Interactive effects of obligate scavengers and scavenger community richness on lagomorph carcass consumption patterns

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Carrion consumption patterns in vertebrate scavenger communities may be influenced by several interacting factors. We assessed the effects of the number of scavenger species and the presence of obligate scavengers (vultures) on carcass detection and consumption times, and the structure (nestedness) of the scavenger assemblage by exploring consumption patterns of lagomorph carcasses provided experimentally. Carcass detection and consumption times were strongly inversely related to vulture presence, whereas scavenger richness had a low contribution, except when interacting with vulture presence. However, none of the scavenger communities presented a nested pattern, perhaps because of the small size of lagomorphs, which prevents large numbers of scavengers and interspecific interactions occurring at one carcass. Our results suggest that scavenger species richness, especially the presence of vultures, increases scavenging efficiency.

Keywords: carrion, community structure, consumption time, detection time, *Lepus* spp., nestedness, *Oryctolagus cuniculus*, small carcass, vulture.

The importance of scavenging by vertebrates in structuring and stabilizing food webs has been highlighted (DeVault *et al.* 2003, Wilson & Wolkovich 2011). However, there remain uncertainties about the main factors structuring vertebrate scavenger communities. Scavenging patterns depend on many interacting factors related to the carcass, the consumer or extrinsic variables (DeVault *et al.* 2003, Selva *et al.* 2005, Wilson & Wolkovich 2011). With respect to consumers, the presence of specialist scavengers and the number of scavenger species might be particularly important. Avian scavengers are considered more specialized in carcass exploitation than mammals, at least for large carcasses, due to their less energy-demanding searching strategies (Houston 1979). Indeed, the world's only obligate terrestrial vertebrate scavengers are vultures (although this group includes the unrelated New World and Old World vultures), which display many adaptations for efficient carrion consumption (Ruxton & Houston 2004). These adaptations make vultures strong competitors in the terrestrial scavenger guild (Houston 1979), and the presence of obligate scavengers can increase interspecific trophic competition, and in turn influence carrion consumption patterns (Cortés-Avizanda *et al.* 2012, Ogada *et al.* 2012). In addition, the number of scavenger species in the community can also influence carrion consumption. Species-rich communities seem to be more efficient in exploiting a given resource (Hooper *et al.* 2005, Griffin *et al.* 2008). In a recent study in an area without vultures, Olson *et al.* (2012) showed experimentally that reduction of facultative scavenger abundance resulted in reduced carcass consumption rates.

Selva and Fortuna (2007) found that the community of (facultative) scavengers feeding on ungulate carcasses in an undisturbed environment was highly structured and presented a nested pattern, which is far from the traditional view of scavenging being a random process (DeVault *et al.* 2003). In nested communities, those species feeding on carcasses visited by few species were subsets of the scavenger assemblage occurring at those carcasses visited by many species. Nested patterns in resource use can relate to competition processes in ecological assemblages; this kind of structure is common as conditions become more competitive (Cook *et al.* 2004). Thus, factors enhancing interspecific competition such as large numbers of consumers (e.g. scavengers) or the presence of specialized consumers (e.g. vultures) might be associated with high levels of nestedness in the resource (e.g. carrion) use pattern. However, no advance in this regard has been made in areas with obligate

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scavengers using carcasses of small animals such as lagomorphs, which are abundant and thus may constitute an important available resource for the scavenger community.

We conducted an experimental carcass monitoring protocol in four areas with different scavenger communities to assess the relative contribution of the presence or absence of obligate scavengers and the overall number of avian and mammalian scavenger species on lagomorph carcass consumption patterns. We predicted that (1) carcass detection and consumption times will be shorter and (2) the structure of the scavenger assemblage exploiting carcasses will be more nested in communities with vultures and that are scavenger species-rich.

METHODS

Study areas and sampling procedures

We studied the vertebrate scavenger community consuming lagomorph (European Rabbit *Oryctolagus cuniculus* and hare *Lepus* spp.) carcasses in four areas: two in Spain (Doñana in southern Spain and the Ebro Valley in northeast Spain), one in the Argentinean Patagonia and one in the state of Victoria, southern Australia. Obligate scavengers (New or Old World vultures) were present in the Ebro Valley and Argentina, but absent in Australia and Doñana (see Supporting Information Appendix S1 and Table S1 for further details).

We monitored feeding activity of scavengers on 85 experimentally provided carcasses of freshly dead rabbits and hares during the most productive seasons of the year (Table S1). Carcasses were monitored using automatic cameras triggered by movement in Doñana and Australia, and were visually inspected and tape-recorded with telescopes in Argentina and the Ebro Valley. Automatic cameras were programmed to take one picture every 2 min throughout each 24-h period, provided that there was some movement (Blázquez *et al.* 2009). Visual observations in the Ebro Valley and Argentina were made during daytime from a vehicle using binoculars (10 × 40) and telescopes (20–60×) at a minimum distance of 300 m to avoid interfering with the scavengers' behaviour (Travaini *et al.* 1998). Additional details on study design and data sampling are given in Supporting Information Appendix S2.

Data analyses

We first constructed species richness curves in the program BIODIVERSITYPRO (James & McCulloch 1990) to assess whether our sample size was sufficient to detect all the scavenger species in a region. We then measured detection time as the time between the placement of the carcass and its first detection by a scavenger, and

consumption time as the time elapsed between carcass placement and its total consumption by the scavengers. To facilitate comparisons among study areas, we grouped consumers into obligate scavengers (vultures), facultative avian scavengers (avian species that can eat carrion but also include other items in their diet) and mammalian scavengers (which are all facultative scavengers).

We used generalized linear models (GLMs; log link and Poisson error distribution) in R 2.14.1 (the R Development Core Team) to compare the detection and consumption times among study areas, and to relate the consumption patterns (detection and consumption times) in each area with the number of species in the scavenger community and with the presence or absence of obligate scavengers. Rabbits and hares are native in Spain, rabbits were introduced into Australia in 1859, and hares have been present in Argentina since the late 19th century. We included carcass origin (native vs. introduced) as a fixed effect to control for this. Study area was not included as a variable because the combination of the variables relating to vulture presence and carcass origin already includes all the information about the four different sites in the analyses. We also calculated the percentage of pure deviances explained by each of the variables following Cushman and MacGarigal (2002).

We also assessed whether the pattern of carcass consumption by the scavenger community of each area was nested using the *NODF* metrics (Almeida-Neto *et al.* 2008). As nestedness may arise from a random community, we compared the *NODF* values with a null distribution of the *NODF* values. We then compared the degree of nestedness between sites using a standardized effect size (SES) of the *NODF* value (Gotelli & McCabe 2002, Ulrich & Gotelli 2007). See Supporting Information Appendix S3 for more details on data analyses.

RESULTS

Species richness curves reached an asymptote in all study areas, suggesting that sample sizes were large enough to include most of the species present in the scavenger community (Supporting Information Fig. S1). Carcass consumption patterns varied among study areas (Table 1). Obligate scavengers fed on 50 and 64% of the carcasses in the Ebro Valley and Argentina, respectively. Facultative avian scavengers were the most frequently detected group in most study areas but the presence of mammalian scavengers was highly variable (Table 2). The order of arrival at the carcasses also varied between areas, with birds usually being the first visitors (Supporting Information Table S2).

Carcasses were detected and consumed faster in regions where obligate scavengers were present (GLMs; explained deviance: 42.0% for detection time, 43.6% for consumption time; all $P < 0.001$). Detection and

Table 1. Summary of the principal characteristics of the studied scavenger communities. *NODF* metrics indicates the nestedness degree of the consumption pattern; *Z*-score standardizes *NODF* with the median nestedness of simulated matrices (see Appendix S3 for details).

	Doñana	Ebro	Argentina	Australia
Obligate scavenger	No	Yes	Yes	No
Scavenger species richness ^a (max. per carcass)	8 (3)	11 (5)	7 (4)	4 (3)
Sample size ^b	27	20	14	13
Detection time ^c (mean $\pm$ sd)	26.6 $\pm$ 24.4	3.25 $\pm$ 2.1	9.3 $\pm$ 23.9	22.4 $\pm$ 17.3
Consumption time ^c (mean $\pm$ sd)	67.4 $\pm$ 39.4	7.9 $\pm$ 2.5	15.6 $\pm$ 13.3	46.2 $\pm$ 19.5
<i>NODF</i> (<i>P</i> -value)	−0.10 (0.68)	0.63 (0.27)	1.27 (0.10)	−1.01 (0.85)
<i>Z</i> -score	15.45 (0.68)	42.43 (0.27)	59.64 (0.10)	31.87 (0.85)

^aNumber of scavenger (obligate or facultative) species using carcasses. ^bNumber of carcasses. ^cIn hours.

Table 2. Percentage of carcasses that were visited by a species belonging to each of the three scavenger groups (obligate avian, facultative avian and mammal scavengers) at each study site. The number in parentheses represents the number of species within each group and at each study site. Note that the sum of the percentages differs from zero because one carcass can be consumed by species of more than one group.

	Doñana	Ebro	Argentina	Australia
Obligate avian	0	55 (3)	64 (2)	0
Facultative avian	48 (5)	70 (7)	100 (4)	80 (3)
Mammal	59 (3)	20 (1)	7 (1)	17 (1)

consumption times were also significantly shorter when there were more scavenger species in the community and at sites where lagomorphs are native (Table 3). However, variance partitioning analysis reflected that the most important factor was the presence of obligate scavengers, while carcass origin barely influenced consumption patterns. The number of scavenger species also had a low contribution, but this was higher when obligate scavengers were present than when they were absent (Fig. 1).

None of the scavenger communities was significantly nested. Although the guilds containing obligate scaveng-

ers had positive *Z*-scores rather than the negative values of communities lacking vultures, *Z*-scores were very close to zero in all cases (Table 1).

DISCUSSION

The results confirmed our first prediction: the number of scavenger species in the community, especially obligate scavengers, was inversely associated with carcass detection and consumption times, whereas carcass origin had little influence on scavenging patterns. Scavenger communities containing vultures led to more rapid exploitation of carrion (i.e. shorter carcass detection and consumption times) than those with only facultative scavengers. This indicates that interspecific competition for carrion is greater in the presence of specialized or dominant carrion consumers (Cortés-Avizanda *et al.* 2012, Ogada *et al.* 2012, Olson *et al.* 2012).

Species richness has often been related to ecosystem function and services (Hooper *et al.* 2005, Hector & Bagchi 2007). This relationship may be the result of three different processes (Hooper *et al.* 2005). A larger number of species may increase the likelihood of the presence of key species, it may increase the number of species with similar foraging strategies or it may increase the complementary use of resources. In our study, we

Table 3. Generalized linear models relating the time needed to detect and consume the carcass to the number of scavenger species at the carcass, carcass origin (native vs. introduced) and the presence of obligate scavengers in the community. We show the coefficient of the model, the standard deviation of the coefficient (SE), the degrees of freedom (df) and the sign of the variable. The reference category for the carcass origin corresponds to an introduced origin of the carrion.

	Detection time (<i>n</i> = 85)				Consumption time (<i>n</i> = 78)			
	Coefficient	SE	df	<i>P</i> -value	Coefficient	SE	df	<i>P</i> -value
Species richness	−0.450	0.003	85	< 0.001	−0.422	0.002	76	< 0.001
Prey origin	−0.644	0.007	86	< 0.001	−0.411	0.006	77	< 0.001
Obligate scavenger	−1.757	0.010	86	< 0.001	−1.717	0.007	77	< 0.001

Figure 1. Results of variance partitioning using partial regression analysis. The values shown in the diagram are the percentages of variation in the proportion of (a) detection time and (b) consumption time explained by the indicated variables (number of scavenger species detected in the community, prey origin and presence of obligate scavengers) by their interactions.

found that the positive effect of species richness on carrion consumption efficiency was associated mainly with the presence of vultures, perhaps supporting the first of these mechanisms. However, further research is needed to clarify the separate contribution of different underlying mechanisms linking scavenger species richness and carcass consumption patterns.

Our second prediction regarding community nestedness could not be validated, as neither species' richness nor obligate scavenger presence was significantly related to scavenger community structure (nestedness). Nestedness has been shown to be high under stressful environmental conditions such as highly competitive environments (Cook *et al.* 2004). Vultures strongly increase not only inter- but also intraspecific competition for carrion (Cortés-Avizanda *et al.* 2012, this study). Therefore, scavenger communities with vultures can be considered relatively competitive, and consequently

could tend towards being organized in a nested pattern. Our failure to identify a nested structure in our scavenger assemblages may be attributable to the small size of lagomorph carcasses. Whereas small carcasses are often consumed by a few individuals, more individuals and scavengers are usually needed to consume large carcasses (e.g. ungulates) completely. Consequently, large carcasses may be partitioned between several species, promoting facilitative and competitive processes (Selva & Fortuna 2007, Cortés-Avizanda *et al.* 2012). Thus, we propose that nestedness in scavenging assemblages could be carcass size-dependent, so that carrion consumption might be organized in a more structured pattern as carcass size increases (Selva & Fortuna 2007). Further studies in more competitive environments (e.g. using data from winter), with bigger carcasses and larger sample sizes could help confirm our hypothesis (see Supporting Information Appendix S4 for discussion on other factors potentially affecting the scavenging patterns found in this study).

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SUPPORTING INFORMATION

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

Appendix S1. Description of the study areas and species detected in this study.

Appendix S2. Further details on study design and data sampling.

Appendix S3. Further details on statistical procedures.

Appendix S4. Supplementary discussion.

Figure S1. Accumulation curves showing how the inclusion of more samples (carcasses) affected the detection of new scavenger species in the four study areas.

Table S1. Summary of the main characteristics of the four study areas and the species detected at each study site.

Table S2. Order of arrival of scavengers at lagomorph carcasses.