

# Temporal resource partitioning mediates vertebrate coexistence at carcasses: The role of competitive and facilitative interactions



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## Abstract

Unravelling how biodiversity is maintained despite species competition for shared resources has been a central question in community ecology, and is gaining relevance amidst the current biodiversity crisis. Yet, we have still a poor understanding of the mechanisms that regulate species coexistence and shape the structure of assemblages in highly competitive environments such as carrion pulsed resources. Here, we study how large vertebrates coexist in scavenger assemblages by adapting their diel activity at large ungulate carcasses in NW Spain. We used camera traps to record vertebrate scavengers consuming 34 carcasses of livestock and hunted wild ungulates, which allowed us to assess also differences regarding carcass origin. To evaluate temporal resource partition among species, we estimated the overlap of diel activity patterns and the mean times of each scavenger at carcasses. We recorded 16 species of scavengers, 7 mammals and 9 birds, and found similar richness at both types of carcasses. Birds and mammals showed contrasting diel activity patterns, with birds using carcasses during daytime (mean= 11:38 h) and mammals mostly at night (23:09 h). The unimodal activity patterns of scavengers showed asynchronous peaks among species. Subordinate species modified their activity patterns at carcasses used by apex species to reduce temporal overlap. Also, diel activity patterns of vultures closely followed those of corvids, suggesting facilitation processes in which corvids would enhance carcass detection by vultures. Two mammal species (12.5%) increased nocturnality at carcasses of hunted ungulates, which could be a response to human disturbance. Our results suggest that both temporal segregation and coupling mediate the coexistence of large vertebrates at carcasses. These mechanisms might lead to richer scavenger assemblages and thereby more efficient ones in driving critical ecosystem functions related to carrion consumption, such as energy and nutrient recycling and biodiversity maintenance.

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**Keywords:** Carrion; Circadian activity; Coexistence; Diel activity; Facilitation; Interference competition; Scavenger community; Temporal segregation

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## Introduction

How ecological communities assemble and maintain biodiversity despite species competition for the same resources has been a central question in ecology for more than a century (e.g. Clements 1916; Gause 1934, Hutchinson 1959; Diamond 1975; Götzenberger et al 2012; Mittelbach 2012; Levine et al 2017). Given the accelerated rates of biodiversity loss we are currently facing (Dirzo et al. 2014; WWF 2020), this question is gaining relevance to shed light on the major mechanisms underlying species interactions and coexistence that support biodiversity (Gaynor et al 2018; Manlick & Pauli 2020; Sévêque et al 2020).

A wealth of evidence shows that interactions between co-occurring species sharing the same resources are key processes governing their coexistence and so local biodiversity (see for example Tokeshi 1999; Krebs 2001; Mittelbach 2012 and references therein). While beneficial interactions such as mutualism and facilitation allow species coexistence, interspecific competition can exclude less-competitive species from the community (i.e. competitive exclusion principle or Volterra-Gause principle; Hutchinson 1957; Hardin 1960; Mittelbach 2012). As a result, in competitive communities, resource partitioning or niche differentiation (i.e. “the degree of differential resource use by coexisting species”; Chase & Leibold 2003) is often proposed as a stabilizing mechanism which facilitates species coexistence by reducing competition for the shared resource (Hutchinson 1957; MacArthur & Levins 1967; Shoener 1974; Chesson 2000; Mittelbach 2012). Studying resource partitioning in competitive environments, where species-rich communities exploit limited resources in space and/or time, offers a good opportunity to gain insight into key ecological processes that contribute to maintain biodiversity and ecosystem functioning.

As a high-quality food resource present across ecosystems (Barton et al 2013; Olea et al 2019a), carrion is consumed by a wide range of invertebrate and vertebrate scavengers that assemble at carcasses. For example, between 2 and 11% of the vertebrate species in an ecosystem are known to scavenge (Mateo-Tomás et al. 2015). Although these are only minimum figures, they suggest that hundreds of vertebrate species (i.e. 675–3,700; Olea et al. 2019a), from very different trophic levels, can scavenge worldwide, participating in key ecosystem functions such as the recycling of matter and energy via carcass removal (Wilson & Wolkovich 2011; Olea et al. 2019a). Furthermore, carrion is an ephemeral resource, i.e. highly-restricted in space and time, which creates therefore “hot spots” and “hot moments” (Subalusky & Potts 2018; Olea et al 2019a) that promote scavenger aggregation. Strong niche overlap is thus expected to occur at carcasses, likely leading to increased competition and lowered coexistence among the species sharing this food resource. Interestingly, high numbers of scavenging species per carcass are often recorded (Mateo-Tomás et al 2015; Olea et al 2019b), – e.g. about 215 beetle species at 18 ungulate

carcasses in the Greater Yellowstone Ecosystem, USA (Barry et al. 2018), and at least 111 individuals of seven large vertebrate species feeding at a single ungulate carcass in the Cantabrian Mountains, Spain (Mateo-Tomás et al. 2017), suggesting that scavenger communities seem to circumvent the high interspecific competition expected for this resource. Several factors, such as the nested structure of vertebrate scavenger assemblages and carrion unpredictability, could alleviate interspecific competition at carcasses (Selva and Fortuna 2007; Cortés-Avizanda et al 2012; Sebastian-González et al 2016). Yet, we have still a poor understanding on the mechanisms that regulate species coexistence and shape the structure of scavenger assemblages at the highly competitive environment of a carcass.

Temporal niche partitioning among competitors for shared resources is known to be one important mechanism which facilitates species coexistence in ecological communities (Shoener 1974; Carothers & Jaksic 1984). In scavenger communities, temporal niche partitioning might occur if circadian (diel) rhythms mediate the interactions among species sharing a carrion; for example, less-competitive scavengers could shift its diel activity to times of the day when dominant scavengers are less active. Yet, while this temporal partition would lead to a dilution of interference competition (e.g. aggressive encounters; Tokeshi 1999), shifting their temporal activity to avoid competitors could imply physiological and ecological costs for the less competitive species (Kronfeld-Schor & Dayan 2003 and references herein; Gaynor et al. 2018). A tradeoff that could be in turn a driver shaping scavenger communities (Mittelbach 2012).

While temporal niche partitioning among seasons has been well-documented in invertebrate scavenger communities (e.g. Loreau 1985), this process remains poorly explored at a smaller scale, i.e. the diel activity patterns, in both invertebrate (but see Kočárek, 2001; Keller et al 2019) and vertebrate scavenger assemblages (but see Blázquez et al 2009; Schlacher et al 2013; Kendall 2014; Bassi et al 2018). The evidence available for vertebrate scavenger communities to date is limited to very specific environments (i.e. small fish carcasses in a sandy shore or mass mortality events; (Schlacher et al 2013; Handler et al 2021) or only one fraction of the scavenger community (i.e. a few mammal or avian species; Blázquez et al 2009; Kendall 2014; Bassi et al 2018; Amorós et al 2020; Handler et al 2021).

To gain insight into the mechanisms that allow species coexistence in highly competitive environments such as large carcasses, we investigate here community-level partitioning of the temporal niche by recording the diel activity patterns of vertebrate scavengers attending ungulate carcasses. We used camera-traps to record the scavenging activity of large vertebrates in a multitrophic community formed by apex species (i.e. predators and vultures), meso-carnivores and medium-sized raptors, and generalists. By studying this species-rich assemblage, we further explore key interspecific interactions such as interference

competition and facilitation. We hypothesize that the apex predators present in our community would exert a top-down control on the scavenging behavior of species at lower trophic levels (i.e. potential prey species; Mateo-Tomás et al 2015; Cunningham et al 2018). The latter would therefore shift their diel activity patterns at carcasses to reduce temporal niche overlap with apex predators. On the other hand, in light of existing evidence highlighting that vultures would rely on other species to find carcasses (e.g. eagles; Kean et al. 2014), we expected that vultures would show different diel activity patterns at carcasses with and without presence of corvids, as producers of information on carcass location.

## Materials and methods

### Study area

We studied the vertebrate scavenger community consuming carcasses of large ungulates in Somiedo and Las Ubiñas-La Mesa Natural Parks, protected areas located in northwestern temperate Spain (Appendix: Fig. 1). The study area holds a complete vertebrate scavenger community, with presence of obligate scavengers, top predators and generalists (Mateo-Tomás et al. 2015, 2017). Griffon *Gyps fulvus* and Egyptian *Neophron percnopterus* vultures breed in the area, while cinereous *Aegypius monachus* vultures are vagrant (Mateo-Tomás et al. 2019). Brown bear *Ursus arctos* and Iberian wolf *Canis lupus* are common apex predators present in the study area, as well as golden eagle *Aquila chrysaetos*. Meso-carnivores such as red fox *Vulpes vulpes* and mustelids (*Martes* spp., *Genetta genetta*), and medium-sized raptors such as common buzzard *Buteo buteo* are also present. Generalists species include wild boar *Sus scrofa*, and corvids like the common raven *Corvus corax*, and the carrion crow *C. corone* (Mateo-Tomás et al. 2015, 2017). This temperate ecosystem covers a wide range of altitudes (i.e. from ~400 to >1200 m.a.s.l.) with a high variety of habitats, from rocky outcrops to oak and beech woodlands and pastures devoted to extensively bred livestock (Mateo-Tomás 2009).

Livestock rearing is a major activity in the study area (~46,000 ha.), dominated by extensive farming of cattle *Bos taurus*, with an official census of ~10,000 heads in 2013, when this study was conducted (SADEI 2019). Additionally, extensive livestock censuses in this year included ~1,400 horses *Equus caballus*, and ~1,800 sheep *Ovis aries* and goats *Capra aegragus hircus* (SADEI 2019). Livestock roam freely most of the year, sharing natural habitats with wild ungulates. Red deer *Cervus elaphus*, chamois *Rupicapra rupicapra*, wild boar, and roe deer *Capreolus capreolus* are hunted in the study area following an official schedule yearly issued by the Regional Government of Asturias. A maximum of 57 red deer, 109 chamois, 8 roe deer and 185 wild boar hunting events were authorized during

the 2012–2013 hunting season in the study area (BOPA 2012; see Appendix: Table 1 for further details).

### Carcass monitoring

We used remote cameras Little Acorn 5210A and 5210M to monitor a total of 34 carcasses of livestock and wild ungulates generated year round in the study area between 2011 and 2013. We monitored 15 livestock carcasses (i.e. 7 horses, 5 cows and 3 sheep) generated in the countryside by predator attacks, illness, accident and other natural causes. We also monitored 19 carcasses of wild ungulates (i.e. 10 red deer, 7 chamois, 1 wild boar and 1 roe deer) all of them resulting from hunting activity (Mateo-Tomás et al. 2015). The monitored carcasses consisted of the entire animal bodies, with the head removed (as a trophy) in most wild ungulates ( $N = 15$ ). As long as livestock and wild ungulates share the same habitats in our study area, the carcasses of both types of ungulates were placed in roughly similar habitat conditions. We did not find significant differences between the locations of livestock and wild ungulate carcasses neither in altitude (Wilcoxon test:  $P = 0.06$ ), nor in open, forest and pasture coverage within a 10 m radius surrounding the carcasses (Wilcoxon test:  $P = 0.60, 0.33, 0.43$ , respectively). While livestock carcasses were generated through natural and unpredictable processes such as predation, illness or accident, the wild ungulate carcasses monitored in this study came from hunting (Mateo-Tomás et al. 2015), a human disturbance associated with shooting noise, human and ammunition scent, hunting dogs, etc., which are known to alter the diel patterns of several mammal species (including scavenging vertebrates) worldwide (see Gaynor et al. 2018 and references therein; corvids and vultures and hunting activity: White 2005; Mateo-Tomás & Olea 2010). Therefore, we separately analyzed the diel activity patterns of scavengers attending the two types of carcass monitored, i.e. livestock and wild ungulates, to further control for possible differences due to the origin of the carcasses.

Carcasses were weighed in the field with portable scales when possible; for carcasses too heavy to be lifted, the weight was estimated according to the age and sex of the individual using existing references on the weight of wild ungulate species and livestock breeds in the study area (Mateo-Tomás & Olea 2010; Mateo-Tomás et al. 2019). See Appendix Table 2 for further details on the types of carcass and their spatiotemporal distribution in the study area.

All the carcasses were located through collaboration with environmental authorities in charge of tracking wildlife damages to livestock and hunting activity in the study area. Briefly, for wild ungulates, we accompanied hunters and/or rangers to place the camera just after the carcass had been generated. Similarly, we put the cameras at unconsumed livestock carcasses within the first 12–24 h after death, just when farmers had informed the authorities of a dead animal. Cameras were removed after carcass consumption or when

only bones and skin remained (Mateo-Tomás et al. 2015, 2017). Cameras were placed near the carrion (4–10 m) and took pictures every minute if movement was detected both at day and night, using no glow infrared sensors to minimise disturbance. Carcasses were staked down with 25–50 cm metal sticks to prevent scavengers from taking them away from the camera before total consumption. A species was considered scavenging a carcass whenever the pictures taken provided unequivocal proof of consumption. When consumption by a species was suspected (e.g. an individual closely inspecting a carcass) but not clearly recorded, we assumed consumption whenever that species was recorded feeding on other monitored carcasses in the study area (see details in Mateo-Tomás et al. 2017).

## Data analysis

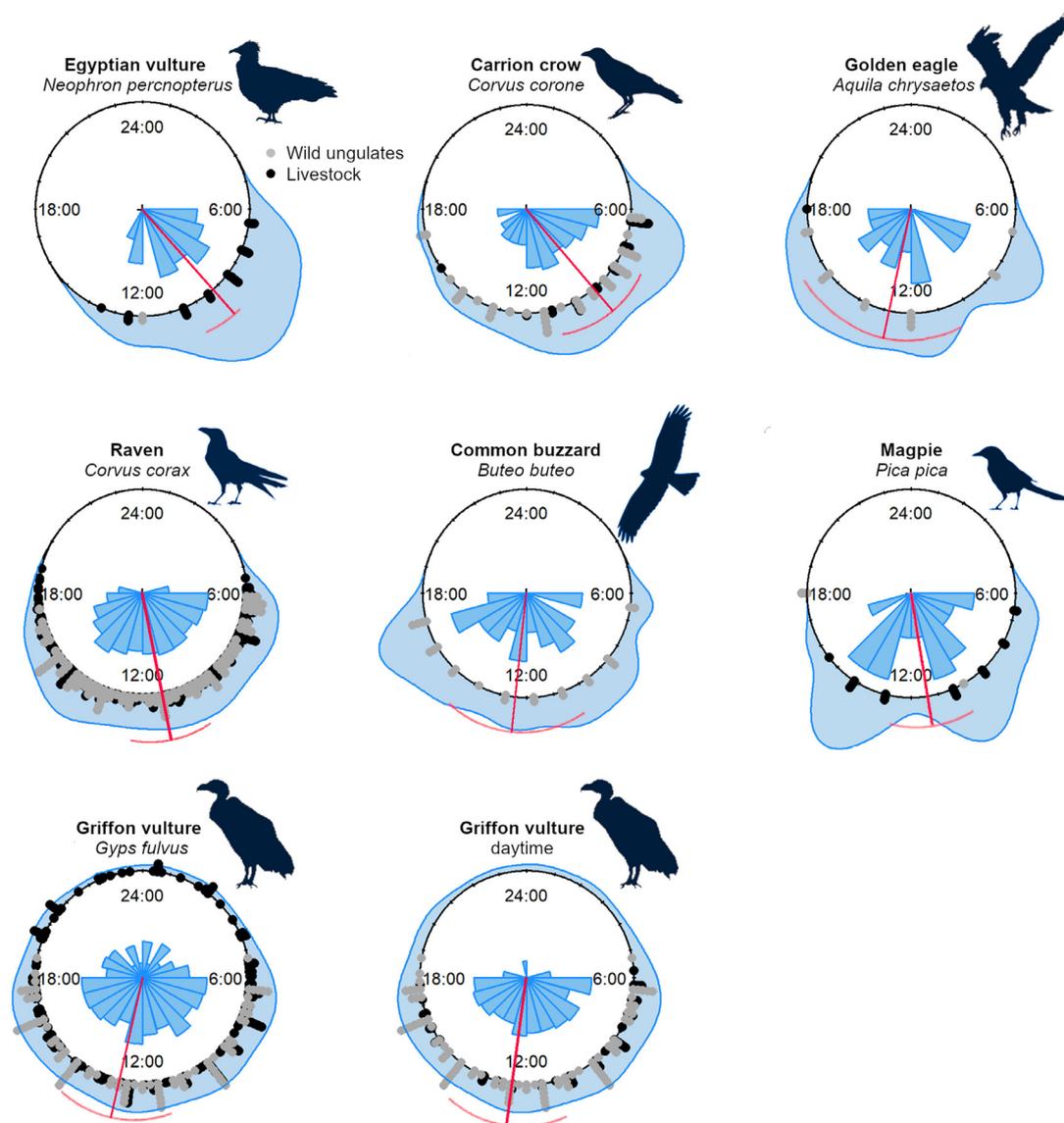
We recorded the species of vertebrate scavengers at each carcass from its generation in the field until total carcass consumption or when only bones and skin remained. Remote cameras allowed us to obtain the time, at the nearest minute (hereafter record), when each species was present at each monitored carcass. Records were grouped into 24 1 h categories and assigned to the nearest hour. Records of the same species at the same time and carcass but on different days were considered different. We recorded UTC time, which was then converted to solar time using the function “sunTime” of the package “overlap” (Ridout & Linkie 2009) in R (R Core Team 2020). Because the times of sunrise, zenith or sunset vary with the time of the year and latitude, the use of solar time is more adequate to analyze diel behavior of animals whose activities are likely driven by light intensity and thus related to the sun position in the sky (Nouvellet et al. 2012).

To assess the existence of daily temporal patterns in the use of carcasses by vertebrate scavengers we used circular statistics. First, we built raw 24-hour circular data plots for each species, with each data point representing the species presence in that hour per day and per carcass (see above); rose diagrams and kernel density were drawn over the plots to support visual inspection of the activity patterns (Agostinelli & Lund 2017) (Figs. 1 and 2). Second, we tested the null hypothesis of uniformity or isotropy, that is, if the records of each species at carcasses were uniformly distributed along the 24-hours period. To do this, we used Rayleigh and Hermans-Rassons tests, which assume that the alternative hypothesis is a unimodal distribution, i.e. shows a single peak (Landler et al. 2018). Both tests perform well under unimodal distributions, but Hermans-Rassons outperforms Rayleigh with bimodal distributions (i.e. two peaks; Landler et al. 2018). Despite being designed for continuous circular data, the Rayleigh test performs well (in terms of error type I and power) with grouped data as those in our dataset, with similar outcomes to those of tests designed specifically for grouped circular data (Humphreys

& Ruxton 2017). If the null hypothesis of uniformity was rejected, we identified when data were concentrated in a single peak by calculating their mean direction. In our study, mean direction was the mean time when a species visited the carcasses. In order to calculate posterior estimates and 95% confidence intervals of the mean times for scavengers attending carcasses, we fitted Bayesian mixed-effects regression models for circular data (Bayesian MERM, i.e. GLMM-type models; Cremers 2020). We also used these models to assess whether species differed in the mean times of attendance at hunted wild ungulate and live-stock carcasses. Carcass was fitted as a random factor in all Bayesian MERMs.

We used Watson’s two-sample test for assessing differences in the usage patterns between carrion types (Pewsey et al. 2013). We considered only temporal data from those species with more than 10 records in total. The two marten species, *Martes foina* and *M. martes*, were considered together as *Martes* spp. due to the difficulty of differentiating them in the black and white photos taken at night.

We performed a second type of analysis to test the existence of competition and facilitation interactions among pairs of vertebrate scavengers attending the carcasses. To test interspecific competition, we examined the temporal overlap of the activity patterns of apex species, such as top predators (i.e. wolf and golden eagle) and obligate scavengers (i.e. griffon vulture) with those of species from lower levels of the food chain (including potential prey: red fox, wild boar, raven and carrion crow). Brown bear was not considered in this analysis because of insufficient sample size. We also examined the possible role of raven and carrion crow as facilitators for griffon vulture to find the carcasses. Concretely, we analyzed the following pairs of species: i) wolf and red fox (present at 12 and 31 carcasses, respectively), ii) wolf and wild boar (14 and 10 carcasses, respectively), iii) golden eagle and raven (6 and 13 carcasses, respectively), iv) golden eagle and carrion crow (6 and 7 carcasses, respectively), v) griffon vulture and raven (25 and 28 carcasses, respectively), and vi) griffon vulture and carrion crow (25 and 17 carcasses, respectively). The degree of overlap of the activity patterns between each pair of species was calculated in two complementary ways: i) comparing the activity patterns of the two species considered, and ii) looking for differences in the activity patterns of the subordinate scavenger species (i.e. generalist for competition or vulture for facilitation) at carcasses with and without presence of the dominant species driving the interaction. The kernel density distribution (KDD) of the dominant species was calculated with records from all the carcasses where present, and compared with the KDD of the subordinate species at carcasses with and without presence of the dominant species. For selecting these records of co-occurrence, we assumed that a potential effect of the dominant species on the presence of the subordinate species would only occur once the dominant species visited the carcass. An alternative more refined analysis further constrained this assumption by



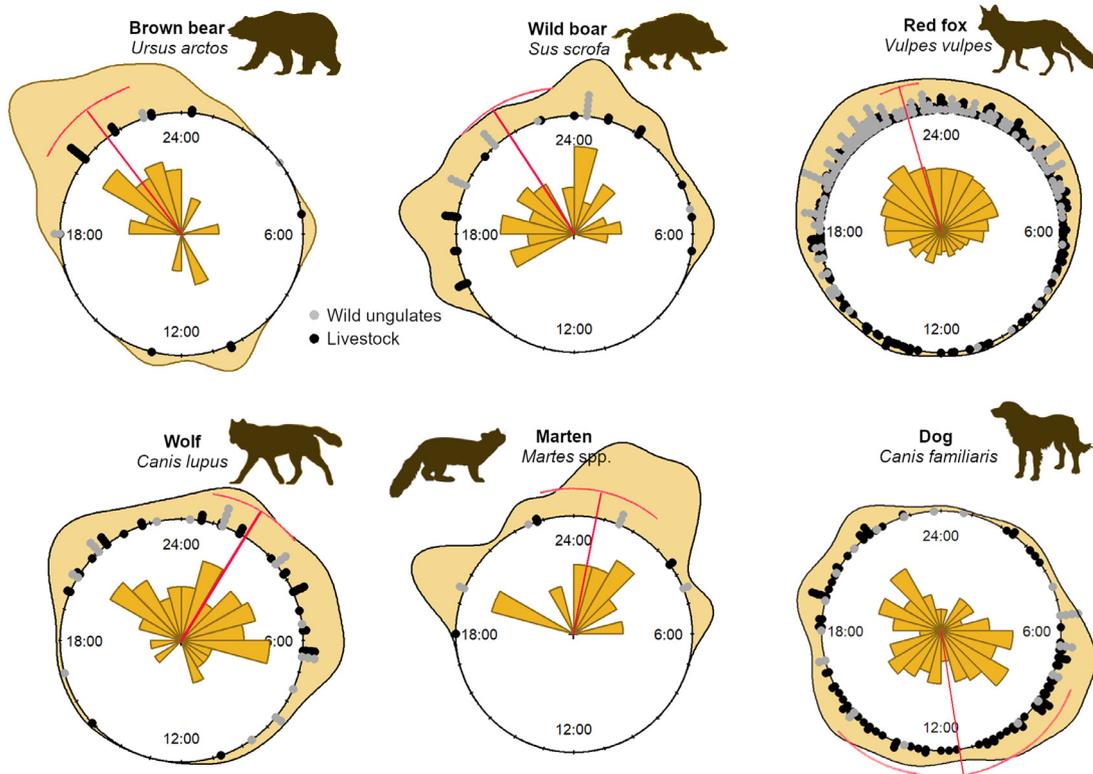
**Fig. 1.** Circular data plots showing hourly distribution of avian scavengers feeding on livestock (black dots) and wild ungulate (grey dots) carcasses; each dot represents a record, i.e. the presence of a scavenger species at an hour, day and carcass ( $N = 742$  records). Rose diagram (central histogram) shows the hourly distribution of records of scavengers at all carcasses (livestock and wild ungulates pooled together); the area of each sector in the rose diagram depicts the relative frequency of records at that hour. The line surrounding the circle represents kernel density estimates of the records for both carcass types together. The mean direction and 95% confidence intervals considering all carcasses together are also shown (red line and arc).

limiting the duration of the influence of the dominant species on the subordinate species at only the same daytime or nighttime period when the dominant species appeared at the carcass. This criterion, however, reduced the sample size in some pairwise comparisons, preventing some analyses using this smaller temporal window (wolf-wild boar, raven-vulture, eagle-corvids). We calculated the degree of temporal overlap, which ranged from 0 (no overlap) to 1 (complete overlap), and the corresponding confidence intervals obtained from 999 bootstrap samples. All analyses were performed with the “circular” (Agostinelli & Lund 2017), “overlap” (Ridout &

Linkie, 2009) and “bpnreg” (Cremers 2020) packages in R (R Core Team 2021).

## Results

We recorded a total of 16 vertebrate scavenging species at the monitored carcasses, 15 species at livestock and 14 at hunted wild ungulates (Appendix: Table 3). Species richness was significantly larger at livestock than at wild ungulate carcasses (i.e. mean: 6 vs. 4 species/carcass, range: 4–9 vs. 2–8; Wilcoxon test:  $W = 72$ ,  $P = 0.01$ ), but, since this value



**Fig. 2.** Circular data plots showing hourly distribution of mammal scavengers feeding on livestock (black dots) and wild ungulate (grey dots) carcasses; each dot represents a record, i.e. the presence of a scavenger species at an hour, day and carcass ( $N = 695$  records). See Fig. 1 for further details.

was marginally correlated with carcass weight (Pearson's correlation  $r_p = 0.32$ ,  $P = 0.07$ ), the difference disappeared when accounting for carcass biomass (i.e. 0.08 vs. 0.12 species/kg, range: 0.01–0.40 vs. 0.02–0.58;  $W = 165$ ,  $P = 0.44$ ).

A total of 1,437 records of vertebrate scavengers were recorded, 951 at livestock and 486 at wild ungulate carcasses (Appendix: Table 3). Similar to species richness, the number of records per carcass was significantly correlated with the weight of the carcass (Pearson's correlation  $r_p = 0.73$ ,  $P < 0.001$ ; mean carcass weight  $\pm$  SE:  $196.3 \pm 57.8$  and  $61.6 \pm 8.3$  kg for livestock and wild ungulates, respectively), thus explaining the significant differences in the mean number of records at livestock and wild ungulate carcasses (mean  $\pm$  SE:  $63 \pm 16$  and  $25 \pm 4$  records, respectively; Wilcoxon test:  $W = 73.5$ ,  $P = 0.02$ ). These differences disappeared therefore when the number of records were corrected for carcass weight (mean  $\pm$  SE:  $0.6 \pm 0.2$  and  $0.6 \pm 0.1$  records/kg, respectively;  $W = 146.0$ ,  $P = 0.92$ ).

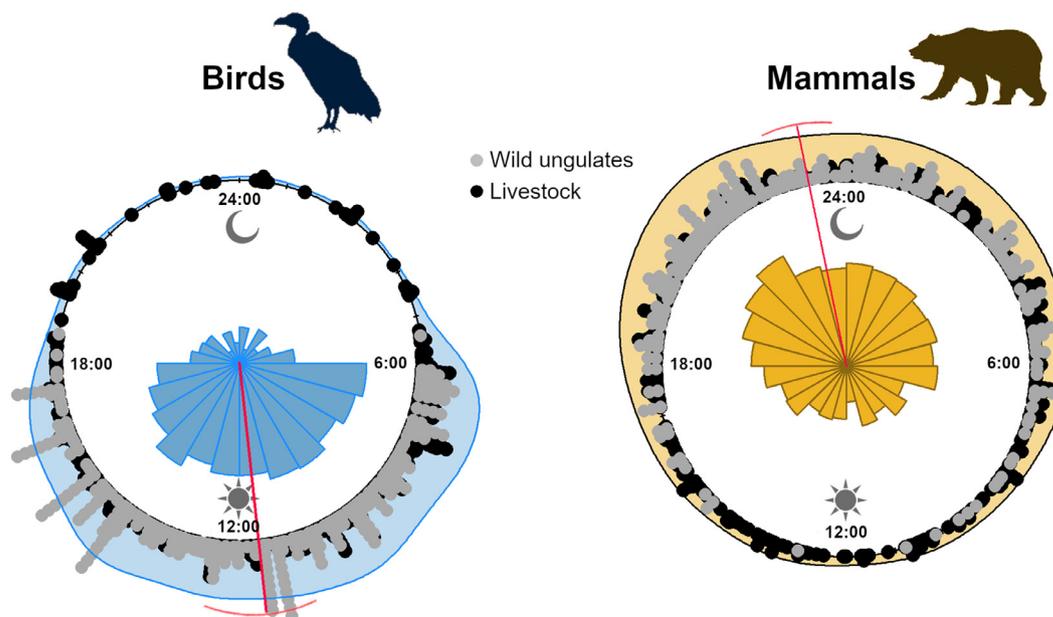
When considering all carcasses together, the 51.6% of the records ( $N = 742$ ) were of birds, while the 48.4% ( $N = 695$ ) corresponded to mammal species. Mammals accounted for a similar number of records ( $N = 478$ , 50.3%) than birds ( $N = 473$ , 49.7%) at livestock carcasses ( $\chi^2 = 0.03$ ,  $df = 1$ ,  $P = 0.87$ ); while birds accounted for more records than mammals at wild ungulates (269 vs. 217, 55.3% vs. 44.7%, respectively;  $\chi^2 = 5.56$ ,  $df = 1$ ,  $P = 0.02$ ).

### Diel activity patterns of scavengers at human-mediated carcasses

Regarding the distribution of their patterns of activity, only raven, griffon vulture and dog showed differences between seasons (spring-summer vs. autumn-winter; raven: Watson's Test = 0.24;  $0.01 < P < 0.05$ ; griffon vulture: Watson's Test = 0.29;  $0.001 < P < 0.01$ ; dog: 0.38,  $0.001 < P < 0.01$ ). However, despite these differences in activity distributions, the mean times of these patterns did not show evidence of differences between seasons: raven (mean spring-summer = 10:55h, CI: 9:52–11:58h; autumn-winter = 11:44 h; CI: 10:32–12:53; GLMM,  $P > 0.05$ ), griffon (mean spring-summer = 13:30h, CI: 11:36–15:18 h; autumn-winter = 10:24 h; CI: 08:16–12:35; GLMM,  $P > 0.05$ ) and dog (mean spring-summer = 10:54h, CI: 08:56–12:48h; autumn-winter = 19:18h; CI: 10:14–06:42 h; GLMM,  $P > 0.05$ ). Therefore, hereafter we show the results of diel activity patterns of scavengers without separating between seasons.

All species showed unimodal distribution in diel activity patterns, as shown by the Rayleigh tests (all  $P < 0.05$ ; Appendix: Table 4), i.e. there was clearly one time of the day most used by the species to attend the carcasses (Figs. 1 and 2).

No species showed statistically clear differences in the mean times of carcass use between livestock and hunted



**Fig. 3.** Circular data plots showing major differences in the presence of mammals, mostly at night, and birds, mostly during daylight, at livestock (black dots) and wild ungulate (grey dots) carcasses; each dot represents a record, i.e. the presence of a scavenger species at an hour, day and carcass. Rose diagram (central histogram) shows the hourly distribution of records of scavengers at both carcass types; with the area of each sector depicting the relative frequency of records at that hour. The line surrounding the circle represents kernel density estimates of the records for both carcass types together. The mean direction and 95% confidence intervals considering all carcasses together are also shown (red line and arc).

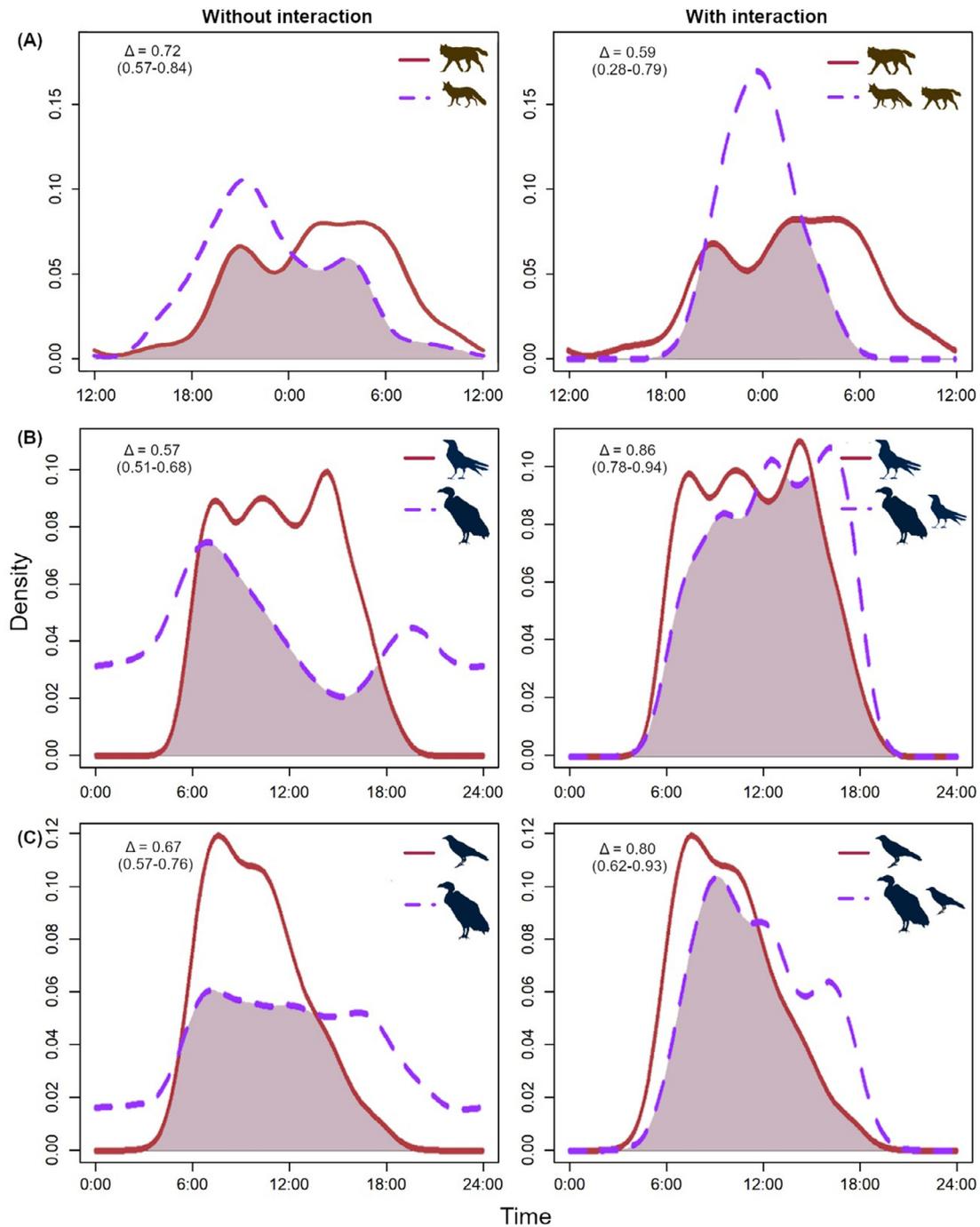
wild ungulates (Figs. 1 and 2; Appendix: Table 5). Regarding the diel patterns of scavengers at carcass, only the griffon vulture, the red fox and the wild boar showed significant differences between livestock and wild ungulate carcasses (Watson's test,  $P < 0.05$  in all three cases; Appendix: Table 5). The differences between carcass types disappeared for the griffon vulture once the two livestock carcasses unusually used at nighttime (Mateo-Tomás & Olea 2018) were removed from the analysis (Watson's Test = 0.125;  $P > 0.10$ ).

As expected, bird and mammal diel activity at carcasses differed significantly (Bayesian MERM:  $P < 0.001$ ; Fig. 3). Birds used carcasses during daylight (mean: 11:38h, CI 95%: 10:42–12:35h), while mammals concentrated at night (mean: 23:09h; CI 95%: 22:27–23:47h). The mean time of carcass attendance differed also among species (Figs. 1 and 2; Appendix: Table 4). Egyptian vulture and carrion crow were on average the earliest to arrive at carcasses during daytime (mean: 09:13h and 9:20h, respectively; Fig. 1) followed by raven (11:14h), magpie (11:24h), buzzard (12:25), golden eagle (12:52h) and griffon vulture (12:53h). Mean time of griffon vulture attending carcasses significantly differed from that of the Egyptian vulture and carrion crow, but not from the rest of species (Bayesian MERM:  $P < 0.001$ ; Appendix: Table 4). Brown bear and wild boar used the carcasses earlier at night on average (21:26h and 21:47h, respectively; Fig. 2), followed by red fox and martens, which appeared around mid-night

(22:59h and 00:41h, respectively). Wolf used carcasses significantly later (02:09h) than the rest of mammal species except martens (Bayesian MERM:  $P < 0.001$ ; Appendix: Table 4).

### Interspecific interactions of scavengers at large ungulate carcasses

The presence of apex predators (i.e. wolf and golden eagle) altered the diel activity patterns of potential prey species at carcasses. The diel activity patterns of wolf and red fox using different carcasses overlapped by 72% ( $\Delta_{\text{wolf-red.fox}} = 0.72$ , CI:0.57–0.84), but this overlap decreased to 59% ( $\Delta_{\text{wolf-red.fox}} = 0.59$ ; CI 95%: 0.28–0.79) at carcasses where the two species co-occurred (Watson's two-test: 0.24,  $P < 0.05$ ). In the presence of wolf, the red fox increased carcass use at midnight, when the wolf reduced its presence (Fig. 4A). As a result, fox activity patterns at carcasses with and without wolf overlapped by 63% (CI 95%: 0.33–0.86), giving rise to a significant change of 37% in the fox activity pattern depending on wolf presence (i.e.,  $\Delta_{\text{red.fox\_WITHwolf-red.fox\_WITHOUTwolf}} = 1 - 0.63 = 0.37$ , CI 95%: 14–67%; Watson's two-test: 0.19,  $P < 0.05$ ) (Appendix: Fig. 3). Wolf and wild boar overlapped at shared carcasses by 49% ( $\Delta_{\text{wolf-wild.boar}} = 0.49$ ; CI 95%: 0.10–0.69) vs. 67% when using different carcasses. The activity patterns showed that the wild boar reduced the use of



**Fig. 4.** Changes in the pair-wise temporal overlap of the diel activity patterns of scavengers at carcasses of livestock and hunted wild ungulates point towards the existence of competitive interactions between apex and potential prey species such as, for example, wolf and red fox (A). Facilitation interactions seem also to occur among the griffon vulture and corvids, i.e. raven (B) and carrion crow (C). Solid lines in the plots show the diel activity patterns of the potentially influencing species driving the interaction (i.e. wolf, raven and carrion crow; solid line); dashed line shows the diel activity patterns of the affected species (i.e., fox, griffon vulture) at carcasses without presence (left plots) and with presence (right plots) of the influencing species. Delta ( $\Delta$ ) represents the coefficient of overlap of the diel activity of the two species compared, and its 95% confidence interval in brackets. See Fig. 2 in Supplementary Information for the remaining pair-wise comparisons.

carcasses between 23:00h and 6:00h, when wolf activity at carcasses peaked (Appendix: Fig. 2). Wolf presence at carcasses could induce changes in the activity patterns of the wild boar in a mean estimated variation of 27%

( $\Delta_{\text{wild.boar\_WITHwolf-wild.boar\_WITHOUTwolf}} = 0.73$ , CI 95%: 0.28–0.89; although these two patterns did not differ significantly: Watson's two-test: 0.05,  $P > 0.05$ ) (Appendix: Fig. 2).

The diel activity pattern of the raven at carcasses was altered by the presence of the golden eagle, peaking in the morning and decreased markedly in the evening at carcasses with presence of the apex predator (Appendix: Fig. 2). While the activity patterns of both species using different carcasses overlapped by 89% ( $\Delta_{\text{eagle-raven}} = 0.89$ ; CI 95%: 0.60–0.98; Watson's two-test: 0.13,  $P > 0.10$ ), this overlap decreased almost by half (to 48%) at carcasses where both species were recorded ( $\Delta_{\text{eagle-raven}} = 0.48$ ; CI 95%: 0.14–0.76); although the activity patterns did not differ significantly (Watson's two-test: 0.13,  $P > 0.10$ ; Appendix: Fig. 2). Eagle presence at carcasses seemed thus to induce change in the activity patterns of the raven in a mean estimated variation of 41% (19–71%) ( $\Delta_{\text{raven\_WITHeagle-raven\_WITHOUTeagle}} = 0.59$ , CI 95%: 0.29–0.81) (Appendix: Fig. 3). A smaller effect was observed for carrion crow, whose diel activity pattern at carcasses with and without golden eagle slightly varied by 26% and did not show significant differences (6–63%;  $\Delta_{\text{carrion crow\_WITH-carrion crow\_WITHOUT}} = 0.74$ , CI 95%: 0.37–0.94; Watson's two-test: 0.09,  $P > 0.10$ ; Appendix: Fig. 2).

Raven but not carrion crow showed significant variation in their activity patterns at carcasses with and without griffon vultures (i.e. 12%, range 3–40%;  $\Delta_{\text{carrion crow\_WITH-carrion crow\_WITHOUT}} = 0.88$ , CI 95%: 0.60–0.97, Watson's two-test: 0.07,  $P > 0.10$ ; 21%, range 8–33%;  $\Delta_{\text{raven\_WITH-raven\_WITHOUT}} = 0.79$ , CI 95%: 0.67–0.92, Watson's two-test: 0.23,  $P < 0.05$ ; respectively; Appendix: Fig. 2). Contrastingly, the presence of both corvid species at carcasses seemed to facilitate the presence of the griffon vulture (Figs. 4B and C). First, vulture increased its presence at carcasses showing two peaks around 12:00h and 18:00h, just after raven peaked, with both species strongly overlapping at shared carcasses ( $\Delta_{\text{raven-vulture}} = 0.86$ ; CI 95%: 0.78–0.94, Watson's two-test: 0.12,  $P > 0.10$ ). Moreover, patterns of vulture activity strongly changed, by 47%, at carcasses with and without raven ( $\Delta_{\text{vulture\_WITHraven-vulture\_WITHOUT raven}} = 0.53$ , CI 95%: 0.47–0.66; Watson's two-test: 1.78,  $P < 0.001$ ; Fig. 4B). Similar changes in the activity pattern of griffon vulture were observed regarding the presence of carrion crow (Fig. 4C). The overlap between the diel activity of both species using different carcasses ( $\Delta_{\text{carrion crow-vulture}} = 0.67$ ; CI 95%: 0.57–0.76) increased at shared carcasses ( $\Delta_{\text{carrion crow-vulture}} = 0.80$ ; CI 95%: 0.62–0.93, Fig. 4C), and differed at carcasses with and without carrion crow ( $\Delta_{\text{vulture\_WITH-carrion crow\_WITHOUT carrion crow}} = 0.73$ , CI 95%: 0.62–0.84; Watson's two-test: 0.31,  $P < 0.01$ ).

## Discussion

Our results show that vertebrate scavengers temporally segregate by using large ungulate carcasses at different times during the day. As expected, birds showed mostly diurnal diel activity patterns (mean time 11:38h), while mammals preferred to use carcasses during the night (mean time

23:09h) (Fig. 3). Temporal segregation occurred also at the species level, since vertebrate scavengers showed different diel activity patterns, characterized by single peaks of activity mostly asynchronous among species (Fig. 1 and 2). This suggests that temporal resource partitioning among scavengers mediates species coexistence, and thereby contributes to shape the structure of scavenging communities at carcasses, where high levels of competition are expected.

Interference competition and facilitation are among the main mechanisms that would drive the coexistence of vertebrates at large ungulate carcasses through temporal segregation and coupling in activity patterns, respectively. Indeed, our results show that apex species such as wolf and golden eagle seemed to alter the diel activity patterns of scavengers at lower trophic levels. For example, red fox modified its temporal activity pattern about 37% to reduce temporal overlap with wolf at shared carcasses (Fig. 4A). Similarly, raven advanced the time of using carcasses with presence of golden eagle, thereby reducing temporal overlap with the predator as much as 41% (Appendix: Fig. 2); these activity patterns are in line with those previously observed for these two species (Blázquez et al. 2009). Overall, these interference competition-induced patterns suggest that the subordinate species exhibit a certain plasticity in their temporal activity patterns to access carrion. This adjustment can mechanistically reduce competition among species and thus enhance species coexistence and biodiversity at carcasses. As a result, circadian temporal niche partition could contribute to the ecosystem functioning through facilitating richer scavenger assemblages that would accelerate carcass removal and the recycling of matter and energy from dead animal matter (Sebastián-González et al 2016; Mateo-Tomás et al 2017; Beasley et al 2019).

Not only species richness but also the presence of functionally dominant species, such as vultures, support the scavenging function in ecosystems (Mateo-Tomás et al 2017; Gutiérrez-Cánovas et al 2020). Thus, facilitation interactions affecting the diel activity patterns of vertebrate scavengers such as those found here between corvids (as information producers) and vultures (as scroungers of such information) (see also Fig. 4, Appendix: Fig. 3) can be also relevant to maintain key ecosystem functions related to carcass consumption. As already described for other birds (e.g. eagles; Kane et al. 2014), earlier detection of carcasses by corvids would increase carcass detectability by vultures, which in turn, could facilitate corvids to access carrion. Although we did not experimentally analyze trophic facilitation between vultures and corvids, our results strongly suggest a facilitation processes from corvids to griffon vultures via carcass detection, as evidenced by the diel activity patterns of vultures closely following those of the raven and carrion crow (Fig. 4, Appendix: Fig. 3). Considering the high ability of corvids to find carcasses (e.g. ravens utilize hunter gunshots to locate hunting remains; White 2005), they can further contribute to rapid carrion disposal through vulture consumption.

Despite previous evidence on corvids taking advantage of hunters to locate hunting remains [White \(2005\)](#), neither raven nor carrion crow showed significant differences in their mean times attending livestock and hunted wild ungulate carcasses. In fact, only 3 (19%) out of the 16 vertebrate species recorded at these carcasses showed significant differences in their temporal activity patterns between the two carcass types. The griffon vulture was one of the species that showed significant differences in its diel activity patterns between hunted wild ungulate and livestock carcasses, but these differences were due to an unusual nighttime activity recorded at two livestock carcasses ([Mateo-Tomás & Olea 2018](#)). Contrastingly, fox and wild boar showed more nocturnal patterns at carcasses of hunted wild ungulates than at livestock carcasses ([Fig. 2](#)). Because both species, and especially the wild boar, are hunted in the study area ([BOPA 2012](#)), they could be warier of being shot ([Wilmers et al. 2003](#)), generating a landscape of fear around hunted carcasses. Indeed, while livestock carcasses were generated through natural processes (predation, illness or accident), the wild ungulate carcasses we monitored came from hunting ([Mateo-Tomás et al. 2015](#)), and thereby this human disturbance could alter the diel patterns of these species as it has been seen in other mammal species around the world ([Gaynor et al. 2018](#) and references therein). Shifting to more nocturnal activity due to human disturbance agrees with previous findings on how those mammals more impacted by human activities increase nocturnality ([Gaynor et al. 2018](#)). Similarly, higher human disturbance through hunting at the wild ungulate carcasses monitored could also explain that mammals accounted for more records than birds at livestock carcasses but not at wild ungulate remains. This result along with the long history of livestock presence in most European ecosystems ([Tresset & Vigne 2011](#)), suggests that the livestock carcasses here monitored (after predator attack, illness or accident) would mimic the natural generation of ungulate carcasses better than that of hunted wild ungulates, whose generation by hunting seems to reflect direct human disturbance (i.e. shooting noise, human scent, hunting dogs, etc.). Nonetheless, this did not lead to major differences in the vertebrate scavenger community. We did not find differences between both types of carcasses neither in species richness nor in the time scavengers spent at each carcass (i.e. number of records) after controlling for carcass size (a factor known to affect vertebrate scavenger assemblages; [Moleón et al. 2015](#); [Turner et al. 2017](#); [Pardo-Barquín et al. 2019](#)). Although our results contrast with other work reporting higher species richness and abundance at livestock than at wild ungulate carcasses ([Arrondo et al. 2019](#)), these differences could be due to methodological biases in that work (e.g. high temporal aggregation of the monitored carcasses, different monitoring techniques between carcass types). Contrastingly, the carcasses analyzed in our study were evenly monitored all year round during the same

years (i.e. 2011–2013; see Methods section) at the time and place where generated. Consequently, they are expected to offer a more accurate picture of the availability of human-mediated carcasses and thus of the associated scavenger assemblages.

Our findings highlight temporal niche partitioning as a mechanism promoting the coexistence of vertebrate scavengers from different trophic levels at carcasses. We show that interference competition and facilitation seem to drive species coexistence in vertebrate scavenger assemblages. Previous evidence of top-down effects of key species on carrion consumption ([Cunningham et al. 2018](#) and references therein) suggests that the changes we observed in the activity patterns of scavengers through interference competition (e.g. wolf-fox, golden eagle-raven) and facilitation (corvids-vulture) could affect carrion consumption. In this line, the role of other interspecific interactions, such as exploitative competition (i.e. reducing resource availability to other species through consumption; [Tokesi 1999](#)), should be further analyzed. Gregarious scavengers such as the griffon vulture are functionally dominant species with a great ability to consume most of the carrion available in an ecosystem ([Mateo-Tomás et al. 2017](#)), a role that could also play large apex predators such as the brown bear or the wolf. Accordingly, these apex species can reduce the availability of the resource to other less-competitive species through exploitative competition. Future studies might deal with the relative contribution of interference *versus* exploitative competition in shaping scavenger communities.

Identifying the factors and mechanisms involved in shaping vertebrate scavenger communities helps to understand the ecosystem functions and services delivered by these assemblages ([Pardo-Barquín et al. 2019](#)). We show here how, once filtered by habitat characteristics ([Turner et al. 2017](#); [Pardo-Barquín et al. 2019](#)), vertebrate scavengers assemble through processes of temporal segregation (competition) and coupling (facilitation) that promote scavenger coexistence and biodiversity at carcasses.

## Author contributions

P.P.O conceived the ideas and designed the study of the manuscript; PMT and PPO performed the field work, P.P.O. analyzed the data and NI and PMT assisted in the analyses. PPO lead the writing, and PMT contributed to it. All authors contributed to revisions of the manuscript.

## Declaration of Competing Interest

The authors declare no competing financial interests.

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## Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2022.01.008.

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