

REPORT

Risk effects cascade up to an obligate scavenger

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Abstract

The effects of predation risk on prey populations have been studied extensively; yet, how risk is manifested in a trophically linked guild—scavengers—has been overlooked. Risk could be particularly consequential for obligate scavengers that are vulnerable while foraging and rely on carrion provisioned by, and shared with, apex predators. We investigated whether Andean condors (*Vultur gryphus*) respond to predation risk in a landscape where the main source of carrion are camelids killed by pumas (*Puma concolor*). We hypothesized that condors would exhibit different behavioral responses to predation risk while they search, encounter, and exploit carrion. We explored condor habitat selection while flying by tracking nine birds with satellite transmitters and monitored via camera traps 41 natural carcasses and 25 experimental carrion stations. We found that condors searched for carrion in areas with a high probability of occurrence of puma kills. However, condors avoided exploiting carrion in areas featuring tall vegetation and steep slopes—selected by pumas to stalk prey—suggesting that condors manage risk primarily through the identification of safe foraging sites prior to landing. Our finding that condors avoided foraging near stalking cover for pumas highlights the importance of risk effects beyond predator–prey interactions, particularly for obligate scavengers.

KEYWORDS

antipredator behavior, carrion, high Andes, predation risk, scavenging, vultures

INTRODUCTION

The risk of predation can affect the physiology and behavior of foragers (Sheriff et al., 2011) and shape the composition of communities and the dynamics of ecosystems (Schmitz et al., 2004). In some cases, the effects of risk may play a larger role than direct

predation, even among species that have evolved morphological defenses (Pokallus & Pauli, 2016) and complex social structures (Pauli & Buskirk, 2007) to avoid predation. The occurrence and strength of risk have been extensively studied on prey species (Schmitz et al., 2004). According to risk level and food value, prey will adjust a repertoire of behaviors to manage risk such as habitat

use, harvest rates, and vigilance (Brown & Kotler, 2004). The behavioral games between predators and prey have sparked debate on the importance of predation risk across communities (Middleton et al., 2013) and revealed the need to investigate risk beyond predator–prey interactions (Sheriff et al., 2020).

Obligate scavenging is a highly specialized terrestrial lifestyle that evolved in two ancestral groups—New (Cathartidae) and Old World (Accipitridae) vultures. Vultures are not adapted for killing but instead rely almost completely on predators and other sources of mortality (e.g., starvation, diseases) to secure food resources (Ruxton & Houston, 2004). Apex carnivores, especially solitary ones, act as a central source of carrion to scavengers by regularly killing large prey (Moleón et al., 2014). Further, predators reduce search and handling time of scavengers by leading them to kills and by stripping the prey of hide (Jackson et al., 2020; Moleón et al., 2014). The fitness of obligate scavengers, then, is intimately linked to predators.

Food-safety tradeoffs may be particularly relevant for vultures. Since carrion is an unpredictable food resource, it is costly for vultures to forego a foraging opportunity. Further, latency to scavenge reduces carrion quality (because it spoils; Houston, 1986) and quantity (because it is consumed by other organisms; Kane et al., 2014). Scavenging, however, presents stark risks. Predators frequently guard kills (since scavengers exact important foraging costs; Elbroch & Wittmer, 2013), and carrion attracts an array of opportunistic carnivores (Prugh & Sivy, 2020). The resultant risk landscape surrounding carrion may be particularly acute for heavy-bodied and volant scavengers, like vultures, whose mobility is compromised on the ground (Ferguson-Lees & Christie, 2001). Further, even fleeing from carrion can adversely impact large vultures because most of these soaring birds' energetic costs are associated with takeoffs from feeding locations (Ruxton & Houston, 2004). As a result of these risks, vultures are typically exceedingly wary of where to forage (Donazar et al., 2018). Although vulture mortality due to predation is infrequent (González-Gallina et al., 2017), this may simply reflect that vultures possess a suite of behaviors to successfully navigate risk while foraging.

The largest obligate scavengers of South America, Andean condors (*Vultur gryphus*), are tightly linked to pumas (*Puma concolor*) and native camelids (vicuñas [*Vicugna vicugna*] and guanacos [*Lama guanicoe*]). Camelid carcasses provisioned by pumas are an important resource for condors (Elbroch & Wittmer, 2012; Perrig et al., 2017). Pumas are ambush predators that use physical features to stalk prey (Bank & Franklin, 1999). In the high Andes, extensive open plains contrast with

structurally complex meadows (high vegetation cover and tall grasses) and hills, mountain peaks, and narrow canyons (shrubs, irregular slopes, and rocky outcrops; Figure 1) where pumas find prime habitat to stalk and ambush prey (Smith et al., 2020). Andean condors might be unresponsive to differences in habitats as the lack of tall vegetation makes the landscape potentially homogeneous for condor foraging. However, if condors perceive pumas as risky, they are faced with choosing to search for and exploit food in sparse canyons and meadows—which provide stalking cover for pumas and hide a large proportion of cached puma kills—or lose profitable resources. The simplicity of this study system provides a unique opportunity to investigate the influence of spatial heterogeneity over predator–vulture interactions.

To evaluate the role of risk throughout the hierarchical process of search, encounter, and exploitation of carrion by vultures, we investigated the foraging behavior of Andean condors inhabiting a pristine landscape of the high Andes. Specifically, we explored condor space use while flying through global positioning system (GPS) tracking data and condor use of carrion through monitoring with camera traps natural carcasses and carrion provided in an experimental setting. We hypothesized that condors would exhibit behaviors to minimize risk that differ between foraging stages (Figure 1). We predicted that condors would maximize their chances of finding carcasses by searching for food in areas with the greatest abundance of puma kills—structurally complex meadows and canyons. We predicted, though, that condors would encounter and exploit more carrion in plains, where vegetation cover and structural complexity are low, than in meadows or canyons. We also predicted higher foraging rates and greater vigilance of condors in meadows and canyons due to the higher predation risk in these habitats relative to plains. Altogether, this study highlights food–safety tradeoffs faced by obligate scavengers and the overlooked effects of predators on higher trophic levels.

MATERIALS AND METHODS

Study area and species

We worked in San Guillermo National Park (SGNP), a 1660-km² protected area at 2000–5600 m above sea level within the Puna and the high Andes ecoregions of central Argentina (29.068° S 69.349° W). Due to its difficult accessibility, human presence in the area is minimal (<100 visitors/year; Donadio & Buskirk, 2016). Vicuñas are the main large mammalian herbivores, and pumas are the sole apex predators (Donadio & Buskirk, 2016). Andean condors are the largest avian scavengers in the area and share

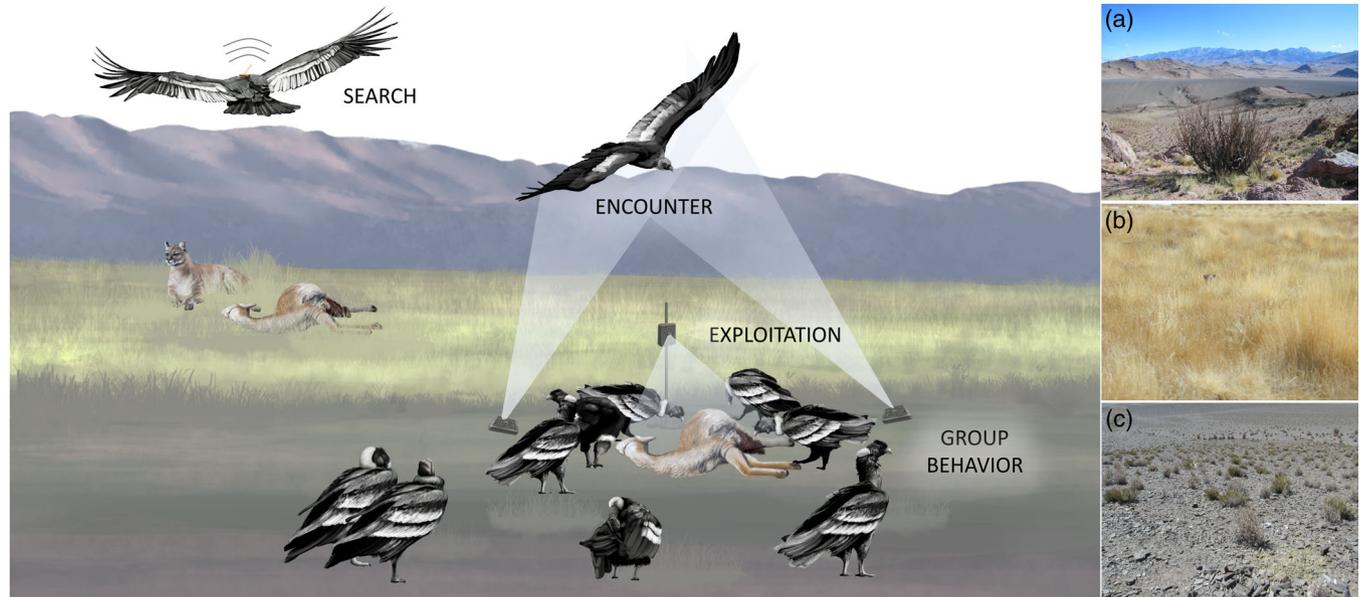


FIGURE 1 We studied Andean condor search, encounter, and exploitation of carrion and the behavior of condors feeding in a pristine landscape where condors rely on puma kills. In particular, we explored condor foraging trips through tracking individuals with satellite transmitters and monitored carrion encounter and consumption via camera traps. We expected to find condors searching for carcasses in sites with (a) complex terrain and (b) tall vegetation, where most puma kills occur, and a higher probability of condors encountering and exploiting carrion in (c) open plains, where visual obstruction and predation risk are low.

carrion resources with mountain caracaras (*Phalacrocorax macrorhynchos*), culpeo (*Lycalopex culpeus*) and chilla foxes (*L. gymnocercus*), and occasionally turkey vultures (*Cathartes aura*). Puma-killed camelids are the main source of carrion in SGNP and constitute 88% of the local diet of condors (Perrig et al., 2017). However, the frequency of kills is habitat dependent: Pumas kill more than expected in meadows (1% of the park; selection ratio [SR] \approx 9) and less than expected in canyons and hillsides (70%; SR \approx 0.8) and in plains (29%; SR \approx 0.3; Smith et al., 2020).

Habitat selection while searching for carrion

We tracked Andean condors using GPS devices to study their habitat selection while flying. We used GPS locations of nine adult birds trapped with baited cannon net traps during 2015–2017 and tagged with 70- or 50-g solar Argos/GPS Platform Transmitting Terminal tags (Microwave Telemetry Inc.) attached as backpacks and set to provide one fix per hour from dawn to dusk. We analyzed Andean condor GPS data inside SGNP with velocity >3 m/s to capture flights (Perrig et al., 2020). We generated 10 random locations per condor GPS position within the boundary of SGNP and compared habitat (normalized difference vegetation index and slope) and food predictors (probability of vicuña presence and puma

kill sites) between used and available locations with a habitat selection function following Muff et al. (2020; Appendix S1).

Predictors of carrion encounter and exploitation

We searched for camelid carcasses using puma cluster analysis (2014–2017) and periodic surveys of the study area (2013–2017). For each fresh carcass found ($n = 41$), we identified the species and age. We then staked the carcass to the ground to monitor its detection by flying condors (hereafter encounter) and consumption (hereafter exploitation; Figure 1). To evaluate encounters, we installed two camera traps (Cuddeback model 1279) ~ 10 m away on opposite sides of the carcass, pointing toward it and facing upward at an angle of $\sim 45^\circ$ (Figure 1); these cameras were set to take one 20-megapixel picture of the sky every 30 s. To evaluate exploitation, we installed a third camera trap (Bushnell Trophy Cam) pointing at the carrion at a distance of ~ 5 m, motion-triggered and programmed to take pictures continuously (Figure 1). We monitored carcasses for variable periods (mean of 3 [range 1–7] days) dependent upon carrion consumption rate and battery duration.

In addition to monitoring camelid carcasses (i.e., natural stations), we deployed standardized carrion stations stratified

by meadows ($n = 14$) and plains ($n = 11$) during January–April of 2017. Experimental stations consisted of four cow heads, obtained from a local slaughterhouse, placed in randomly selected locations of puma-killed camelids registered for this and other studies ($n = 415$). We ensured a minimum distance of 1 km between stations deployed simultaneously. We monitored carrion encounter and exploitation as described previously, and camera traps were active between 7 and 15 days.

We recorded species and number of individuals in the photos obtained from natural and experimental stations. We characterized in the field microhabitat features where each carrion station was located: topographic slope, mean vegetation height and percentage cover, and distance to puma stalking cover (hereafter visual obstruction). We estimated the amount of biomass available for scavengers and used camera trap pictures to document the presence of mountain caracaras and turkey vultures (Appendix S1). We investigated the probability that a condor would exploit carrion via a single-season, multistate occupancy model fitted with the R (R Core Team, 2020) package unmarked (Fiske & Chandler, 2011). The states considered per survey were “not encountered” (state = 0), “encountered” (state = 1), and “exploited” (state = 2). We used a multistage modeling selection approach based on the Akaike information criterion (AIC). We included the number of days a station was monitored as a predictor for the probability of detecting encounters. The most complex model for the encounter occupancy state included vegetation height, presence of other avian scavengers, and number of days that the station was monitored for encounters. For the exploitation occupancy state, we included microhabitat predictors, available biomass, and whether carrion was experimental or natural. We validated the predictive performance of the exploitation state of our model using an independent data set of 20 carcasses (Appendix S1).

Foraging behavior

For stations exploited by condors ($n = 33$), we recorded the minimum number of birds registered in each photo. Given our large data set of consecutive condor pictures ($n = 14,994$), we subsampled photos taken at least 2 min apart before recording condor behavior. We only considered birds located less than ~10 m from the carcass and recorded how many individuals were scanning and feeding (Appendix S1: Table S1). For every record of condors foraging, we multiplied the number of condors feeding by the time between photos as a proxy of group foraging rate; time lapses of >3 min were not considered. We ran generalized linear mixed models (Brooks et al., 2017) to

analyze group foraging rate (gamma distribution) and proportion of condors vigilant (beta-binomial distribution). We included station ID as a random effect and used AIC to select among models that included microhabitat characteristics, available biomass, whether the station was experimental or natural, the number of condors present, and, for group foraging rates, the time since a condor first fed in the station (Appendix S1: Table S2). Predictors were not correlated ($r < 0.6$) and were centered and standardized.

RESULTS

Habitat selection while searching for carrion

We analyzed condor habitat selection during foraging flights (16–489 flight locations per individual). We found a higher relative probability of condors searching for food in sites featuring a low relative probability of vicuña daytime presence (β [SE] = -0.38 [0.11]) and a high relative probability of puma kill-site locations (0.13 [0.03]) (Appendix S1: Figure S3). The relative probability of condor use increased with topographic slope (0.11 [0.12]) (Appendix S1: Figure S3), but the confidence interval of this variable overlapped zero (Figure 2). An out-of-sample evaluation indicated good predictive performance of this final model ($r = 0.68$ [0.28]).

Predictors of carrion encounter and exploitation

We analyzed 66 carrion stations to study condor encounter and exploitation of carrion. Of these stations, 18 (10 natural and 8 experimental) were neither encountered nor exploited, 20 (12 and 8) were encountered but not exploited, and 28 (19 and 9) were encountered and subsequently exploited by condors. Our top-ranking model included all predictors considered (Appendix S1: Table S3). Condors exhibited a lower probability of encountering carrion when avian scavengers were present (-3.08 [1.52]) and when vegetation height was high (-1.35 [0.96]), principally when vegetation was taller than 40 cm (Appendix S1: Figure S4), though this confidence interval overlapped zero (Figure 2). The probability of condors exploiting carrion was reduced by tall vegetation (-12.01 [5.50]) and steep slopes (-1.62 [0.74]). In particular, the probability of condors exploiting a station declined when vegetation height was >20 cm and slopes steeper than 15° (Figure 2). We found weak evidence that the probability of condors exploiting a station increased

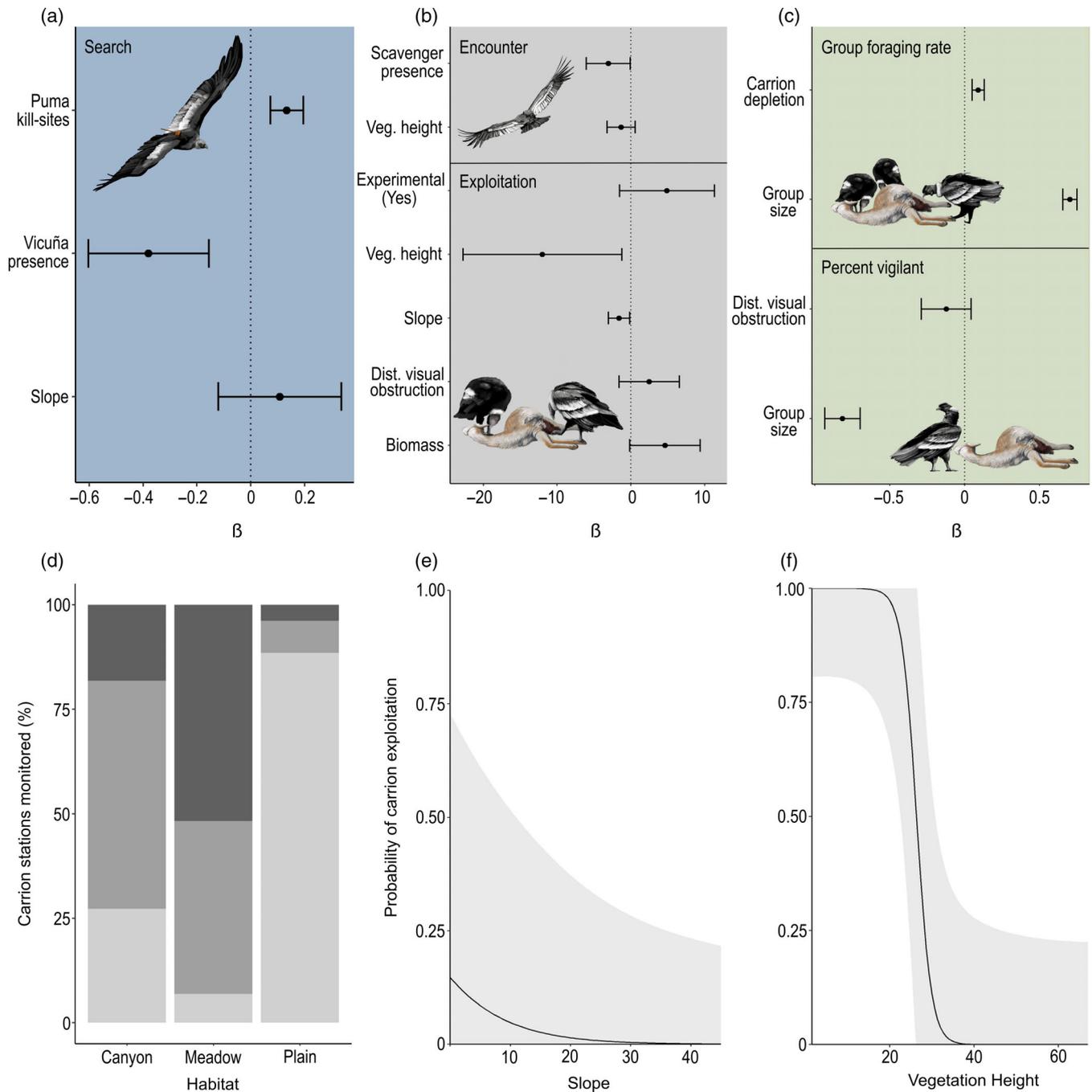


FIGURE 2 Andean condor behavior at different stages of foraging. Beta coefficients (and 95% confidence intervals) of (a) Condor habitat selection while searching for carrion from a mixed-effects Poisson process model, (b) condor relative probability of encountering and exploiting carrion from a multistate occupancy model, and (c) condor group foraging rate and proportion of individuals vigilant based on generalized linear mixed models. Predictors considered include the probability of puma kill-site location (puma kill sites), probability of vicuña presence during the day (vicuña presence), slope, presence of avian scavengers other than condors (binomial; scavenger presence), vegetation height (cm; veg. height), estimated biomass (kg; biomass), distance (m) to meadows or rocky outcrops (dist. visual obstruction), number of condors present in a camera trap photo (group size), carrion depletion due to condor foraging (carrion depletion), and if stations were experimental or natural (experimental [yes]). (d) Number of stations not encountered, encountered, and exploited by condors (from dark to light gray) in canyons ($n = 11$), meadows ($n = 29$), and plains ($n = 26$). (e) Partial-residual plots (with 95% confidence intervals in gray) for the statistically significant predictors of the multistate occupancy model showing that slope and (f) vegetation height decreased the probability of condors exploiting carrion.

with increasing carrion biomass (4.59 [2.44]), especially with carcasses heavier than 50 kg, and when carrion was located more than 200 m from visual obstructions (2.45 [2.08]; Appendix S1: Figure S4), although confidence intervals for both variables overlapped zero (Figure 2). We found weak evidence of condors showing higher probability of exploiting experimental carrion stations than camelid carcasses (4.87 [3.28]). Our final model showed adequate fit and good predictive capacity of condor exploitation (area under the receiver operating characteristic curve = 0.97).

Foraging behavior

We analyzed condor vigilance behavior in 1651 photos from 33 carrion stations. We found that the foraging rate of condor groups increased with a larger number of individuals (0.7 [0.02]) and as carrion depleted (0.09 [0.02]; Figure 2). Vigilance among condors increased when fewer conspecifics were present (−0.82 [0.06]; Figure 2) and slightly decreased farther from visual obstructions (−0.12 [0.08]; Figure 2). The remaining predictors in top-ranking models (<2 Δ AIC) (Appendix S1: Tables S4 and S5) had confidence intervals overlapping zero.

DISCUSSION

Our findings indicate that Andean condors perceive sites where pumas hunt as risky. Condors rarely exploited carrion in areas with grasses taller than 20 cm and slopes steeper than 15°. In particular, condors did not exploit 57% of the carrion stations monitored that were associated with these habitat features, 30% of which they had encountered. Vegetated areas and slopes are selected by pumas to stalk their prey and are predictive of high predation risk (Smith et al., 2019). It appears, then, that predation risk imposed by pumas prevented condors from exploiting carrion resources, highlighting that apex predators can exert strong risk effects on the foraging decisions of obligate scavengers.

The lower probability of condors descending to feed at sites associated with puma stalking cover could simply indicate that condors have low chances of encountering carcasses under these conditions. However, we defined carrion encounter when we registered at least two pictures of condors flying <100 m above carrion, when condors almost certainly detected the food given their high visual acuity (Lisney et al., 2013). Additionally, we found that the presence of facultative scavengers decreased the probability that condors would encounter carrion. Other avian scavengers in our study area use visual and

olfactory cues to find food and should detect most, if not all, carrion available (Ferguson-Lees & Christie, 2001). We expected condors to rely on interspecific cues to locate food (Kane et al., 2014). It is likely, though, that condors are not drawn to carrion stations located in risky areas despite the presence of scavengers, creating a negative relation between carrion encounter by condors and the presence of other scavenging raptors. It appears, then, that food–risk tradeoffs, and not detectability, influences carrion encounters. Regardless, condors avoided exploiting carrion encountered at sites with complex terrain. It is improbable that condors did not descend due to difficulties in landing, walking, or taking off since they feed in shrublands elsewhere (Perrig et al., 2020) and high spatial heterogeneity allows condors to easily walk in and out of carcass sites. Further, we found weak evidence of condors using experimental stations more than natural ones, which may indicate that condors respond to cues of puma presence. Altogether, our results support the idea that condors respond to risk by allocating time to safe foraging sites, selected prior to descending to the ground.

Foraging is a multistage process (Sheriff et al., 2020), and Andean condors responded to risk differently at each stage of the foraging sequence. Condors generally searched for carrion in locations with a high probability of having puma kills. Indeed, condors flew slightly more in canyons than expected, as expected in meadows, and less than expected in plains (Appendix S1: Figure S5). Yet, it is possible that high visibility over plains enables condors to scan for carrion from a greater distance without having to fly above this habitat. The association of flying condors to puma kills could be due to better soaring conditions in canyons, which we could not model at a sufficiently fine spatial scale. However, a nonsignificant relationship between condor searching probability and slope suggests that the birds do not use canyons merely for efficient flying. Meadows do not offer high visibility or useful soaring conditions, and they were used as (or slightly more than) available. Our data, then, suggest that condors search for food in areas with complex terrain, where most puma kills occur. However, most carrion stations in meadows and canyons—featuring tall vegetation and steep slopes—were not exploited by condors, even when detected. We found no differences in condor vigilance behavior or foraging rates related to environmental features, probably because carrion exploited by condors was mostly in areas of low vegetation height and cover (Appendix S1: Figures S6 and S7). Our results suggest that scavengers drawn into risky foraging sites tend to forego foraging entirely when faced with heightened risk, mirroring mesocarnivores (Klauder et al., 2021).

Similarly to vultures, many mesocarnivores rely on large predators for scavenging opportunities, especially in

periods of prey scarcity. However, a negative correlation between the abundance of large and small carnivores indicates that top predators limit more than facilitate subordinate species (Prugh & Sivy, 2020). Low intraguild mortality rates suggest that nonconsumptive effects have a central role in the net suppressive effect of large carnivores (Prugh & Sivy, 2020). Vultures are adapted to scavenging and cannot easily switch to hunting their own prey, as carnivores can (Ruprecht et al., 2021; Ruxton & Houston, 2004). Being responsive to cues of risk may be key for these long-lived birds to avoid mortality from the same predators that provision them with food or with whom they share carrion resources (Creel & Christianson, 2008; Moleón et al., 2014). Risk effects, though, can be shaped by environmental context.

Our findings support the idea that puma–condor interactions are mediated by spatial heterogeneity (Elbroch & Wittmer, 2013). Specifically, pumas in SGNP preferred to hunt in meadows and canyons (Smith et al., 2020), whereas the probability of condors exploiting a puma kill seems lower in these habitats compared to plains. Thus, meadows may act as a spatial refuge that protect pumas from kleptoparasitism by condors, whereas plains appear to act as a spatial refuge for condors from predation. Negative, small-scale association with apex predators can result in a positive association at a large spatial scale, and vice versa (Sivy et al., 2017). This may be particularly consequential in human-dominated landscapes, where vultures are unintentionally poisoned while consuming predator kills that have pesticides delivered by humans to retaliate against predators (Pauli et al., 2018). It is of increasing importance to understand how risk affects predator–vulture interactions for the effective conservation of these guilds.

The reward versus risk tradeoff faced by any scavenger when foraging depends upon the probability of finding alternative carrion sources and the current energetic state of the animal (Ruprecht et al., 2021). We found that the available biomass on a site influenced the probability that condors would exploit carrion (Charnov, 1976). Furthermore, most of our study took place during a mange outbreak that increased vicuña mortality, resulting in abundant carrion resources for condors (Monk et al., 2022). We also provisioned experimental carrion stations simultaneously, augmenting available foraging opportunities. Condors may have been more responsive to risk because the marginal value of carrion decreased and there was enough food available in safe habitats. In areas with paucity of carrion, energy is more valuable and condors may expose themselves to greater risks (Speziale et al., 2008). The low density of vicuñas in our study area after the mange outbreak (a period not covered in this study) not only reduced carrion

availability for condors but also changed the spatial patterning of vegetation (Monk et al., 2022). Future research in SGNP would shed light on the food and risk tradeoffs made by Andean condors and how adaptable obligate scavengers are to changing conditions.

Our results suggest that the main behavioral strategy used by condors to manage risk is microhabitat selection. Although condors avoided feeding in risky sites, we did not find evidence that condors changed their group foraging rate to mitigate perceived riskiness and they decreased vigilance only slightly farther from visual obstructions. This result contrasts with previous studies conducted in human-dominated landscapes of the Argentine Patagonia, where condors spent twice as much time scanning when feeding near than far from roads, a risky landscape feature (Speziale et al., 2008). Quantifying quitting harvest rates, something that we were unable to do in this study, would provide valuable insights on how individual condors titrate food and risk (Brown & Kotler, 2004). We found that condors in small groups spent more time vigilant. This was expected, since larger groups can diffuse risk effects (Lima, 1995). As the density of Andean condors continues to decline due to human impacts (BirdLife International, 2020), it is plausible that an Allee effect emerge whereby smaller groups of birds suffer negative fitness consequences as a result of spending less time foraging (Stephens & Sutherland, 1999). Further, condors' group foraging rate increased in larger groups and as carrion depleted. The slower consumption of carrion due to declining populations of vultures can impact food webs, nutrient cycling, and disease dynamics (Buechley & Şekercioglu, 2016).

A growing body of evidence has demonstrated that carrion is a risky food resource and that direct and indirect effects of predators on scavengers can ultimately shape the functioning of ecosystems (Prugh & Sivy, 2020). However, research has focused on facultative scavengers; few studies have linked risk of predation to vulture behavior (Gavashelishvili & McGrady, 2006). Our work shows that predation risk can influence carrion use by an obligate scavenger and that landscape features are reliable cues for scavengers to avoid predation. These results highlight that the risk of exploiting carrion is not only ephemeral but also spatially variable. More generally, our findings show that the effects of predation risk propagate to higher trophic levels and are potentially as important for these interactions as they are for predator–prey dynamics. Indeed, the balance between food and risk appears to be highly relevant for obligate scavengers; Andean condors ignored profitable resources to avoid foraging near stalking cover for pumas. Our findings likely extend to other predator–scavenger systems in which scavengers

are tightly tethered to carrion provisioned by, and shared with, large carnivores. Our study complements a large body of literature showing that tradeoffs of food and safety are pervasive across foragers (Sheriff et al., 2020). Future research investigating how risk manifests in scavengers globally will help to reveal the full effects of predation risk on ecological communities.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Perrig et al., 2022) are available in Figshare at <https://doi.org/10.6084/m9.figshare.16783048>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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