Behavioral Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2016), 27(4), 1041–1052. doi:10.1093/beheco/arw010

Original Article

Behavioral coexistence and feeding efficiency drive niche partitioning in European avian scavengers

Rubén Moreno-Opo,[a] Ana Trujillano,[b] and Antoni Margalida[c,d]

[a]Evolution and Conservation Biology Research Group, University Complutense of Madrid, E-28049 Madrid, Spain, [b]Bearded Vulture Study and Protection Group, Apdo. 45, E-25520 El Pont de Suert, Spain, [c]Department of Animal Science (Division of Wildlife), Faculty of Life Sciences and Engineering, University of Lleida, E-25198 Lleida, Spain, and [d]Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, CH-3012 Bern, Switzerland

Received 5 August 2015; revised 16 December 2015; accepted 7 January 2016; Advance Access publication 8 February 2016.

The mechanisms that determine the evolutionary adaptations of scavengers to carrion exploitation have been well established. In contrast, little is known about coexistence during carrion exploitation based on behavioral traits and considering obligate and facultative species together. This study revisits the hypotheses of behavioral organization within the guild of necrophagous birds in light of the adaptive processes of specialization to carrion exploitation. We used a detailed dataset of observations from high-quality video recordings in the 2 regions with the most diverse and abundant populations of European avian scavengers. Active feeding time varied between species, with the obligate scavengers spending more time eating. The way that scavengers ate the food (i.e., on the ground or carrying away) diverged among species, with species with longer and more pointed beaks and a greater prehensile ability (of talons to grip things) carrying the remains away more often. We recognized the diversity and complementarity of strategies aimed at exploiting the same resource by different species and age classes. Scavenger species were clustered according to the relationship between the time active at the feeding site and the number of feeding pecks, leading to a decrease in competition for resource exploitation, as well as an occupation of specialized trophic niches. The study of active-consumption rates showed that eagles and vultures obtained most and a half, respectively, of their daily energetic requirements from each feeding event, reinforcing the important role of this relevant food source from ecological, evolutionary, behavioral, and conservation standpoints.

Key words: **behavioral ecology, carcasses, facultative scavengers, obligate scavengers, supplementary feeding sites, vultures.**

INTRODUCTION

Resource exploitation triggers complex networks of relationships at both intraspecific and interspecific levels and is key in the development of many ecological processes (Bascompte 2010). In the case of food webs, the adaptive processes necessary to obtain and exploit the same trophic resource fit the traits and life histories of individuals and communities, due in part to the influence of coevolutionary behavioral mechanisms such as competition, predation, and mutualism (Stouffer et al. 2012; Thompson et al. 2012).

Carrion provides an interesting model for studying food webs: It is a pulsed food source of unpredictable occurrence in space and time, offers a high nutritive biomass but is not globally widespread across all habitats and territories, and can be considered free because it does not require a large physical investment as would occur during predation (Ostfeld and Keesing 2000; DeVault et al. 2003; Selva and Fortuna 2007; Barton et al. 2013; Moleón, Sánchez-Zapata, Margalida, et al. 2014). As a result of these features, organisms feeding on this resource have developed morphological and behavioral adaptations to optimize its exploitation (Hertel 1994; DeVault et al. 2003; Moreno-Opo et al. 2015a), establishing guilds of species as is the case of carrion-eating birds (Simberloff and Dayan 1991; Selva and Fortuna 2007). In addition, in these species, social information transfer can lead to important nontrophic interactions among species and highlights important potential links among social evolution, community ecology, and conservation biology (Kane et al. 2014).

Interspecific mechanisms determining evolutionary adaptations to carrion exploitation—mainly competition and facilitation—have been explored in various studies (Wallace and Temple 1987; Kirk

Address correspondence to R. Moreno-Opo. E-mail: rmorenoopo@gmail.com.

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source: https://doi.org/10.7892/boris.93836 | downloaded: 12.10.2024

and Houston 1995; Jackson et al. 2008; Cortés-Avizanda et al. 2014; Kane et al. 2014; Kendall 2014). Thus, vulture species have been ecomorphologically characterized according to resource partitioning and prey selection (König 1983; Hertel 1994). However, and with the exception of dominance and hierarchy aspects (Wallace and Temple 1987; Cortés-Avizanda et al. 2012; Kendall 2013), detailed knowledge of the intraguild relationships in carrion exploitation is weak with regard to behavior and performed activity, especially considering obligate and facultative avian scavengers jointly (but see Kane et al. 2014). Thus, it is particularly interesting to evaluate the mechanisms of coexistence within the avian scavenger guild, given its evolutionary implications and the interactions that arise within food webs. A key challenge is to identify the diversity and complementarity of strategies aimed at exploiting the same resource by different species and age classes, which is relevant from ecological, evolutionary, behavioral, and conservation standpoints.

This study revisits the hypotheses of behavioral organization within the avian scavenger guild on the basis of adaptive processes for carrion exploitation (Kruuk 1967; Houston 1975, 1988; Wallace and Temple 1987; Hertel 1994). With the aim to identify patterns of specialization in carrion exploitation, we studied the activity performed by different species in the European guild of avian scavengers considering different age classes and/or breeding status, and including both obligate (i.e., vultures) and facultative (i.e., corvids, eagles) species. We tested various hypotheses (Table 1) about how different species are predicted to adopt different feeding strategies including variation in time spent at the carcass, mode of feeding, selection of specific parts of the carcass, and energetic efficiency of ingestion according to active-consumption rates (defined as the mass of food consumed per time unit actively feeding, active-consumption rates [ACR], Wilmers and Stahler 2002; Wilmers et al. 2003).

METHODS

Study area

The study was carried out in Spain, home to >90% of obligate European avian scavengers (Margalida et al. 2010). We selected 4 supplementary feeding sites (hereafter SFS), 2 in the Pyrenean Mountain range (northeastern Spain [N-E], Buseu 42°18′26″N, 1°7′13″E and Soriguera 42°24′12″N, 1°10′14″E; 12.8 km of distance between them) and 2 in the Mediterranean sector of the Iberian Peninsula (central-western Spain [C-W], Fuencaliente 38°32′9″N, 4°26′17″W and Cabañeros 39°19′41″N, 4°25′26″W; 91.5 km of distance between them). The 2 sampled Spanish regions were chosen to include representative populations of 10 of the most common carrion-eating species comprising the European avian scavenger guild with the exception of the white-tailed sea-eagle *Haliaaetus albicilla* and the imperial eagle *Aquila heliaca*, which are not present in Spain (Moreno-Opo et al. 2015a, Table 2).

Study design and variables considered

From May 2009 to April 2011, we provided carrion on a monthly basis at each SFS totaling 100 inputs. Carrion was supplied during the day (randomly from 7:00 to 19:15 h GMT+1) alternating different input traits (prey species, biomass, scattering) homogeneously among the different points. We sequentially provided carcasses/remains from ovine–caprine (total inputs = 34), porcine–bovine (n = 30), and wild ungulates (n = 36) as prey species, a range of

Table 1

Hypotheses made in this study on the feeding activity within the European guild of avian scavengers, expected results, and a summary of the main results obtained

Hypotheses	Expected results	Observed results
In terms of cost–benefit balance, the length of stay and active feeding versus ingested biomass and percentage of individuals that feed will vary depending on the adaptability of birds to scavenging.	Obligate scavengers and adult age groups are more effective in carrion exploitation due to a better adaptability to exploit the resource.	• Obligate scavengers stayed longer at carcasses and fed longer, but facultative scavengers spent proportionally more time actively feeding with respect to total time at the carcass. • Adults and nonadults showed no differences either in time spent at carcasses or in percentage of birds that ate.
The morphological traits and scavenging nature will determine selection for different carrion parts, the way of feeding (on the ground/carrying food, quickly or slowly) and the feeding rate (pieces ingested per unit of time).	Grouping species according to their feeding behavior is possible according to the ecological niches within the avian scavenger guild.	• Morphology determines carrying ability of carrion: species with more pointed beaks and a greater prehensile ability took more pieces away. • Facultative scavengers preferred more abundant and soft parts of the carcasses as opposed to specialized vultures. • Feeding rate (gram per minute) was higher in facultative species with respect to vultures.
The proportion of satisfied energetic requirements from each feeding event will vary depending on the obligate or facultative nature of the scavengers.	Obligate scavengers will satisfy a greater percentage from each event, in relation to facultative species that can obtain food from other sources.	• Obligate scavengers fulfilled approximately half of daily biomass required (20.0–50.4%) per feeding event. • Facultative scavengers completed their daily energetic requirements from each feeding event, except for nonadult individuals of eagle species.
Feeding efficiency and biomass exploited will be greater during periods with higher energy needs.	For all species and age classes, this should be higher during winter. Efficiency will be greater during prelaying and chick rearing.	• A longer stay around the carcass was generally observed outside the breeding season for all the species, although the proportion of birds that ate was higher during the breeding season.

Table 2

European avian scavengers studied

Species	Type of scavenger	Range in Spain	Breeding population in Spain (pairs)	% with respect to European population	Body mass (g)	Prehensile ability of the claw	Beak strength	Hardness of selected parts	Beak capacity (in mm^3) for this study's analyses
BV	Obligate	N-E	121[a]	67.0	5750	0	2	2.85	396 396
CV	Obligate	C-W	2068	96.3	7800	0	0	1.50	396 396
EV	Obligate	All	1452	36.3	2200	0	3	0.50	141 680
GV	Obligate	All	24 609	91.2	7650	0	0	0.60	396 396
SIE	Facultative	C-W	409	97.6	3900	3	1	1.60	141 680
GE	Facultative	All	1553	15.3	4300	3	1	1.20	141 680
RK	Facultative	All	2176	9.2	1050	2	1	1.00	—
BK	Facultative	All	10 300	16.1	875	2	1	0.50	—
RA	Facultative	All	84 000	18.7	1200	1	2	0.75	—
CC	Facultative	N-E	700 000	8.3	520	1	2	0.55	—

For each species, the degree of specialization in carrion exploitation (obligate/facultative) (González 1991; Donázar 1993; Heinrich 1994; Del Hoyo et al. 1994; Cramp 1998; Del Hoyo et al. 2009), the range in Spain (N-E; C-W; all, present in all of the Iberian Peninsula), the breeding population in Spain[b,c] and its proportion to the European population (BirdLife International 2004; Deinet et al. 2013), and the average body mass (González 1991; Donázar 1993; Heinrich 1994; Del Hoyo et al. 1994; Cramp 1998; Del Hoyo et al. 2009) are shown. Categorical variables of different morphological traits are as follows: prehensile ability of the claw (González 1991; Donázar 1993; Heinrich 1994; Del Hoyo et al. 1994; Cramp 1998; Del Hoyo et al. 2009) (0 = no prehensile capacity to 3 = high prehensile capacity), beak strength (Kendall 2013) (0 = very high; 1 = high; 2 = medium; 3 = low), and hardness of parts of the carrion selected (data derived from this study, assigning a mean value from all feeding of each of the different parts of carrion considered—bones = 3, greater hardness; skin/tendons = 2; mixed remains = 1; meat/viscera = 0, lesser hardness). Beak capacity (mm^3) was calculated through average biometrics (in mm) of the beak length, width, and height for 2 groups of species: large vultures—BV, CV, GV—and eagles—EV, SIE, GE[d] (García 2013).

[a]Breeding units.

[b]Official Spanish Working Groups for endangered species.

[c]See http://www.seo.org/2012/07/02/monografias-seuimiento-de-aves/.

[d]Other own unpublished data from field measurements for CV, GV, BV, and SIE.

40–470 kg per feeding event (mean 92.9 kg ± 78.9 standard deviation [SD]) and either concentrated (<2 m radius, n = 48) or scattered (≥2 m radius, n = 52) (Moreno-Opo et al. 2015a). Birds present at the sampled points were monitored from the time of the provision of food until 3 days later through a high-resolution video camera (Arecont Vision Megavideo® AV5100) connected to a computer, hard disk drive, and rechargeable lithium batteries. The camera was located within 20 m from the point of supply, allowing the observation of a wide area around the carrion with the 120° display angle of the camera (see Moreno-Opo et al. 2015b for further details). The recordings of each feeding event were visualized thereafter through the AV program v.5.1.4.239 Application Manager (Arecont Vision, Glendale, CA) by registering the activity of individuals of the 10 targeted scavenger species (Table 2). Video analysis was performed by the same person to avoid biases from differences in the data interpretation between different observers. We randomly selected 1 individual per species and age class (adults—birds showing typical adult plumage—and nonadults—birds exhibiting juvenile, immature, or subadult phases of plumage) attending to the SFS for each feeding event regardless of the hour and the time after the carrion provision. Thus, we monitored the behavior of 564 individuals (103 bearded vultures *Gypaetus barbatus* [BV], 93 cinereous vultures *Aegypius monachus* [CV], 9 Egyptian vultures *Neophron percnopterus* [EV], 200 griffon vultures *Gyps fulvus* [GV], 16 Spanish imperial eagles *Aquila adalberti* [SIE], 18 golden eagles *Aquila chrysaetos* [GE], 8 red kites *Milvus milvus* [RK], 10 black kites *Milvus migrans* [BK], 79 common ravens *Corvus corax* [RA], and 28 carrion crows *Corvus corone* [CC], see Table 3) from the time they arrived at the SFS until they departed. We were able to complete the study of the whole potential number of birds present at carrion inputs only for the GV (n = 200) because the rest of the species attended to only a subset of the 100 inputs. In the case of the most abundant and gregarious species—that is, GV and CV—we chose those birds exhibiting distinctive features in their plumage or nonfeathered parts as well as marks (plastic rings or wing tags) to optimize their individualization and avoid visual loss in the crowd during the entire period of stay.

Several variables were sampled during the observational monitoring of each bird on the basis of their linkage to individual feeding behavior and the energetic performance in avian scavengers (Cortés-Avizanda et al. 2010; Duriez et al. 2012; Kendall 2013, 2014; Moreno-Opo et al. 2015b). The following response variables were considered: *total time spent at the feeding site* in minutes, *time active at the feeding site* (i.e., searching for, ingesting, or fighting for food) in minutes, *general activity* (eats/does not eat), *way of feeding* (on the ground/take away/both), *type of ingested carrion* (bones/meat–viscera/skin–tendons/mixed remains, including several of the former categories and/or other type of remains), the *total number of feeding pecks*, and the *number of feeding pecks directed at the following categories of pieces of carrion*: *≤10*, *11–100*, *and >100 g*. These latter categories were assigned through visual estimates by zooming into the high-resolution images (5 megapixels). To deepen the relationship of the behavioral traits to components of intraguild resource partitioning, we accounted for the *species* and their *level of specialization on carrion* (facultative/obligate), the *age class* (adult/nonadult), and other morphological characteristics of the studied avian scavengers (Table 2) as explanatory covariates. The *subregion* (N-E, C-W) and the 4 climatic *seasons* in which carrion was provisioned were also included as fixed variables in the analyses (Zuur et al. 2007).

An estimate of the mean biomass consumed per feeding event by each individual was made following ACR assigned for each group of species: corvids–kites (<1500 g body mass, BK, RK, RA, CC), eagles (1500–5000 g, EV, SIE, GE, Wilmers et al. 2003), and greater species (>5000 g, BV, CV, GV, Table 2). ACR was calculated by multiplying the number of pecks during the whole period of stay per gram per peck assigned to each species. We based gram per peck for raven and eagle-sized species on Wilmers et al. (2003). For vultures—BV, CV, and GV—we considered their average beak capacity in cubic millimeter with respect to that of eagles through skull measurements: beak length, width, and height in millimeter (García 2013 and own unpublished data, Tables 2 and 3). We then extrapolated the gram per peck from eagles to vultures directly from the relationship of beak capacity in cubic millimeter between the 2 groups (eagles vs. vultures, Table 3). We decided not to correct gram per peck for the texture/stages of the *type of ingested carrion* (bones/meat–viscera/skin–tendons/mixed remains) despite its implication in ACR because data on gram per peck rates by texture was only available for ravens (Wilmers et al. 2003). As 84.6% of feeding events of BV were on bones, and this type of carrion does not fit the assumptions made for determining beak capacity and gram per peck (Wilmers et al. 2003), we could not consider this species for analyses on biomass consumed per feeding event. We also discarded for this latter analysis species that took food away in >50% of events due to the inability to determine the biomass ingested outside the study area.

Lastly, we calculated the rate of the daily energetic requirements fulfilled by comparing the estimated mean biomass consumed per feeding event to the daily biomass required by each species: BV = 0.40 kg, EV = 0.20 kg, CV = 0.57 kg and GV = 0.52 kg (Donázar 1993), SIE = 0.26 kg (González 1991), GE = 0.30 kg, BK = 0.17 kg and RK = 0.20 kg (Cramp 1998; Nagy 2005), RA = 0.40 kg (Heinrich 1994), and CC = 0.18 kg (estimated from Nagy 2005).

Statistical analyses

We first performed generalized linear mixed models (GLMMIX) to evaluate the *total time spent at the feeding site* and *time active at the feeding site* in relation to the species, their scavenging behavior, the season, subregion, and their interactions. We then established competing GLMMIX, 1) to assess *general activity* of birds present at SFS by choosing a logit-link function and a binomial distribution, 2) to consider the way birds fed on the carcasses (*way of feeding* and *type of ingested carrion during the entire presence*) by applying a logit-link function with a multinomial distribution, and 3) to determine the effects on the *total number of feeding pecks* (and *feeding pecks per minute*) with a log-link function and Poisson distribution. The explanatory covariates included in all the models were the *species*, the *level of specialization* (facultative or obligate), the *age class* of the individual, the *season*, the *subregion*, and for some analyses those covariates referred to in Table 2. The requirement of the maximum number of explanatory variables introduced in a multivariate analysis according to the existing sample would be violated in the case of considering jointly all the explanatory variables in the same model (Zuur et al. 2007). Thus, we established subsets of competing models considering the variables *species*, *season*, and *subregion* on the one hand and *level of specialization* and *age* on the other. We used the Akaike's information criteria (AIC; Burnham and Anderson 2002) to determine the most parsimonious model. We subsequently selected those combinations with the lowest AIC value and evaluated the estimates (β ± SD) for each level of the variables to determine their relationship (+/−) to the response variable as well as the Type 1 likelihood-ratio (LR)

Table 3

Results of the activity carried out by different species of European avian scavengers, distinguishing the age classes

Species	Age	Time present (min)	Time feeding (min) and % respect time present	% birds eat	% feeding activity			n	Total feeding pecks	Pecks/min	Gram/peck	Biomass per feeding event (g)	ACR (g/min)	% of required daily biomass fulfilled per feeding event
					On ground	Take away	Both							
BV	Adult	3.3 ± 0.7	1.2 ± 0.3 (36.3%)	38.2	9.6	58.1	32.3	34	2.1 ± 1.0	3.0 ± 1.8	8.81	—	—	—
	Nonadult	6.5 ± 0.8	2.0 ± 0.5 (30.7%)	43.1	28.9	46.1	25.0	65	1.8 ± 0.6	0.8 ± 0.2				
CV	Adult	34.5 ± 10.7	12.4 ± 3.2 (25.8%)	90.0	100.0	0.0	0.0	30	30.3 ± 6.9	2.5 ± 0.5	8.81	267.0	22.0	46.8
	Nonadult	34.4 ± 6.0	11.7 ± 2.4 (34.0%)	80.9	100.0	0.0	0.0	63	21.8 ± 4.5	1.8 ± 0.3		192.0	15.8	33.7
EV	Adult	47.2 ± 16.9	42.0 ± 17.1 (88.9%)	100.0	70.0	0.0	30.0	9	32.0 ± 30.7	3.2 ± 2.5	3.15	100.8	10.1	50.4
GV	Adult	17.6 ± 3.7	6.3 ± 1.2 (37.8%)	83.3	93.1	0.0	6.9	72	11.8 ± 3.2	5.7 ± 0.9	8.81	103.9	50.2	20.0
	Nonadult	26.7 ± 4.0	9.5 ± 1.4 (35.5%)	82.8	93.0	0.0	7.0	128	16.5 ± 3.1	4.9 ± 0.4		145.3	43.1	27.9
SIE	Adult	36.9 ± 9.5	12.6 ± 4.6 (34.1%)	75.0	100.0	0.0	0.0	8	141.1 ± 49.7	4.9 ± 1.2	3.15	444.4	15.4	170.7
	Nonadult	13.1 ± 5.4	2.6 ± 1.8 (19.8%)	71.4	80.0	0.0	20.0	7	29.5 ± 20.0	2.3 ± 0.5		92.9	7.2	35.7
GE	Adult	15.1 ± 4.8	12.3 ± 4.0 (81.4%)	66.6	50.0	33.3	16.7	12	100.1 ± 34.8	5.9 ± 0.8	3.15	315.3	15.7	100.0
	Nonadult	13.3 ± 4.8	7.6 ± 3.7 (57.2%)	83.3	40.0	0.0	60.0	6	45.3 ± 19.3	3.0 ± 0.7		142.7	9.4	45.7
RK	All	1.5 ± 0.8	1.4 ± 0.8 (93.3%)	37.5	42.8	57.2	0.0	8	20.5 ± 12.6	11.6 ± 1.9	1.15	—	—	—
BK	All	40.7 ± 10.7	28.3 ± 8.2 (69.5%)	90.0	100.0	0.0	0.0	10	173.2 ± 79.9	8.2 ± 1.6	1.15	199.2	9.4	117.1
RA	All	20.2 ± 4.9	9.0 ± 1.6 (44.5%)	84.8	81.1	0.0	18.9	79	37.9 ± 6.5	5.9 ± 0.5	1.15	43.6	6.8	109.0
CC	All	3.2 ± 0.5	1.7 ± 0.4 (53.1%)	100.0	89.3	0.0	10.7	28	14.2 ± 3.1	4.7 ± 0.5	1.15	16.3	5.4	90.5

The median ± SD of the time present and time spent actively feeding on carrion are shown, as well as the percentage of cases—from birds randomly selected per carrion event—in which individuals fed. Regarding feeding activity, the percentage of cases in which individuals of each species fed on the ground, took the food away, or alternated these methods to total observations at carrion inputs are indicated. In relation to feeding pecks, the median ± SD of total pecks and pecks per minute at each feeding event, and the percentage of pecks to the different size categories of ingested pieces are shown. In addition, biomass consumed per event is shown, calculated by multiplying the total number of pecks by the mean biomass per peck (gram per peck). Finally, ACR (biomass ingested in gram per min) and the percentage of daily nutritional requirements (in terms of biomass) satisfied per each event are shown (data of daily required biomass of each species have been extracted and adapted from González 1991; Donázar 1993; Heinrich 1994; Cramp 1998; Nagy 2005, see Supplementary Material).

test (χ^2) to know the significance value (P) of the covariates jointly included in the most parsimonious model.

To determine how the ratio of *time active* to *total time spent at feeding site* was influenced by the *species* (nested in its *level of specialization*), we performed 1-way analyses of variance. Lastly, we applied a nonparametric analysis of multiple dependent samples to meet the frequency distribution (χ^2) of the different categories (<10, 11–100, and >101 g) of the *number of feeding pecks* depending on the *species*. The statistical analyses were conducted with Statistica 6.1 (StatSoft, Tulsa, OK).

RESULTS

The time spent at the feeding site and actively feeding varied between species, with EV and BK spending more time feeding per each event ($F_{6,528}$ = 2.55; P = 0.019 for *total time spent at the feeding site* and $F_{6,518}$ = 2.42; P = 0.025 for *time active at the feeding site*, in both cases for the interaction of species with *season* and *subregion*, Table 3) and with a longer stay at SFS during periods outside of the breeding season—summer and fall. The ratio between *time active* and *total time spent at the feeding site* was also mediated by species ($F_{9,557}$ = 10.30; P < 0.001, Figure 1). In addition, obligate scavengers (vultures) ate for proportionally more time than facultative ($F_{1,4,3646}$ = 10.58; P = 0.027). The age of the individual, however, was not a significant factor in the length of stay (P = 0.769).

The results related to the activity of birds at carcasses (eat/do not eat) showed that all variables considered were included in the most parsimonious model (AIC = 521.37; LR χ^2_8 = 172.60, P < 0.001), with significant variations between the interaction of the different species, seasons, and subregions (χ^2_2 = 14.72, P = 0.006, Table 3 and Supplementary Table S1). Thus, almost all EV, CC, CV, and BK ate during their stay around carcasses. In addition, there were differences in the proportion of birds that ate depending on the time of year, being higher during the breeding season (β ± SD, winter 15.55 ± 10.88; spring 7.92 ± 10.70; summer −24.88 ± 132.23). On the other hand, the way the birds obtained the food (on the ground/take away/both) was more robustly influenced by species, seasons, and subregions (AIC = 409.47; LR χ^2_{17} = 330.87, P < 0.001). Species also varied in the way they obtained food (χ^2_{16} = 192.21, P < 0.001, Table 3 and Supplementary Table S1), with BV, GE, and RK taking carrion pieces away more frequently and the rest of the species eating in situ (Figure 2). The capacity to carry carrion away from the feeding site was conditioned by the morphological traits of the different species and the selection for the characteristics of the carcass (AIC = 175.80; LR χ^2_8 = 128.87, P < 0.001, Supplementary Table S1). Thus, birds with longer and more pointed beaks (0.65 ± 0.11; EV, RA, CC, and BV, Table 2) and a greater prehensile ability (0.32 ± 0.06; SIE, GE, RK, and BK, Table 2) carried proportionately more pieces away, mainly from the hardest parts of the carrion (0.71 ± 0.07).

The selection of the *type of ingested carrion* (bones/meat–viscera/skin–tendons/mixed remains) was more accurately explained by the combination of species + subregion + season variables (AIC = 879.34; LR χ^2_{12} = 308.69, P < 0.001, Supplementary Table S1), with significant differences between species (χ^2_{32} = 316.99, P < 0.001, Figure 3). Similarly, the scavenging character also had a high explanatory robustness regarding the type of parts consumed (AIC = 992.67; LR χ^2_4 = 17.27, P = 0.006, Supplementary Table S1): The facultative species positively selected meat/viscera and mixed remains (β ± SD, 1.33 ± 0.91 and 0.78 ± 0.19, respectively) and negatively selected bones and skin/tendons (−0.94 ± 0.33 and −0.56 ± 0.28, respectively).

The number of feeding pecks (total or per minute) depended on species × subregion × season ($F_{6,526}$ = 4.72, P < 0.001 for total pecks and $F_{4,15,2112}$ = 3.16, P = 0.044 for pecks/min, Table 3). Thus, facultative scavengers (1.26 ± 0.02 and 0.35 ± 0.09 for total pecks and pecks/min, respectively) from the adult age class (nonadults: −0.30 ± 0.01 and −0.23 ± 0.05 for total pecks and pecks/min, respectively) and with a larger body size (0.00031 ± 0.00001 and 0.00020 ± 0.00004 for total pecks and pecks/min, respectively) showed more rapid and numerous pecks (AIC = 21007.05; LR χ^2_4 = 5724.08, P < 0.001 for total pecks and AIC = 1282.60; LR χ^2_4 = 44.27, P < 0.001 for pecks/min, Supplementary Figure S1 and Supplementary Table S1). In addition, scavenger species were clustered according to the relationship between the time spent actively feeding and the number of feeding pecks (r = 0.351, P < 0.001, Figure 4).

Finally, the proportion of feeding pecks to the size of pieces considered (≤10, 11–100, and >100 g) varied between species (χ^2_2 = 19.54, P < 0.001). The results related to the biomass consumed per feeding event allowed us to determine the ACR and the percentage of the daily amount of biomass required for each of the species (Table 3).

DISCUSSION

The integrated approach of our study, taking into account different variables and species (see Methods and Table 2), provides a new perspective for revealing patterns of feeding behavior in avian scavengers. Few previous studies have analyzed these effects in an integrated way. In addition to the above parameters, there are others that affect the dynamics of feeding of necrophagous birds not included in our analysis (time of carrion input, species of origin of the carrion, biomass provided, and scattering), although these were considered in the design of our experimental field work. We discarded their inclusion in the analyses because 1) they have been the subject of recent studies already showing significant effects on feeding behavior (Cortés-Avizanda et al. 2010, 2012; Duriez et al. 2012; Moreno-Opo et al. 2015a, 2015b), 2) the frequency of inputs from different categories of these variables was homogeneously (for prey species, scattering and biomass) or randomly (time of input) distributed (see Methods for details), in order to standardize the variability of situations as much as possible and to avoid biases in the results, and 3) increasing the number of explanatory variables included in the multivariate analyses for species with a relatively small number of studied events (n < 30) was not possible, according to the selection of parsimonious models using intuitive rather surrogate variables, which is much more advisable than other analytical processes such as principal components whose interpretation is more complex (Zuur et al. 2007). Furthermore, the experimental design was planned by randomly choosing and studying a single individual by species and age group, with the purpose of considering the greatest variability of situations and to avoid possible pseudoreplication effects in the samples. It should be borne in mind that attendance of certain species occurred only to some of the carrion inputs, as they were not distributed in all sampled locations or because migratory species are absent for part of the year. This reduced the final sample size for some species—EV, RK, BK, and SIE, in comparison with the maximum potential samples obtained for GV, BV, and CV.

Behavioral patterns of carrion exploitation at the species level

The studied species showed a highly differentiated feeding behavior with general implications for intraguild niche partitioning: While species such as EV and BK spent a significant amount of time in the vicinity of the carrion, others such as BV, CC, and RK invested a much shorter stay. All species spent more than a third of their time feeding at the carrion, due to the need to optimize resource exploitation (MacArthur and Pianka 1966; Cortés-Avizanda et al. 2012; Spiegel et al. 2013). However, highly specialized species, such as CV and GV, or SIE, were inactive at the feeding events longer than other species, such that their presence at these feeding events

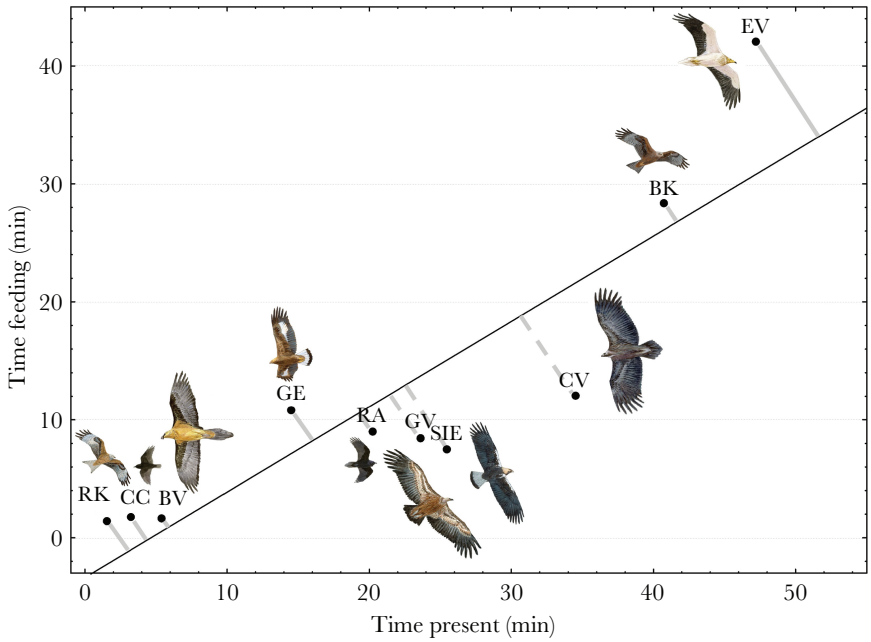

Figure 1
Linear regression (black line) of the relationship between the time present and the time active at carrion inputs by different species of European avian scavengers (BV, EV, CV, GV, SIE, GE, RK, BK, RA, and CC). Distances to the regression line of each species are shown so that greater distances imply higher (continuous gray line) or lower (dashed gray line) proportion of time spent in active feeding with respect to the time present around the carcass (species drawings: J. Varela).

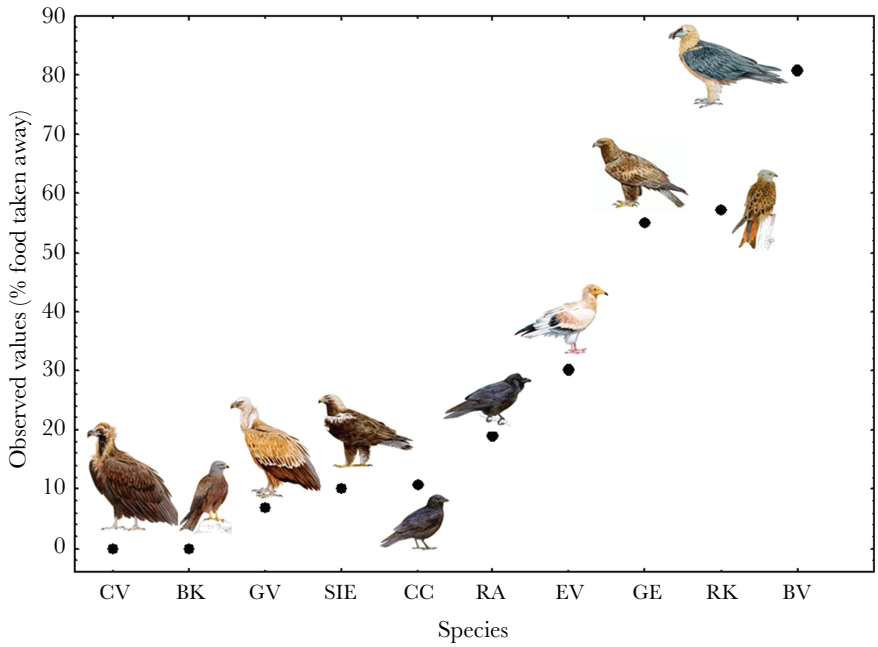

Figure 2
Observed values of the percentage of events of capture and transport of food outside the carrion site by European avian scavengers (BV, EV, CV, GV, SIE, GE, RK, BK, RA, and CC). Higher percentages (top right) correspond to species showing more carrier activity, whereas lower percentages (below left) are those that feed primarily on the ground (species drawings: J. Varela).

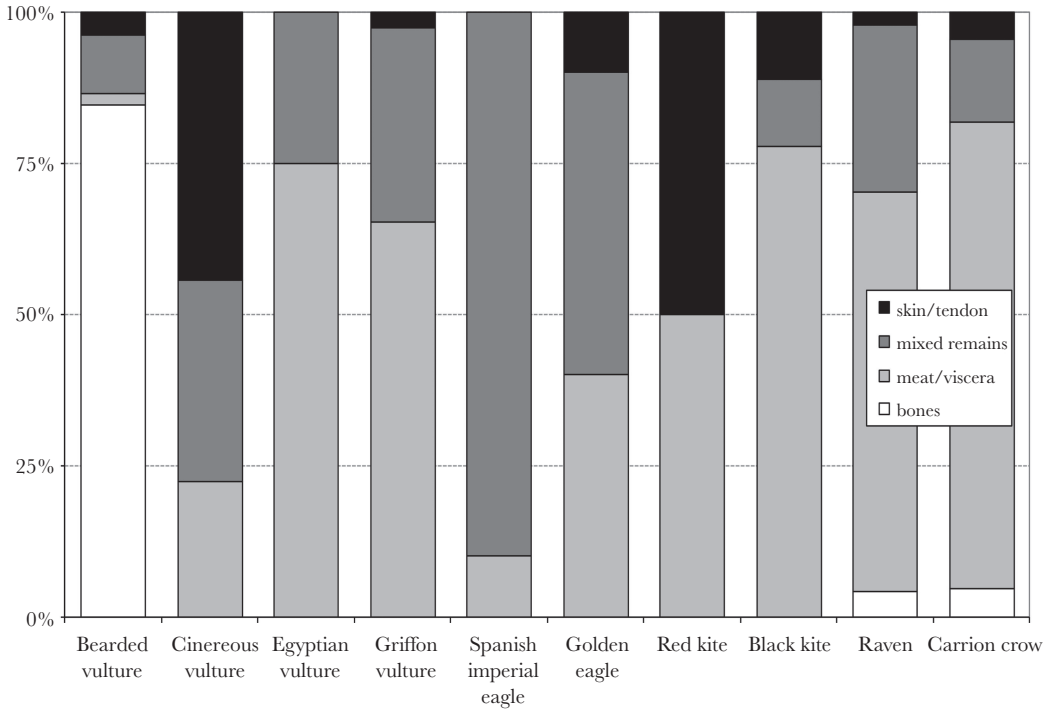

Figure 3
Percentage distribution of types of consumed parts of the carcasses by each species for the total feeding events in which its behavior was observed, grouped into the categories skin/tendons, mixed remains, meat/viscera, and bones.

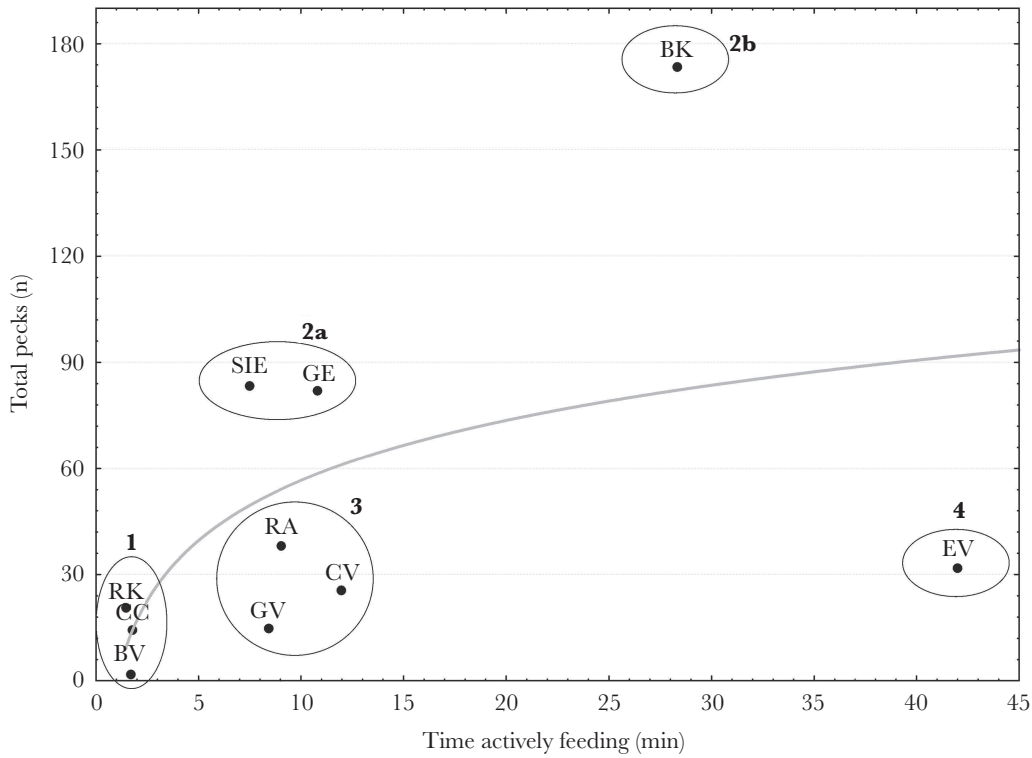

Figure 4
Allocation of European species of avian scavengers according to the ratio between the number of feeding pecks and time of active feeding (i.e., searching for, ingesting, or fighting for food) and logarithmic regression of the results (gray). Species are grouped into 1 = *urgent eaters* (short feeding time and very few pecks; BV, RK, CC); 2 = *restless peckers* (many pecks, and 2a = in short time—SIE, GE—or 2b = in long time—BK); 3 = *balanced scavengers* (few pecks over a moderate amount of time; CV, GV, RA); and 4 = *parsimonious* (few pecks over a very long time; EV).

could have implications other than nutrition. For example, there may be implications related to social interactions and gregariousness (Deygout et al. 2010; Dermody et al. 2011), or this may be a consequence of less pressure from other vital activities such as breeding in nonadult individuals (Carrete et al. 2006; García-Heras et al. 2013). The number and speed of feeding pecks also allowed clustering different species: Although large eagles and kites showed a large number of pecks throughout their presence at the carcasses, kites are the only birds that exhibited a much higher speed of pecks than the other species. Following this pattern, species were grouped according to the pecking activity (number of pecks vs. time spent, Figure 4), such that the following groups could be defined: *urgent eaters*, characterized by short feeding time and very few pecks, including BV, RK, and CC; *restless peckers*, including species showing many feeding pecks over a short time, including SIE and GE, or over a long time such as BK; *balanced scavengers*, species performing a few pecks over a moderate time, including CV, GV, and RA; and *parsimonious*, with a small number of pecks over a very long time, including EV. The relationship of the variables time of stay/time of active feeding and the number of feeding pecks also enabled the segregation of avian scavengers, leading to a decrease in competition and conflicts for resource exploitation, as well as an occupation of specialized trophic niches (Houston 1975; Cortés-Avizanda et al. 2014; Kendall 2014). Moreover, competition may also explain the differences observed in the feeding activity: The larger species with greater hierarchical status and better adapted to scavenging consumed carrion in situ, whereas those with less ability for fighting (Wallace and Temple 1987; Kendall 2013) and specific morphological traits (i.e., a greater prehensile capacity) were more likely to be carrion carriers.

Most individuals (>75%) of the different species obtained food when they attended the feeding event, except BV (<45% of individuals fed) which may be explained by its ecological and behavioral characteristics in the exploitation of bone remains, a resource that may be preserved in good condition for longer (Houston and Copsey 1994). This is linked to the way the different species feed and is related to the results of selection for different parts of the carcass. Vultures with strong beaks that feed on meat scraps, skin, and viscera (CV, GV) ate almost exclusively on the ground, whereas vultures specializing in bones (BV), skin, and other remains (EV) with longer beaks and more prehensile capacity took pieces of the carcass away from the feeding site (Margalida 2008). This way of feeding of BV and EV reduces their overall interspecific competition for food through an elusive behavior with respect to the other more abundant and aggressive vulture species (Houston and Copsey 1994; Meretsky and Mannan 1999). These species also differ in the way they feed their offspring: While CV and GV regurgitate, BV and EV carry the food (in their claws and/or beak) to the nest. Because of the greater prehensile ability of claws (Fowler et al. 2009) facultative species also took resources for consumption to areas in the surroundings of the feeding site.

Although no differences in feeding patterns among juveniles and adults were observed, adults spent less time feeding but obtained in general higher yields, by eating a greater amount of biomass per minute and for the whole stay (Table 2). This suggests a greater efficiency in more experienced birds (Wallace and Temple 1987; Kirk and Houston 1995).

Finally, the results showed the influence of season on feeding behavior, related to the life-cycle stage of the species. During the breeding season (winter, spring, and/or summer) the *total time spent at the feeding site* was lower, whereas the number of feeding pecks and the percentage of birds that fed were proportionally greater. This indicates that individuals try to optimize the acquisition of food during periods in which parental investment is essential (Moreno-Opo et al. 2010; Spiegel et al. 2013).

Trophic efficiency

As a result of the estimated biomass consumed, we found that, in general, vulture species obtained nearly half of their daily requirements at each feeding event (20.0–50.4%). It should be expected that these percentages would be higher, given the feeding strategies of obligate scavengers that cope with patterns of pulsed and unpredictable occurrences of carcasses (DeVault et al. 2003; Selva and Fortuna 2007; Cortés-Avizanda et al. 2012). Vultures are adapted to ingest large amounts of food at each feeding event and, subsequently, may go several days without eating (Spiegel et al. 2013). In this sense, we found in our study that 28.1% (for CV, $n = 64$), 15.0% (for GV, $n = 113$), and 50.0% (for EV, $n = 2$) of individuals actively feeding at carcasses, respectively, exceeded their daily required biomass.

Several factors may have influenced our results and might even have effects at a global scale in recent times: 1) increasing populations of CV and GV may have boosted competition for resources, such that the requirements of a large number of birds present at each feeding event would not be satisfied and/or 2) increasing the availability of carcasses at locations with a frequent and predictable presence of food would promote higher visit rates to these feeding points by vultures (Deygout et al. 2010), implying less of a need to ingest large quantities of food at a single event. The latter may explain, in particular, the situation for BV and EV, for which behavioral or demographic shifts have been shown resulting from their preferred selection for predictable feeding sites (Meretsky and Mannan 1999; Carrete et al. 2006; Margalida et al. 2014). The bone-based feeding by BV, and the presence of this type of carrion at feeding sites beyond 3 days after depositing the carcass, would extend the time for which this resource is available.

Given the greater plasticity of food sources for facultative species (Wilson and Wolkovich 2011; Oro et al. 2013), it would be expected that the percentage of daily biomass satisfied at the feeding event would be lower than vultures. However, for large eagles, BK, and corvids, exploiting resources at carrion meant fulfilling daily energetic requirements, reinforcing the important role of this food source for apex predators (Sánchez-Zapata et al. 2010; Moleón, Sánchez-Zapata, Selva, et al. 2014; Mateo-Tomás et al. 2015).

Preferences for different carrion parts

The selection for different parts of the carcass showed an interspecific resource partitioning such that parts offering a higher global biomass (meat and viscera) are exploited by most of the species, both obligate and facultative (Moreno-Opo et al. 2010; Cortés-Avizanda et al. 2014; Moreno-Opo et al. 2015a). Our results allowed us to link the characteristics of hardness and texture of consumed parts of carrion to the morphology of the feeding apparatus, mainly beaks and the structure of the head (König 1983; Hertel 1994). The different species thus distribute their exploitation, and even their abundance at carrion depending on the properties of the available parts (Moreno-Opo et al. 2015a). The most abundant species, the GV, takes soft parts from the body (viscera and meat), which provide a greater biomass (Duriez et al. 2012). This positive association between abundance level and relative biomass availability could explain the population growth of this species over

others in recent decades, in a European context. The CV selects, in addition to soft parts, other tougher and scarcer tissues (skins and tendons), thanks to its effective tearing capacity. EV is specialized in collecting peripheral small remains of the most abundant parts, by pecking around the point of carrion location (Meretsky and Mannan 1999). The BV preferably selected bones avoiding competition with other vultures for the same parts (Houston and Copsey 1994). The facultative species with less robust or weaker beaks (kites and corvids) consumed the most abundant available soft tissues (viscera and meat), whereas large eagles included more heterogeneous and hard parts (mixed remains) due to their rending capability (Fowler et al. 2009).

Differences between obligate and facultative scavengers

The feeding patterns of obligate and facultative scavengers differed in several respects. Vultures, as obligate scavengers, stayed longer in the surroundings of the carrion, both feeding and not feeding. As these species are evolutionarily adapted to their presence at carcasses, and have a stronger social character (DeVault et al. 2003; Dermody et al. 2011; Kendall et al. 2012), these times were higher than those of facultative species except in the case of RA and BK, who also exhibit a strong gregarious behavior (Sergio and Penteriani 2005; Fraser and Bugnyar 2011). This social component could also explain the fact that facultative species performed more pecks (total and per unit of time) and spent a greater proportion of time actively feeding (mean 61.3% ± 22.7 of time feeding, $n = 6$) due to the urgency to avoid situations of competition or other disadvantageous interactions for their survival and feeding efficiency (Wallace and Temple 1987). In addition, the most abundant parts of the carcasses (viscera, meat, and other remains) were exploited to a greater extent by facultative species, demonstrating their generalist nature in the exploitation of these resources (Wilson and Wolkovich 2011; Mateo-Tomás et al. 2015). Obligate scavengers are more specialized and diversed in the use of different parts of the carcass depending on the species, showing a complementary niche partitioning derived from facilitatory processes for finding and exploiting carrion (Selva and Fortuna 2007; Jackson et al. 2008; Deygout et al. 2010; Sánchez-Zapata et al. 2010; Kendall 2013; Cortés-Avizanda et al. 2014; Kane et al. 2014).

Implications on behavioral organization and food webs

Our findings improve the knowledge about the functioning and ecological implications of food webs related to carrion resources. The presence of this trophic resource of great isolated and abundant biomass and partially unpredictable in the ecosystem (Barton et al. 2013), results in complex relationships among species during its exploitation. Using avian vertebrates as a study model, a nested structure of species has been observed whose composition and abundance are complementary during the exploitation event (Cortés-Avizanda et al. 2012; Kendall et al. 2012). These species have developed evolutionary mechanisms leading to the establishment of various life strategies: On the one hand, several species are specialized in the use of certain limited parts of the carcass benefitting from particular morphological and physiological adaptations (Hertel 1994; Moreno-Opo et al. 2015a). On the other hand, generalist species have a wider ecological plasticity and feed on the most abundant parts of the carcass (Wilson and Wolkovich 2011), which would result in a greater efficiency at the feeding event. In addition, the phenomena of competition and facilitation determine the species abundance and composition (Jackson et al. 2008): Facultative species have developed strategies that minimize the risk of aggression through a lower time of presence and a faster food intake, reducing the costs associated with interspecific and intraspecific interactions.

In short, obligate scavengers stay in the vicinity of the carrion longer, feed on more specific parts of the carcass taking advantage of their morphological adaptations and obtain a comparatively lower yield per feeding event. In contrast, facultative species spend less time to obtain a greater fulfillment of their daily trophic requirements, avoiding body interactions with obligate species, behave as generalists in the selection of the parts of the carcass, and are more efficient in the use of the resource. Several factors may have contributed to these patterns because it is not expected a priori that species evolutionarily better adapted to scavenging will satisfy less energy requirements (DeVault et al. 2003; Selva and Fortuna 2007). It is possible that food availability does not constitute a limiting resource for vultures in the study area, favored by mechanisms such as the increased mobility of individuals for searching for other scavenging events, social facilitation, or anthropogenic management practices in promoting supplementary feeding points (Deygout et al. 2010; Margalida et al. 2014).

Environmental and behavioral patterns of avian scavengers associated with the occurrence of ephemeral food resources in time and space but abundant in biomass are potentially similar to those from other biological systems. In the field of scavenging, taxa such as invertebrates (mainly arthropods), microorganisms, or plants could respond to the same patterns as vertebrates, with regard to their obligate/facultative and specialist/generalist nature, with a special relevance for aspects such as competition and facilitation (Barton et al. 2013). In this sense, some necrophilous invertebrate species depend on decaying biomass for the development of some life-cycle stages (i.e., Watson and Carlton 2003), whereas others feed on a facultative basis (Kaiser and Hiddink 2007). The bacterial community and associated nitrophilous vegetation associated with carcass rottenness also exhibit specific temporal dynamics (Barton 2015). Other similar phenomena, such as overlapping in fruiting plant species (i.e., masting) or variation in abundance cycles of prey species (i.e., rodents, zooplankton), may be comparable with scavenging because such temporal but abundant occurrences of heterogeneous resources generates specialization, and intraspecific and interspecific competition in its exploitation and even demographic effects (Korpimäki and Krebs 1996; Herrera et al. 1998; White 2008).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

FUNDING

A.M. was supported by a Ramón y Cajal research contract from the Ministry of Economy and Competitiveness (RYC-2012-11867).

This work was carried out within the framework of the project *Technical basis and guidelines for a strategy on feeding of endangered scavengers* (Spanish Ministry of Environment). L.M. González, J.J. García, A. Arredondo, P. Montoto, J. Muñoz, J. Canut, L. Baquedano, J. Alay, D. Sánchez, J. de Lucas, C. García, D. García-Ferré, J. Ruíz-Olmo, Á. Gómez, M. Carrasco, J. Palau, J. Fernández, and I. Mosqueda provided valuable support to perform the field work. The comments of A. Kane, A. Jackson, and 2

anonymous reviewers improved a previous version of this manuscript. We specially thank J. Varela (http://www.juanvarela.com/) for providing the pictures of the studied species.

Handling editor: David Stephens

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