





ORIGINAL RESEARCH

Scavenger assemblages are structured by complex competition and facilitation processes among vulturesL. Naves-Alegre^{1,2} , Z. Morales-Reyes^{1,3} , J. A. Sánchez-Zapata¹  & E. Sebastián-González² ¹Department of Applied Biology, Centro de Investigación e Innovación Agroalimentaria y Agroambiental (CIAGRO-UMH), Miguel Hernández University of Elche, Elche, Spain²Ecology Department, Alicante University, Alicante, Spain³Instituto de Estudios Sociales Avanzados (IESA), CSIC, Córdoba, Spain**Keywords**

coexistence; exploitative competition; interspecific facilitation; inter-guild interactions; interspecific interactions; scavengers; niche differentiation; neotropical vultures.

Correspondence

Lara Naves-Alegre, Departamento de Biología Aplicada. Universidad Miguel Hernández de Elche., Avda. Universidad s/n 03202 Elche, Spain. Email: laranavesalegre@gmail.com

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Abstract

Understanding the factors that allow multiple species to coexist and share resources is an outstanding question in community ecology. Animals that share resources tend to use different strategies to decrease potential competition, through morphological adaptations, establishment of hierarchies, behavioral adaptations or spatial or temporal segregation. The main objective of this study was to infer interspecific processes of competition and facilitation through the study of species co-occurrence patterns in a vertebrate scavenger guild in de Brazilian *cerrado*. We analyzed patterns of spatial and temporal co-occurrence between species pairs, both qualitatively and quantitatively, and determined the activity patterns of the different scavenger species. For this purpose, we placed and monitored 11 large (i.e. goat) and 45 small (i.e. chicken) carcasses by camera-trapping, obtaining a total of 27 448 images. Our results show complex competitive and facilitative relationships among scavenging species in the Brazilian *cerrado* that are influenced by carcass size and change depending on the spatial and temporal scale at which they are analyzed. The scavenger assemblages that consumed large and small carcasses were different, evidencing resource partitioning between obligate and facultative scavengers. Furthermore, as an alternative to reduce competition levels, most species showed differences in their scavenging patterns, in addition to a strong temporal segregation during carcass consumption. Regarding New World vultures, our results suggest a strong interference competition between species with clear differences in their ecological traits (e.g. size, social behavior). However, we also found evidence of facilitation processes between vulture species in the location and access to the interior of the carcasses. Our findings highlight the role of obligate scavengers both in competition and facilitation processes in this vertebrate scavenger community. Future research should focus on investigating which species play the most important role in the structure and dynamics of this community, also considering intraspecific and behavioral patterns.

Introduction

Understanding the factors that allow multiple species to coexist and share resources is an outstanding question in community ecology (Bascompte, 2010; Kneitel & Chase, 2004). Several studies have found that the coexistence of interacting species may be driven by both agonistic (e.g. prey–predator dynamics, competition for resources) and facilitative (e.g. mutualistic interactions) processes (Harrison & Whitehouse, 2011; Prugh & Sivy, 2020; Ullas Karanth et al., 2017; Veit & Harrison, 2017). Among agonistic interactions, interspecific competition may be especially important in situations of strong

competition because organisms must develop diverse strategies to prevent it (Davies et al., 2007). One of the most important strategies adopted is niche differentiation, where two organisms living in the same environment use different ecological niches to coexist, differing in what, where or when they eat (Finke & Snyder, 2008; Roughgarden, 1975).

Competition between coexisting species that belong to the same guild is especially interesting, because the more similar the ecological niche of two species is, the larger the competition among them (May & MacArthur, 1972). Animals that share resources tend to use different foraging strategies to decrease this potential competition, through morphological

adaptations, establishment of hierarchies, behavioral adaptations or spatial or temporal segregation (Carrete *et al.*, 2010; Sogbohossou *et al.*, 2018). In this sense, the scavenger guild is an interesting assemblage because carrion offers highly nutritive biomass concentrated in space and time, which tends to be unpredictable and ephemeral (DeVault *et al.*, 2003; Moleón *et al.*, 2019). All these characteristics result in many individuals of different species being able to consume carrion and thus potentially sharing the same resource (Cortés-Avizanda *et al.*, 2012; Kane *et al.*, 2014).

Within the scavenger guild, we can find obligate (i.e. vultures) and facultative scavengers (i.e. generalist species such as other raptors, corvids, mammals or reptiles). This implies a high richness of potential coexisting scavenger species resulting in high levels of interspecific competition (Allen *et al.*, 2014; Ruxton & Houston, 2004). To reduce competition, coexisting scavengers may use different strategies, such as establishing hierarchy patterns in the use of the resource, with the hierarchical order of the species depending on their ecological traits (Houston, 1988; Kendall *et al.*, 2012; Kruuk, 1967). For example, body size may facilitate dominance during aggressive interactions, so larger species will lead consumption at carcasses (Allen *et al.*, 2014; Moreno-Opo *et al.*, 2020). Species with low competitive capacities (e.g. small body size) may reduce competition in carcasses through other strategies, such as by conspecific aggregations in the resource or by avoiding direct confrontations by changing their spatial or temporal foraging patterns (Blázquez *et al.*, 2009; Kendall, 2014). Specifically, vultures are most specialized species in the consumption of carrion, sharing many physiological and morphological adaptations that make them very efficient when exploiting this resource (DeVault *et al.*, 2003). They have also developed some strategies to decrease competition, for example having different morphologies in the beak, that allow them to feed on different parts of the carcass (Kendall, 2014; Kruuk, 1967) or segregating in space and time.

Spatial and temporal segregation has been described both within Old and New World vultures (Cortés-Avizanda *et al.*, 2012; Kendall *et al.*, 2012; Kruuk, 1967; Moreno-Opo *et al.*, 2016). Also, some works have shown how some facultative species reduce costs related to interactions by spending less time in the carcass and increasing the speed at which they consume it, thus avoiding obligate scavengers which stay longer in the vicinity of the carcass (Moreno-Opo *et al.*, 2016). In addition, in areas where obligate scavengers are absent, differences in scavenger consumption patterns both in time and space have been described among facultative bird scavengers with different competitive capacities (Blázquez *et al.*, 2009).

One way to understand these patterns of facilitation or exclusion that occur between species that coexist in the same habitat and that consume the same resource, is through co-occurrence patterns. These patterns can indicate the presence of direct and indirect interactions between species (Gotelli & McCabe, 2002). It has been described that a negative co-occurrence between two species may reflect a competitive exclusion among these species, while a positive co-occurrence could indicate a process of facilitation (Sebastián-González *et al.*, 2010; Sfenthourakis *et al.*, 2006). Despite the abundance

of research on competitive interactions among scavengers, studies at community level, including all vertebrate scavenger species, are not available. Such community-level studies are needed to understand the patterns of competition and facilitation that influence vertebrate community structure and functioning (Sebastián-González *et al.*, 2016). The main objective of this study is to determine competitive and facilitation processes between species, by analyzing spatio-temporal co-occurrence patterns of the vertebrate scavenger species at carcasses in the Brazilian *cerrado*. In this way, we want to answer the following questions: Are facilitation processes occurring between species with different carcass opening skills, and/or between species with different foraging strategies? How do species with different competitive capacities manage competition at different scales? We establish specific hypotheses related to these questions (see Table 1 for hypotheses and further details). As a specific objective, we describe the daily activity patterns and the mean time of arrival to the carcasses of the different scavenger species in the community. These results will allow us to know the role of each species in the competition and facilitation processes that may occur during carrion consumption and, therefore, in the structure of this vertebrate assemblage.

Materials and methods

Study area and scavenger community

The study was carried out in the *cerrado* grasslands of North-eastern Brazil (Piauí state). Our study area contains a mosaic of vegetation ranging from woodlands to dry and gallery forests to savannas and grasslands (Ribeiro & Walter, 1998). There is a rainy season from December to March and a dry season from April to November. Annual rainfall ranges from 1200 to 1300 mm and the average annual temperature is 23°C. In our study area, we find four species of New World vultures (Cathartidae), turkey (*Cathartes aura*), lesser yellow-headed (*C. burrovianus*), American black (*Coragyps atratus*) and king (*Sarcoramphus papa*) vultures. We also find at least 14 species of facultative scavengers, from medium-sized mammals (e.g. hoary foxes *Lycalopex vetulus*), several raptor species (e.g. southern caracara *Caracara plancus*) and some reptiles (see Naves-Alegre *et al.*, 2021 for details on the study area and the scavenger assemblage).

Study design and variables considered

We studied the co-occurrence patterns between scavenger species through the placement of carcasses monitored by automatic cameras (Browning Strike Force pro HD). All cameras were placed approximate 1.5 m from the carcass, tied to a tree and configured to take 2 photographs per trigger with a delay of 30 seconds, as long as there was movement in front of the lens. Since carrion size is one of the factors that most affects the structure and functioning of scavenger assemblages (Moleón *et al.*, 2015; Naves-Alegre *et al.*, 2021), we placed 56 fresh carcasses during November 2018, distinguishing two sizes: (1) large, that is domestic goats (*Capra hircus*) weighing

Table 1 Facilitation and competition processes that may be occurring in a vertebrate scavenger community related to the co-occurrence patterns and hypotheses established in this work

Process	Description of the process	Co-occurrence	Hypothesis	References
Facilitation	Some species can access and open hard skin carcasses (i.e. goat carcasses) by passing through the skin, allowing the access to other species.	Positive co-occurrence patterns	1. There will be facilitation processes and thus species with a larger body size or stronger beaks (i.e. king vultures) and species with less ability to open carrion (e.g. <i>Cathartes</i> species, American black vultures) will positively associate in the same carrion, even at the same time.	(Kruuk, 1967; Selva <i>et al.</i> , 2003)
Facilitation	Species with higher search efficiency, due to differences in flight ability or sensory ability (e.g. olfactory capacity), will serve as a visual cue of the presence of carrion for other species.	Positive co-occurrence patterns	2. The presence in a carcass of species with olfactory capacity (i.e. turkey, lesser yellow-headed vultures and southern caracara) and with lower flying height (i.e. <i>Cathartes</i> species) will serve as a signal for other species of the community to locate the carrion, giving rise to positive co-occurrence of these species.	(Cortés-Avizanda <i>et al.</i> , 2012; Houston, 1988; Kane <i>et al.</i> , 2014; Kruuk, 1967; Veit & Harrison, 2017)
Competition	Exploitative competition or resource competition, i.e. when organisms consume and therefore compete for the same resource.	Negative spatial co-occurrence patterns	3. Exploitative competition will result in spatial segregation between species. Thus, species with greater consumption capacity (e.g. larger body size, specialists) may consume some carcasses completely or monopolize its consumption, precluding the use of the resource by other species.	(Gorelli <i>et al.</i> , 2010; Moreno-Opo <i>et al.</i> , 2016; Palomares <i>et al.</i> , 2016)
Competition	Interference competition, i.e. one species reduces the ability of other species to exploit a shared resource by direct interactions (e.g. aggressive interactions).	Negative spatio-temporal co-occurrence patterns	4. There is a hierarchy whereby some species are competitively superior (e.g. larger species), and therefore competitively inferior species will avoid co-occurring on the same carcass at the same time (i.e. temporal segregation) to avoid direct confrontations.	(Blázquez <i>et al.</i> , 2009; Kronfeld-Schor & Dayan, 2003; Moreno-Opo <i>et al.</i> , 2020)

20–40 kg ($n = 11$), and (2) small, that is entire chickens or chicken fragments (*Gallus gallus*) weighing between 0.075 and 2 kg ($n = 45$), (see study area map in the Appendix S1, Figure S1). All carcasses were placed randomly, large ones at a minimum distance of 1.5 km among them (Morales-Reyes *et al.*, 2017). Small carcasses were placed at a minimum distance of 150 m and in higher numbers to more realistically simulate the dynamics of a natural system, where smaller organisms are found at higher densities and have higher mortality rates due to their shorter life span (Rossberg *et al.*, 2008; White *et al.*, 2007). The independence of the samples was confirmed by analyzing the spatial autocorrelation between them and confirmed their spatial independence (see Naves-Alegre *et al.*, 2021 for further details).

We obtained 27 448 images (24 980 images for large carcasses and 2468 images for small carcasses). All the images were visualized, and we extracted several variables. First, we identified the *presence per carcass* and *presence per image* of all detected species, that is presence (1) or absence (0) of a scavenger at a carcass or image level (see the list of species in the Appendix S1, Table S1). For quantitative analyses, we established the *abundance per carcass* for each detected species, which was defined as the maximum number of unequivocally different individuals from a species that appeared simultaneously in the same image or that could be individualized during the consumption of the carcass because of age/sex differences, color patterns or distinct marks (e.g. injuries). We also calculated the *abundance per image* for each species, defining it as the total number of individuals of a species observed in an image.

For the quantitative analyses, we also considered two other covariables that are known to affect the relations between species (Naves-Alegre *et al.*, 2021): (i) *vegetation cover*, defined as the percentage cover of trees and shrubs within a 5-m radius of the carcass location, the (ii) *time of carcass placement*, differentiating between carcasses placed during the *morning* (i.e. from sunrise to 12:00 h) and the *afternoon* (i.e. from 12:00 h until sunset). Because the main scavengers in this community are diurnal (i.e. vultures and facultative raptors), being preferentially active during the hottest hours of the day, the time of carcass placement could affect consumption patterns. Finally, we also used (iii) the *day of consumption* (i.e. whole days from the date the first scavenger species appears until carcass total consumption), because competition levels may vary during the consumption of the resource.

Activity patterns and time of arrival

We represented the activity patterns of scavenger species throughout the day, measured as the percentage of photographs in which a species appears throughout the hourly periods that compose the 24 hours of the day (i.e. we divided the 24 hours into 1 hour periods) out of the total number of photographs in which that species appears. To simplify these results, we grouped the scavenger species into (a) vultures, (b) facultative birds (i.e. all birds except vultures), (c) mammals and (d) reptiles. In addition, we represented the activity of each vulture species (i.e. turkey, American black, lesser yellow-headed and

king vultures) according to the *day of consumption* of the carcass. Finally, we calculated the mean *time of arrival* of each species at the carcasses in which they were recorded, that is minutes from the time the carcass was placed until the first individual of each species appears in a carcass.

Co-occurrence analyses

We used co-occurrence analyses to identify possible associations between species. We used the ‘coocur’ package in R (Griffith *et al.*, 2016), which uses the probabilistic model of species co-occurrence by Veech (2013). This approach utilizes presence/absence data, and it calculates an expected probability that two species coincide, determining whether the co-occurrence of the different pairs of species is therefore higher (positive co-occurrence) or lower (negative co-occurrence) than expected, or if it is random. Using this method, we studied the co-occurrence between species pairs both spatially (*i.e.* species occurring at the same carcass) and spatio-temporally (*i.e.* species occurring in the same image: same time at the same carcass) for large and small carcasses separately.

a) Spatial co-occurrence

Initially, to determine whether to perform the co-occurrence analyses for large and small carcasses separately or together, we used permutational multivariate analysis of variance (PERMANOVA), to determine whether there was a segregation between species in the consumption of the two carcasses sizes. On the one hand, we used the Jaccard dissimilarity that only considers the presence or absence of the species, that is *presence per carcass*, and on the other hand, the Bray–Curtis dissimilarity, which contemplates the abundance of each of the species, that is *abundance per carcass*. For both PERMANOVAs, we used the ‘adonis’ function of the ‘vegan’ package (Oksanen *et al.*, 2019).

Subsequently, we analyzed the co-occurrence of species by the variable *presence per carcass* of those species that appeared in more than 7 carcasses for both large and small carcasses (see Table S2 for further details).

b) Spatio-temporal co-occurrence

For all spatial–temporal co-occurrence analyses, we used the variable *presence per image* of those species that appeared in more than 100 images (see Table S2b). First, due to the long consumption times of large carcasses, we analyzed the spatio-temporal co-occurrence patterns for each different *day of consumption* separately (*i.e.* first, second, third or fourth). We divided all the images according to the day of consumption to which they belonged. Because we had a very different number of images for each *day of consumption*, we selected a sub-sample of pictures from each day by using ‘sample’ function in R. We determined the minimum number of photographs required to carry out the analyses, by repeating the co-occurrence analyses for different numbers of photographs from each *day of consumption* (*i.e.* 200, 400, 800, 1000, 1500), obtaining that the minimum number of images required for

consistent results is 1000. In this way, we decided to use the maximum number of images above 1000, so we randomly selected 1500 photographs from the first, second and third day of consumption, and 1184 images from the fourth day (maximum number of images obtained). Images from day 5 and 6 were not considered because they were not enough to run reliable analyses (52 and 2, respectively).

Second, we analyzed the spatio-temporal co-occurrence for large carcasses throughout all their consumption period. Since we previously found differences in co-occurrence patterns between consumption days, we used the ‘sample’ function to obtain a sub-sample of images for each of the days of consumption, in the same way as the analysis described above (*i.e.* 1500 images for days 1, 2 and 3, and 1184 for day 4). In this way, we considered the same approximate proportion of images during the entire period of carcass consumption. We ran the co-occurrence analysis for large carcasses using all the selected images together (5684 in total). Finally, we also analyzed the spatio-temporal co-occurrence patterns for the small carcasses, for which we used all the images obtained ($n = 2468$).

Quantitative analyses

As co-occurrence analyses only use presence and absence data, we quantitatively analyzed associations between pairs of species by using generalized linear models (GLMs) for the spatial scale and generalized linear mixed models (GLMMs) for the spatio-temporal scale, to study the possible effect that the number of individuals of a species has on the presence and abundance of another species. These analyses were carried out for large and small carcasses separately (see Table S2 for further details).

a) Spatial analyses

For the spatial analyses, we ran a GLM for each species that appeared in more than seven carcasses using as response variable its *abundance per carcass*. We made this selection because to fit the models we need each species to have enough positive occurrences in the total of carcasses. We used as explanatory variables the *abundance per carcass* of all the other species that also appeared in more than seven carcasses, together with two covariables: *vegetation cover* and *time of carcass placement*.

For the spatial models referring to large carcasses, because we only had a sample of eleven carcasses, we performed one-predictor GLMs with each of the explanatory variables. For the large carcass models, we used as response variable the *abundance per carcass* of the following species: (1) turkey vulture, (2) king vulture, (3) American black vulture and (4) southern caracara. For turkey, king and American black vultures’ models we used a negative binomial distribution (log link function), and for Southern caracara models we used a Poisson distribution (log link function).

In contrast, several-predictor models were performed for the spatial models of the chicken carcasses ($n = 45$). For these carcasses, we used as response variables: (1) turkey vulture, (2) lesser yellow-header vulture, (3) king vulture and (4) southern

caracara. All models were fitted to a Poisson distribution (log link function).

b) Spatio-temporal analyses

For the spatio-temporal analyses, we ran a GLMM for each species that appeared in more than 100 images using as response variable its *abundance per image*. We used as explanatory variables the *abundance per image* of the other species that also appear in more than 100 images of each carcass size, together with two covariables: *vegetation cover* and *day of consumption*, and the carcass identity as random factor.

For large carcasses, we ran multivariate mixed models using as response variable the *abundance per image* of the following species: (1) turkey vulture, (2) lesser yellow-headed vulture, (3) king vulture, (4) American black vulture and (5) southern caracara. We used a Poisson distribution (log link function) for all species' models.

For small carcasses, we used all the images obtained. We ran several-predictor GLMMs using as response variable the *abundance per image* of the following species: (1) turkey vulture, (2) lesser yellow-headed vulture, (3) king vulture, (4) southern caracara and (5) yellow-headed caracara. We used Poisson distribution (log link function) for all the species.

We used the *glm* and *glmer* functions in 'lme4' package for spatial GLMs and spatial-temporal GLMMs analyses, respectively (Bates *et al.*, 2015). For several-predictor GLMs (i.e. small carcasses analyses), we selected the best models based on Akaike's information criteria for small samples (AICc) from all potential models. We only selected the models with an AICc value <2. In cases where we obtained more than one model, we calculated the model-average coefficients using the *model.avg* function in the *MuMIn* package (Bartoń, 2019).

Results

We detected 18 scavenger species in the carcasses (see Table S1 for complete list of species). Four of these were New World vultures (i.e. obligate scavengers; family Cathartidae), that is turkey (*Cathartes aura*), lesser yellow-headed (*C. burrovianus*), American black (*Coragyps atratus*) and king (*Sarcophagus papa*) vultures. We also found 14 species of facultative scavengers, seven facultative birds (e.g. southern caracaras *Caracara plancus*), five medium-sized mammals (e.g. hoary foxes *Lycalopex vetulus*) and two reptiles (e.g. black-and-white tegu *Salvator merianae*).

Activity patterns and time of arrival

Vultures showed a mainly diurnal activity (Fig. 1). The lesser yellow-headed vulture was exclusively detected during the day, with two peaks of activity between 10 a.m. and 12 p.m. and between 3 p.m. and 5 p.m. The turkey vulture maintained its activity throughout the day, being around 81% of its detections between 8 a.m. and 5 p.m. The American black vulture had a very similar activity to turkey vulture, being active mainly during the day, between 6 a.m. and 7 p.m. However, American

black vulture showed some nocturnal activity during the consumption of one of the carcasses. Finally, the king vulture was detected between 6 a.m. and 6 p.m., with a peak of activity during the early morning hours (i.e. 40% of its activity recorded between 6 a.m. and 9 a.m.) (Fig. 1a). Facultative birds were mainly diurnal, being more active in the morning, between 8:00 a.m. and 1:00 p.m. (59% of the detections). Mammals showed a mainly nocturnal activity pattern (83%). Reptiles were diurnal, focusing 100% of their activity between 8 a.m. and 3 p.m. (Fig. 1b).

In large carcasses, not all vulture species appeared at the same carcass consumption timeline. The lesser yellow-headed vulture focused its activity during the first day of carcass consumption, while the turkey vulture was mainly active on the first and second days. American black and king vultures had a longer lasting activity, being more active on the second day than on the first. For all vulture species, from the third day onwards, the activity dropped (Fig. 1c).

Species' mean arrival times at carcasses were highly variable (Table S3). We detected the shortest arrival times for the species of the genus *Cathartes*, that is Turkey vulture and Lesser yellow-headed vulture, with mean arrival times at carrion of 77 and 82 minutes, respectively. While the longest detection times were those of two facultative species, that is ocelot and red-legged seriema, with 6105 and 10 620 minutes, respectively.

Spatial co-occurrence

PERMANOVA results showed that there was a segregation between species that consume large and small carcasses (Table S4). For large carcasses, we did not find positive or negative associations, meaning that the 6 species pairs co-occurred randomly (Fig. 2). In contrast, GLMs (quantitative analyses) for large carcasses showed a positive relationship between the *abundance per carcass* of turkey and king vultures, and a negative relationship between the abundance of the king vulture and the southern caracara (Fig. 2, Table S5).

For small-sized carcasses, we only obtained one positive association between turkey and king vultures out of 6 species pairs (Fig. 2). Quantitative analyses also showed a positive relationship between these two species. We also found a positive association between the *abundance per carcass* of king and lesser yellow-headed vultures (see Fig. 2, Table S6). None of the covariates had a significant effect on either large or small carcasses (see Tables S5 and S6).

Spatio-temporal co-occurrence

We obtained diverse patterns of spatio-temporal co-occurrence in small and large carcasses. For large carcasses, we recorded 1 positive and 8 negative associations out of 10 species pairs. Quantitative GLMMs showed predominantly negative relationships between species' *abundance per image* except for the positive relationship between king and American black vultures. On the contrary, the variable *day of consumption* had significant effects for most of the species, while the *vegetation cover* did not seem to have any effect (Fig. 2, Table S7).

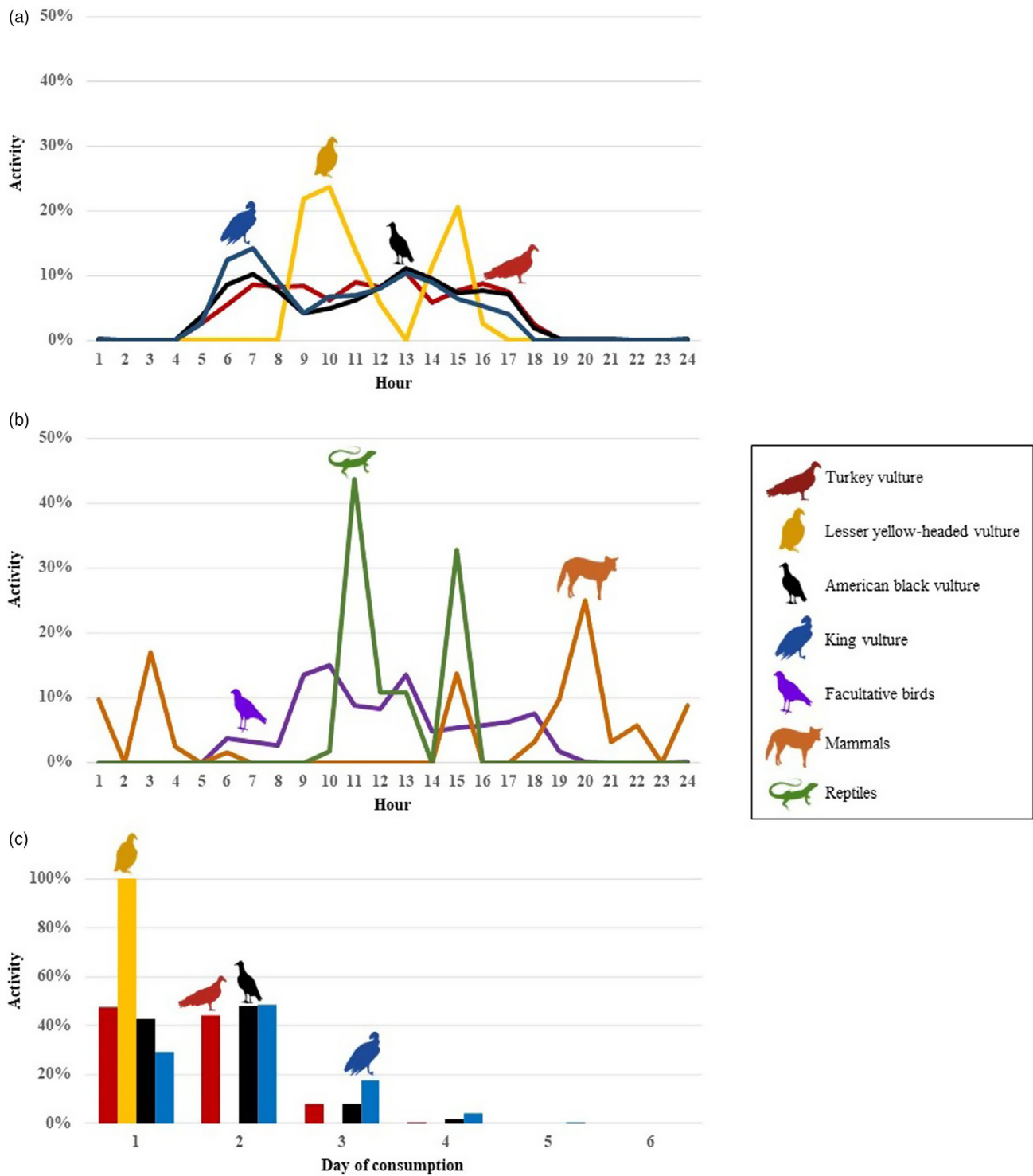


Figure 1 Daily activity patterns represented as the percentage of activity of scavenging species in the Brazilian *cerrado*, differentiating between (a) obligate and (b) facultative scavengers. (c) Activity patterns of the four species of vultures found in this scavenger community through the different days of consumption of the two sizes carcasses.

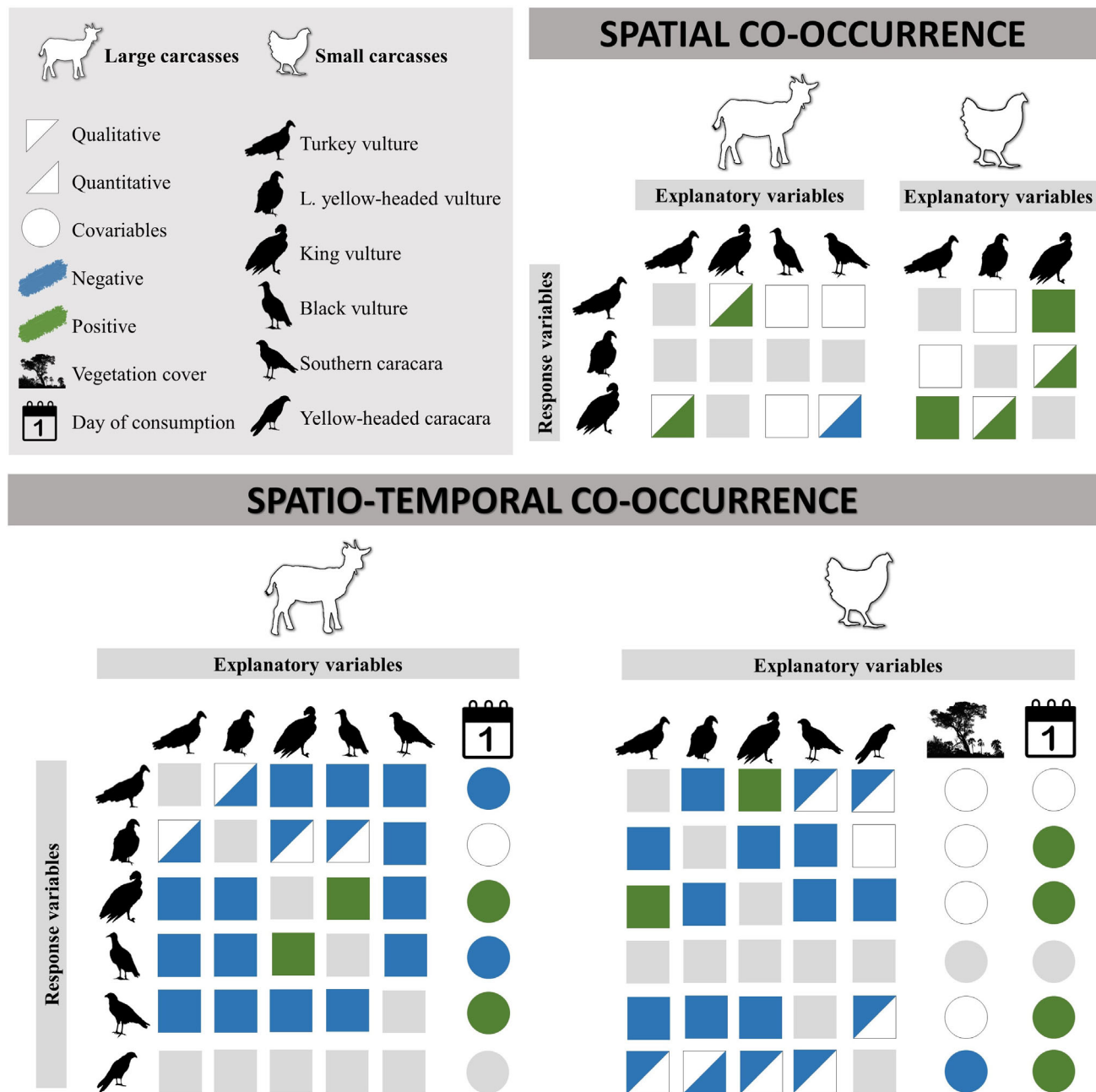


Figure 2 Results of the spatial and spatio-temporal co-occurrence analyses between pairs of species, both qualitative co-occurrence and quantitative GLMs (spatial co-occurrence) and GLMMs (spatio-temporal co-occurrence) that relate the abundances of the species. Negative associations are shown in blue and positive associations in green. Only the species associations (squares) and covariates (circles) incorporated in the GLMs and GLMMs that were significant for any of the species were represented. For more details, see [Appendix S1 \(Tables S5–S8\)](#).

We also obtained variations in the co-occurrence patterns among the 10 pairs of species obtained as a function of the *day of consumption* for large carcasses (Fig. 3). During the first day of consumption, we obtained mainly negative patterns (8 negative associations), as opposed to two positive relationships. On the second day, the number of negative relationships between pairs of species was lower (4), and the positive

relationships were maintained between the same species. On the third day, negative co-occurrence relationships continued to predominate (4), as opposed to positive ones (1). Finally, during the fourth day, the negative relationships decreased (3), and there were two positive relationships (Fig. 3).

For the small carcasses, we could test associations between 10 species-pairs. Eight showed negative associations while only 1

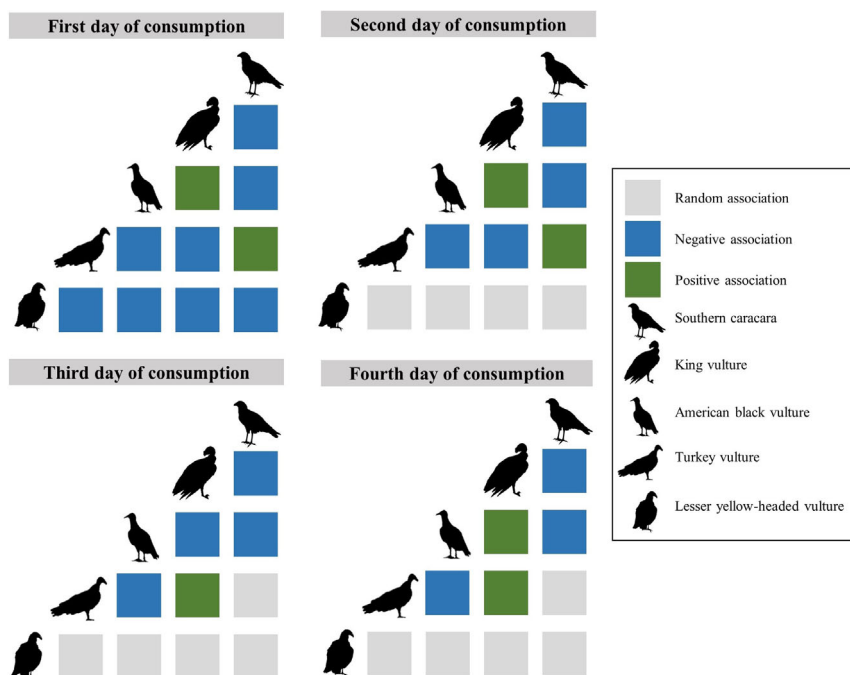


Figure 3 Spatio-temporal co-occurrence for the different days of consumption at large carcasses. Yellow-headed caracara is not included because it only appeared in one of the photographs used for this co-occurrence analysis.

was positive (Fig. 2). The results of the quantitative GLMMs support positive relationships between king and turkey vultures. The remaining quantitative relationships between species were negative and concordant with the qualitative co-occurrence results (Fig. 2, Table S8). The variables *day of consumption* and *vegetation cover* significantly affected the *abundance per image* of some species (for more details, see Fig. 2).

Discussion

Competition and facilitation relationships between species belonging to the same guild are fundamental because they determine community's functioning and ultimately shape its structure (Bascompte, 2010). By examining fine-scale spatio-temporal co-occurrence patterns among scavenging species in the Brazilian *cerrado*, our results show complex patterns of competition and facilitation that were mainly affected by carcass size. Most scavengers in this community showed differences in their activity patterns in addition to a strong spatio-temporal segregation between them during carcass consumption. Vultures co-occur at all large carcasses although both temporal association and segregation might modulate facilitation and intraguild competition for this resource.

Facilitation processes

Our results evidence that two different facilitation processes may be taking place between vulture species and that their relative importance changes with the size of the carcass. First, the spatial and spatio-temporal association in large carcasses among species with different abilities to open hard skin carcasses seems to

evidence a facilitation process in the access to the carcass interior, supporting our first hypothesis (see Table 1). In this way, species that cannot open carcasses (i.e. turkey vulture or American black vulture) would benefit from the presence of larger species or species with stronger beaks (i.e. king vulture), as has already been described in other communities (Kane et al., 2014; Selva et al., 2003; Stahler et al., 2002).

Secondly, although we also found positive associations (both spatially and temporally) among vultures in small carcasses, it is unlikely that the same facilitation process is occurring given that the skin of this carcass type is easily penetrable by all species and given the differences in the average consumption times of both types of carcasses (large carcasses: 48.41 hours, vs. small carcasses: 13.55 hours) (Naves-Alegre et al., 2021). Indeed, these associations include vultures with developed olfactory capacity (e.g. turkey vulture) and vultures that only rely on sight. This would support our second hypothesis (see Table 1), suggesting a facilitation process in carrion location in which species with keen searching abilities would signal the presence of small carcasses to other species (Gomez et al., 1994; Houston, 1985, 1988; Wallace & Temple, 1987). Such positive spatial associations have already been described in other systems, such as in Africa, being explained by facilitation processes when finding carcasses, or due to a preference for the consumption of certain parts of the carcass (Kendall et al., 2012). It is important to mention that this facilitation effect could also be playing a role in the localization of large carcasses, but more studies are needed to confirm these processes.

Common associations of species eating the same carrion at the same time (i.e. positive spatio-temporal co-occurrence) may not always suggest a facilitation process between the species

involved. These results could have two alternative explanations: (a) species are competitively equal in direct confrontation, for example when the difference in size between them is compensated by the social nature of one of them or its higher aggressive behavior; (b) the species are specialized in the consumption of different parts of the carcass (e.g. king vultures feed mainly on skin and tendons while American black vultures remove soft tissues) (Del Hoyo *et al.*, 1992; Houston, 1988), as found for other scavenger species (Kendall, 2014; Kendall *et al.*, 2012; Moreno-Opo *et al.*, 2020). Therefore, behavioral studies are necessary to be able to discern exactly what type of processes are taking place at any given moment, given that the process of facilitating the carcass localization will be important in the early stages of the carcass, moving on to a situation of competition between species as it is being consumed.

Vegetation structure has been described as a fundamental factor that shapes vertebrate scavenger communities at different scales (Pardo-Barquín *et al.*, 2019). Our results support a previous study showing that this factor has no effect on interspecific interactions due to the high efficiency of the *cerrado* scavenger community (Naves-Alegre *et al.*, 2021). However, we found a mainly negative effect of vegetation structure on the recruitment capacity of the species, that is on quantitative co-occurrences at the spatio-temporal level. Thus, a denser vegetation cover means a lower abundance of some species in a carcass at a given time. This may be due to interference in the transmission of intraspecific visual information, or as described above, dense vegetation cover may complicate access to carrion and thus limit the facilitation processes between species (Pardo-Barquín *et al.*, 2019; Ruzicka & Conover, 2012).

Competition processes

Many papers have described processes of exploitative competition between species sharing the same resources, which in many cases give rise to different scales of spatial segregation (Gotelli *et al.*, 2010; Palomares *et al.*, 2016; Tsunoda *et al.*, 2017). Contrary to these previous studies and to our own third hypothesis (see Table 1), our findings showed no evidence of spatial segregation between species, although the small sample of large carcasses may be masking some process. However, PERMANOVA analyses showed a strong differentiation between the scavenger communities that consumed the two carcass types. Vultures monopolized large carcasses, while small carcasses were consumed by multiple species (Moleón *et al.*, 2015; Naves-Alegre *et al.*, 2021). This is an evidence of resource partitioning, which allows facultative species with a lower competitive capacity to consume small carcasses where the risk of interaction with other species is lower (Tsunoda *et al.*, 2017). Resource partitioning among vertebrate scavenger species has previously been described in diverse ecosystems, such as the Mediterranean (Blázquez *et al.*, 2009) or in temperate forests of Europe and North America (Moreno-Opo *et al.*, 2016; Van Dijk *et al.*, 2008).

Contrary to what has been observed for spatial co-occurrence patterns, our results highlight temporal segregation patterns between multiple species, a process described in other

systems (Blázquez *et al.*, 2009; Kendall, 2014). According to our fourth hypothesis (see Table 1) this process would be a result of the interference competition derived from the hierarchy among species, segregating the competitively inferior ones (e.g. facultative scavengers or turkey vulture) to avoid direct confrontations with larger species (i.e. king vulture) and with social vultures that appear in large groups (i.e. American black vultures) (Kronfeld-Schor & Dayan, 2003; Moreno-Opo *et al.*, 2020). In large carcasses, because of their long consumption times, these spatio-temporal relationships between pairs of species change during the consumption timeline, indicating that competition levels do not remain the same throughout the consumption of the resource (Moleón *et al.*, 2019; Moreno-Opo *et al.*, 2015). On the contrary, many negative spatio-temporal relationships detected in small carcasses could be driven by these being mainly consumed by a single species, so that, in general, different species do not coincide at the same time on the same carcass.

Time partitioning is described as an important mechanism for reducing competition between coexisting species (Frey *et al.*, 2017) and has been evidenced in previous studies on scavengers (Butler & du Toit, 2002; Ruxton & Houston, 2004). Thus, we did not find many spatio-temporal patterns among facultative species (e.g. mammals or reptiles), highlighting the differences in activity patterns between mammals, reptiles and birds. We found that mammals were mainly nocturnal, while reptiles and all bird species, both facultative and obligate scavengers were active mainly during the day. Moreover, the co-occurrence in carcasses of certain facultative species may be low because they are competitively displaced by the obligate scavengers (Ulrich *et al.*, 2014), reducing the number of interactions between obligate scavengers and most of the facultative species (Moreno-Opo *et al.*, 2016; Sebastián-González *et al.*, 2013). By contrast, in other systems, facultative or smaller species have been found associated with some carnivores that open carrion (e.g. Selva *et al.*, 2003; Stahler *et al.*, 2002).

Conclusions

This work highlights how the *cerrado* scavenger community structure is governed by complex processes of facilitation and competition. These interactions between species seem to be very influenced by carcass size (Moleón *et al.*, 2015; Naves-Alegre *et al.*, 2021) and also change depending on the spatial and temporal scale at which they are analyzed, as previous research has shown (Kneitel & Chase, 2004; Ullas Karanth *et al.*, 2017). However, it is noteworthy that most species showed a strong temporal segregation during carcass consumption, as an alternative to reduce competition levels (Kronfeld-Schor & Dayan, 2003). The fundamental role of obligate scavengers in these processes is also emphasized, as these species were involved in most of the species-pair associations, especially in facilitation processes (i.e. location and access to the carcasses). In addition, these inter-species relationships do not always appear to be bidirectional, but rather one of the species is the trigger for the attraction or repulsion of another, that is the facilitation or competition process. Further work is needed

to determine which species play the most important role in the structure and dynamics of this community, for example by considering the order of access to carcasses (Alvarez *et al.*, 1976; Hunter *et al.*, 2007). It is also necessary to study the interactions of vertebrate and invertebrate scavengers, especially in those systems where there are no obligate or large scavengers, as in these systems carcasses remain available for longer time periods, facilitating their use by invertebrates. Also, in the future it will be important to determine not only the interspecific patterns but also the intraspecific ones, because they may also affect the functioning of this guild.

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Supporting Information

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

Figure S1. Map of the study area in Piauí, Brazil. We show the locations of all carcasses placed in the field, differentiating between large carcasses (orange, $n = 11$) and small carcasses (red, $n = 45$).

Table S1. Species recorded consuming carrion in this study. For each of them, we specified the common name, the scientific name, the taxonomic group (vulture, other bird, mammal or reptile) and the functional group (obligate or facultative scavenger).

Table S2. Summary of the analyses used and the species included in each analysis. (a) Analyses performed at different

scales, for which the R package and function used, the type of data, the unit of analysis, and the sample size for large and small carcasses are specified. (b) For each of the vertebrate scavenger species detected in the community we determined: the spatial and temporal co-occurrence models for large and small carcasses in which they were included; and for the spatial and spatio-temporal quantitative models (also for large and small carcasses), those species included as response variables. Included species are represented with an X, missing species were not included in these analyses because of their low sample size.

Table S3. Mean *times of arrival* at the carcasses of all detected species (i.e., 18 scavenger species) represented in minutes and ordered from smallest to largest.

Table S4. Results of the PERMANOVA analyses testing dissimilarity in the vertebrate scavenger community depending on carcass size (large vs. small). All P -values were calculated based on 9999 permutations. The degrees of freedom (d.f.), sum of squares (SS), pseudo R^2 , pseudo F -statistic and the P -value. Significant P -values are in bold.

Table S5. Model coefficients for large carcasses by means of generalized linear models (GLMs) showing the relation between the *abundance per carcass* of turkey, king and American black vultures and southern caracara and the other species abundance, *time of carcass placement* and *vegetation cover*. The estimate of the parameters, the standard error (SE) and significance (P -value) are shown. Significant P -values are in bold.

Table S6. Model-averaged coefficients for small carcasses by means of generalized linear models (GLMs) showing the relation between the *abundance per carcass* of turkey, king and lesser yellow-headed vultures and southern caracara and the other species abundance, *time of carcass placement* and *vegetation cover*. The estimate of the parameters, the standard error (SE) and significance (P -value) are shown. Significant P -values are in bold.

Table S7. Model coefficients for large carcasses by means of generalized mixed models (GLMMs) showing the relation between the *abundance per image* of turkey vulture, lesser yellow-headed vulture, king vulture, black vulture, southern caracara and the other species abundances, *day of consumption* and *vegetation cover*. The estimate of the parameters, the standard error (SE) and significance (P -value) are shown. Significant P -values are in bold.

Table S8. Model coefficients for small carcasses by means of generalized mixed models (GLMMs) showing the relation between the *abundance per image* of turkey vulture, lesser yellow-headed vulture, king vulture, southern caracara and yellow-headed caracara, *day of consumption* and *vegetation cover*. The estimate of the parameters, the standard error (SE) and significance (P -value) are shown. Significant P -values are in bold.