging groups prove to be complex sociobiological events, not fully understood and worth further investigation (Figure 3). For this, we believe they are approachable within a framework of fission–fusion processes (Silk et al. 2014) in vulture sociality (van Overveld et al. 2020b), and that the ultimate question to answer is whether these events are stochastic or if they follow defined patterns, and if so, what are the optimal group sizes. Our study suggests that some patterns appear to emerge, but further studies are needed to ascertain the factors governing the formation of foraging groups, for

which the questions deployed in Figure 3 could help. Amidst the unrestricted impacts of human activities that condition the survival of vultures globally, we hope to motivate future research on this topic, relevant not only to increasing our knowledge about the role of the foraging group formation in the ecology and conservation of the Andean Condor but also about the rest of the members of this irreplaceable guild that aggregate to feed on carrion, an unpredictable critical pulsed resource, delivering a key ecosystem service.

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Conflict of interest

The authors declare that there is no conflict of interest.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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