

Carcasses provide resources not exclusively to scavengers: patterns of carrion exploitation by passerine birds

RUBÉN MORENO-OPPO^{1,†} AND ANTONI MARGALIDA^{2,3}

¹*Vertebrate Biology and Conservation Group, University Complutense of Madrid, Madrid 28049 Spain*

²*Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Bern 3012 Switzerland*

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Abstract. Carrion provides energy transfer to food webs as a primary trophic resource for many taxa. Ecological relationships around this pulsed resource are highly complex and are influenced by many factors, including those related to its availability and the management of carcasses by humans. In recent years progress has been made in understanding the scope, implications and value of carrion ecology, mainly using scavenger birds and arthropods as study models. However, carrion is important for other facultative scavengers, and even for other non-scavenger species, which may be influenced by the onset of the resources generated. The objective of this study was to evaluate the patterns of attendance of passerine birds, including the non-scavengers, at carrion inputs in order to divulge the importance of this resource, its relationship to other species, and to reveal its ecological implications. Individuals of the Corvidae family, recognized facultative scavengers, showed a similar trophic behavior to obligate scavenger raptors regarding the selection of carcass characteristics (i.e., format, scattering, biomass), the surrounding landscape and spatiotemporal conditions. Furthermore, corvids mismatched their presence with vultures, benefitting through commensalism from the generation of residual small pieces and scraps. The non-scavenger passerines avoided simultaneous presence with vultures and delayed their attendance to carcasses from the time of input. Non-corvid passerines profited from carrion opportunistically, especially through predation on scavenger arthropods. Thus, their appearance was linked to seasons and conditions with an increased abundance of invertebrates, and coincided with periods of higher energy demand (migration and wintering). Similarly, inter-specific competition in carrion exploitation as well as a decrease in abundance of arthropods may determine the segregation between non-corvid passerines and scavenger raptors.

Key words: arthropod productivity; carcasses; carrion ecology; corvids; decomposition; opportunistic trophic behaviour; passerines; scavenging; Spain; supplementary feeding sites.

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³ Present address: Department of Animal Production (Division of Wildlife), Faculty of Life Sciences and Engineering, University of Lleida, Lleida 25198 Spain.

† **E-mail:** rmorenoopo@gmail.com

INTRODUCTION

Carrion plays a key role in food webs, and is an extensively used trophic resource providing high nutritional levels in terrestrial ecosystems

(DeVault et al. 2003, Leroux and Loreau 2008). This importance is reflected, for example, in the existence of a higher overall energy transfer between organisms through scavenging rather than through predation (Wilson and Molkovich

2011). As a result, many taxa feed on the organic material of carcasses (Selva and Fortuna 2007, Barton et al. 2013) and cadaver decomposition itself is a driver of soil alteration through the transfer of nutrients and minerals (Carter et al. 2007). In carrion ecology, the discipline that assesses the relationships between animal organic material in decomposition and ecosystems as well as its importance for biodiversity and ecological processes (Barton et al. 2013), various key aspects have been identified and a greater knowledge of these would allow an accurate understanding of the ecological links generated by carrion and, when appropriate, the proper management of the resources offered. These issues include the recognition of the net energy contribution of different types and sizes of carcasses at different space-time scales, the assessment of the stability of ecological relationships at the community level, the analysis of the influence of the different ecosystem traits on the energy transferred, and knowledge of the effects of human activities on the occurrence of different types of carcasses in the wild (Cortés-Avizanda et al. 2010, Margalida and Colomer 2012, Barton et al. 2013).

Carcasses are a pulsed resource whose occurrence patterns in ecosystems are subject to variable spatiotemporal predictability depending on many factors (Nowling et al. 2008, Cortés-Avizanda et al. 2009a). These are, among others, the mortality rates and their causes, the abundance, location and distribution of wild animal species, as well as the intensity and methods of their socio-economic uses (DeVault et al. 2003, Deygout et al. 2009, Margalida and Colomer 2012). All of these determine carrion availability, triggering adaptive changes in the morphology, behaviour, interactions, distribution and population dynamics of species linked to this resource (i.e., Wilmers et al. 2003a, Selva et al. 2005, Shivik 2006, Cortés-Avizanda et al. 2009a, Deygout et al. 2010, Margalida et al. 2011).

Scavengers exploit carrion at different levels of intensity, which defines them as either obligate or facultative depending on their degree of dependence on this resource and their own adaptive traits (DeVault et al. 2003, Wilson and Wolkovich 2011). In general, due to the unpredictability in the availability of carcasses, there are few obligate scavengers. On the other hand, a large

number of species, including almost all carnivores, benefit to some degree from carrion as a trophic resource, and are therefore considered facultative scavengers (DeVault et al. 2003, Wilson and Wolkovich 2011). Scavenger species have been used as study models in carrion ecology research, mainly focusing in mammals, birds and arthropods (Ives 1991, Selva and Fortuna 2007, Ulrich et al. 2008). For other animals, including non-scavengers, plants, microbes or different elements of ecosystems such as soil or water, there have been many fewer studies on nutritional relationships with cadavers (Shivik 2006, Barton et al. 2013). Carrion may also provide resources to non-scavenger species—considered as those not feeding on the organic biomass provided by the carcass—due to the increased density of food elements located in its surroundings. These resources may appear in various forms such as the concentration of scavenger animals around the carcass and, therefore, a higher predation success of such scavengers (Selva et al. 2005, Cortés-Avizanda et al. 2009b), or by increasing the concentration of nutrient compounds in the soil which determines the growth rates and survival of certain plant communities or species (Carter et al. 2007, Melis et al. 2007).

The passerines are the most species-rich order of birds, which means that the group shows a high level of heterogeneity in foraging adaptations and requirements. Regarding carrion use, most passerine species are not scavengers except for the family Corvidae, in which common carrion consumption has been shown (Soler and Soler 1991, Read and Wilson 2004). The facultative scavenging nature of the corvids varies depending on the species and according to non-exclusive factors such as the geographical scope, habitat characteristics, territorial behaviour, inter- and intra-specific competitive mechanisms, or the availability of carcasses (Heinrich 1988, Read and Wilson 2004). In some cases other non-corvid passerines that are not considered scavengers are active participants in the process of carrion consumption (Selva et al. 2005), exploiting the side-effects of these pulsed resources, such as a higher concentration of scavenger invertebrates (Melis et al. 2007, Barton et al. 2013). However, no specific studies have addressed in detail the factors that determine the



Fig. 1. Study area in the Iberian Peninsula (Spain). The locations (dots) where experimental carrion inputs were controlled are shown, within northeastern (1 = Tremp; 2 = Buseu; 3 = Alt Pirineu Natural Park) and central-western (4 = Cabañeros National Park; 5 = Alcudia-Sierra Madrona Natural Park; 6 = Sierra de San Pedro) sub-regions.

presence of (mainly non-corvid) passerines at carcasses for feeding purposes.

This paper discusses, for the first time, the patterns of occurrence of passerine species with feeding activity at experimental carrion inputs. It aims to reveal the factors that determine their presence and abundance depending on (1) the characteristics of the carrion, the surrounding landscape and spatiotemporal conditions, and (2) their relationship with other scavengers to analyze potential competitive interactions. Specifically, we tried to recognize the behavioral association between passerines and scavenger raptors regarding their simultaneous abundance at carcasses and the sequence of consumption since the carrion was supplied. Due to differences between corvids and non-corvids in relation to their scavenging status, the two groups of passerines were considered separately in the analyses.

METHODS

Study area

The study was carried out at six sites in the Iberian Peninsula (Spain), three in the northeast (Pyrenean mountains range) and three in central-west (Sierra Morena, Montes de Toledo-Sierra de San Pedro ranges; Fig. 1). These two Iberian regions, of varied climate, vegetation, altitude and land use, were selected so as to include a wide diversity of bird species, both scavengers and non-scavengers, in the study (Del Moral and Martí 2003). The northeastern area is situated between the Mediterranean continental and the high-altitude mountain climatic sub-regions. Mean temperature in winter (January) is 2.9°C and in summer is 20.3°C (July). The altitude of the study locations ranged between 1045 and 1330 m asl. The vegetation of the surroundings was mainly formed by *Pinus sylvestris* forests, subalpine grasslands and a series of shrub-tree

Table 1. Independent variables regarding the characteristics of the provided carrion in experimental inputs, considered to assess their influence on the presence and relative abundance of passerine birds with feeding activity.

Variable	Type	Description	Categories
Season	categorical	Season of the year	Winter (December, January, February) Spring (March, April, May) Summer (June, July, August) Autumn (September, October, November)
Format	categorical	Type/characteristics of the provided carrion	Whole carcass (one or more) Carcass/es divided into, at least, six pieces Remains (guts, legs and various pieces) including meat and bones Meat remains (guts and various soft tissues) Bone remains (legs, backbones, etc.)
Scattering	categorical	Radius of dispersion of the carrion parts/remains from a central point	Concentrated (<2 m radius) Not concentrated (2–10 m radius) Dispersed (>10 m radius)
Region	categorical	Region of provision of carrion	Northeastern Spain Central-Western Spain
Predictability	categorical	Frequency of carrion inputs at the supplementary feeding point before starting and during the experimental assay apart from the inputs monitored fortnightly in the present study	Weekly (at least one input per week) Monthly (approximately one input per month) Non-periodic (without exact frequency and with periods of no inputs)
Biomass (kg)	continuous	Weight of the carrion provided measured through a digital scale or a visual assessment	

developments. The main socioeconomic land-uses are extensive grazing, ecotourism and, to a lesser extent, big game harvesting. The central-western subregion has a continental Mediterranean climate with hot summers, with an altitude ranging between 521 and 686 m asl. Mean temperature in winter (January) is 5.7°C and in summer is 25.4°C (July). The prevailing vegetation corresponds to *Quercus rotundifolia* and *Quercus suber* accompanied by other typical Mediterranean species, shaped as pasturelands (dehesa) or as unmanaged forests, and grasslands. Big game hunting, logging activities mainly from cork exploitation and extensive grazing are the main incomes for the local population.

Experimental sites were selected on active supplementary feeding points maintained within the frame of official conservation programs to favor scavenger bird species. These points were chosen because a different type of management was carried out before the start of the essay (*predictability* variable; Table 1). The species of avian scavengers and forest passerines within the study area show relative abundances high enough to consider their presence at the supplementary feeding points as representative of the

whole Iberian Peninsula. Thus, for vulture species, within the northeastern sub-region an average of 347 pairs of Griffon Vulture *Gyps fulvus*, five of Cinereous Vulture *Aegypius monachus*, 18 of Egyptian Vulture *Neophron percnopterus* and 15 of Bearded Vulture *Gypaetus barbatus* were registered in a 25 km radius around the three locations of carrion inputs (R. Moreno-Opo and A. Margalida, *unpublished data*). For the central-western sub-region the average numbers of breeding pairs of the species mentioned above in the three locations were, respectively, 90, 148, 7 and 0 (R. Moreno-Opo and A. Margalida, *unpublished data*). Other bird species were not the subject of population estimates in our field work. Nonetheless, there is a widespread occurrence of different species typical of forest environments in the vicinity of the tested points (Del Moral and Martí 2003). Furthermore, according to distribution patterns of bird species richness based on environmental (habitat, weather, productivity), geographical and human characteristics (González-Taboada et al. 2007, Moreno-Rueda and Pizarro 2010), there should be a higher richness and relative abundance of birds in the central-western subregion, in comparison to the northeastern one.

Study design and data collection

Between May 2009 and April 2011 an experimental program of carrion inputs at supplementary feeding points for avian scavengers was performed. Carrion was supplied at each point every 15 days, controlling its characteristics and combining inputs sequentially (mainly *format* and *scattering* variables; Table 1). In addition, other carrion remains were provided within the schedule of the management program of the supplementary feeding sites. These were not monitored but considered ahead regarding its possible influence on the attendance of birds to the experimental sites (*predictability* variable; Table 1). Thus, at the end of the two-year experiment, a similar number of inputs with each of the combinations of the studied variables was implemented. The provided carrion consisted of cadavers and remains of livestock, mainly Sheep *Ovis aries*, and wild ungulates such as Red Deer *Cervus elaphus* and Wild Boar *Sus scrofa*. The management of the animal by-products was developed in accordance with current sanitary legislation (European Commission 2011).

Carrion exploitation was continuously recorded from the time of its provision until three days later, during the daytime from sunrise to sunset. For this purpose, we installed a high-resolution videocamera (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 due to the 120° display angle of the camera. The recording quality was controlled, so that images occurred in a sequence of 20 frames per second with a resolution of 5 megapixels. This high resolution allowed zoom images to capture accurate data on the studied variables (see sections below). Images were stored on the hard disk drive for subsequent visualization and study, through the AV program v.5.1.4.239 Application Manager (Arecont Vision, Glendale, California, USA).

Response and explanatory variables

The recordings of each three-day event of carrion consumption were visualized by registering different independent and response variables. The first were addressed to determine the number of passerines showing feeding activity.

Thus, the following were considered: (1) bird counts in each 10-min period (i.e., every 10 min a census of the birds was carried out); and (2) the total number of birds that visited the carrion after each input, expressed as the sum of birds recorded in the different 10-min periods. Passerines were identified to the species level, although some small-sized species had to be assigned to their genus or families. The following were selected as independent variables, depending on the analysis performed: (1) the number of individuals of scavenger raptors present (Griffon Vulture, Cinereous Vulture, Bearded Vulture, Egyptian Vulture, Black Kite *Milvus migrans*, Red Kite *Milvus milvus*, Spanish Imperial Eagle *Aquila adalberti*, Golden Eagle *Aquila chrysaetos*, Common Buzzard *Buteo buteo* and Montagu's Harrier *Circus pygargus*) recorded using the same procedure as passerines; (2) the number of hours since the provision; and (3) carrion characteristics and space-time circumstances (Table 1). For the purposes of this study, it was considered as *obligate scavengers* those individuals of vulture species, as *facultative scavengers* other raptors different to vultures and passerines of the Corvidae family, and as *non scavengers* passerines not belonging to the Corvidae family.

The numerical relationships between occurrence of passerines (we also observed, and so included in this category, two non passerine species the Hoopoe *Upupa epops* and Wood Pigeon *Columba palumbus*) and raptors feeding on carrion were first analyzed, to evaluate possible exclusion-competition-facilitation mechanisms that could occur between the two groups. To this end, this relationship was assessed in each 10-min period in which individuals of any of the two groups (passerines and/or scavenger raptors) were present. Pseudoreplication between subsequent counts of 10 min that could lead to the lack of independence of the observations was discarded. Based on the analysis and data gathering from the images, it was observed that the permanence of individuals was dynamic and continuously changing (Cortés-Avizanda et al. 2010). In fact, in most cases, the residence time of individuals was less than 10 min, especially for passerines (*personal observations*). Due to the large distances between sampling points within the same study sub-regions and to the weekly interval between inputs at different points,

spatial autocorrelation therein was dismissed. Furthermore, the temporal progress of attendance of passerines to the carcasses was assessed with the objective of recognizing possible excluding relationships between species. This was obtained by calculating the mean number of birds counted from the time of the input at 0.1 h intervals.

In addition, the influences of different variables (Table 1) on the total number of passerines that came to each input—as the sum of the birds recorded in the different 10-min periods—were analyzed. These variables were selected in order to elucidate possible effects related to the study area, the time of year, the management performed at the supplementary feeding point or the carrion characteristics. In all cases corvids, whose opportunistic and facultative scavenging behavior is common (Soler and Soler 1991, Heinrich 1998), and other passerine species not considered scavengers were analyzed separately.

Analytical procedures

To determine whether the presence of scavenger raptors conditioned the presence of passerine birds, trends of both variables were compared, taking as a unit the number of birds of each group simultaneously counted in each 10-min period. The variables were not log-transformed to adjust to a normal distribution because of the large number of cases ($n = 7286$) and the robustness of the regression analysis itself, both ensuring the accuracy of the analysis (Zuur et al. 2009). Similarly, the temporal pattern of occurrence of passerine birds (corvids and non-corvids separately) was evaluated, with the number of hours from the time of the carrion input used as the independent variable and the mean number of birds in each time category (0.1 h intervals) as the response variable. In these cases, multiple regression models were performed (Sokal and Rohlf 1995).

To determine the effect of different characteristics of the carrion inputs on the number of passerines feeding, a multivariate analysis (Generalized Linear Models GLM, sigma-restricted parametrization, sum of squares Type VI) was performed in which independent variables were the categorical *season*, *format*, *scattering*, *region* and *predictability*, and the continuous *biomass* (Table 1). This latter variable was $\log_{10} + 1$

transformed to obtain normality. Between effects of the above-mentioned variables were not integrated into the models since the number of independent variables exceeded one-tenth of the studied events (Harrell et al. 1996). A principal component analysis that could reduce the number of variables and improve the discriminating power of the model was not considered since variables were conceptually different implying difficulty in the interpretation of results (Jolliffe 2002).

Lastly, in order to recognize time differences in the relative abundance of passerines attending to carrion inputs, stated as the sum of birds every 10 min per day and grouped into their corresponding month, analysis of variance (one-way ANOVA, Sokal and Rohlf 1995) of the trend of birds per month was performed. Continuous response variables—total passerines (n), passerines no corvids (n) and corvids (n)—were $\log_{10} + 1$ transformed to ensure normality. The statistical analyses were conducted with Statistica 6.1 (StatSoft, Tulsa, Oklahoma, USA).

RESULTS

A total of 144 inputs of carrion with a total of 6,772 kg of biomass were supplied and distributed homogeneously among the studied geographic areas and locations. From these inputs over 10,000 h of video-recordings were obtained which, once visualized, allowed the counting of 55,885 individual scavenger raptors and 21,214 passerines. We identified 18 species of passerines (six corvids and 12 non-corvids) and two related species (Table 2). The species most frequently attending carrion inputs was the Raven *Corvus corax* (71.4% of contributions), and among non-scavengers the White Wagtail *Motacilla alba* (19.0%). In relation to non-corvid passerines, their presence was recorded in more than 50% of inputs.

The abundance of passerines at carcasses was significantly influenced by the number of scavenger raptors present ($R^2 = 0.143$, $F_{2,7286} = 54.088$, $p < 0.001$). Thus, the number of corvids was positively related to the simultaneous presence of scavenger raptors ($r = 0.082$, Fig. 2) while, on the other hand, non-corvids shied away from higher abundances of scavenger raptors and were more abundant when fewer raptors occurred ($r =$

Table 2. Passerine and related species observed feeding during experimental carrion consumption events. The number of inputs attended by each species, their proportion with respect to the total number of inputs in the assay, the maximum number of registered birds and the percentage distribution of birds between seasons (W: winter, Sp: spring, Su: summer, A: autumn) are shown.

Species	Inputs attended (n)	Percentage from total inputs	Max. counted birds/input (median)	Max. counted simultaneously	Birds/season (%)			
					W	Sp	Su	A
Passerines								
Corvids								
<i>Garrulus glandarius</i>	8	5.4	35.5	16	27.2	32.4	24.3	16.2
<i>Pica pica</i>	27	18.3	130.9	17	11.1	26.7	33.1	29.1
<i>Cyanopica cyana</i>	17	11.5	113.1	38	41.4	44.1	0.0	14.4
<i>Pyrrhocorax pyrrhocorax</i>	1	0.6	4.0	2	0.0	100.0	0.0	0.0
<i>Corvus corone</i>	54	36.7	39.3	22	39.8	31.1	15.3	13.9
<i>Corvus corax</i>	105	71.4	38.5	54	26.9	30.1	18.8	24.2
Unidentified corvids	30	20.4	20.5	9	55.2	16.7	12.9	15.2
Non-corvids								
<i>Lullula arborea</i>	1	0.6	1.0	1	0.0	0.0	0.0	100.0
<i>Motacilla alba</i>	28	19.0	40.3	16	47.4	18.2	4.7	29.7
<i>Sturnus unicolor</i>	21	14.3	123.9	50	37.9	0.0	9.4	52.8
<i>Turdus merula</i>	18	12.2	14.5	12	27.8	17.7	20.6	33.9
<i>Turdus philomelos</i>	5	3.4	9.8	2	58.9	0.0	0.0	41.1
<i>Turdus viscivorus</i>	7	4.7	112.0	31	0.0	22.2	17.2	60.6
<i>Saxicola torquata</i>	2	1.3	2.0	2	100.0	0.0	0.0	0.0
<i>Fringilla coelebs</i>	6	4.0	50.3	10	72.3	27.7	0.0	0.0
<i>Erithacus rubecula</i>	3	2.0	12.6	4	65.7	0.0	0.0	34.3
<i>Lanius meridionalis</i>	7	4.7	1.7	2	10.1	38.8	30.0	21.1
<i>Phoenicurus ochruros</i>	2	1.3	7.0	2	0.0	0.0	0.0	100.0
<i>Calandrella brachydactyla</i>	1	0.6	2.0	2	0.0	0.0	100.0	0.0
<i>Galerida</i> spp.	3	2.0	1.3	2	0.0	43.1	33.4	23.5
Unidentified lark species	8	5.4	6.0	4	8.8	33.7	39.1	18.4
Unidentified passerines	79	53.7	33.9	30	35.3	25.9	13.9	25.0
Related								
<i>Upupa epops</i>	10	6.8	44.8	14	0.0	15.2	35.2	49.6
<i>Columba palumbus</i>	1	0.6	2.0	1	0.0	0.0	100.0	0.0

-0.089, Fig. 2). The elapsed time since the input of the carrion determined the number of individuals of passerine species feeding on carrion ($R^2 = 0.206$, $F_{2,677} = 89.205$, $p < 0.001$). Whereas corvids were active in greater numbers shortly after the carrion was supplied ($r = -0.132$; Fig. 3), non-corvids increased their presence as time progressed ($r = 0.110$, Fig. 3).

Regarding the effects of the characteristics of the carrion inputs on the abundance of passerines, non-corvids were significantly influenced by the format of the carrion ($F_{4,143} = 6.245$, $p = 0.001$), with carcasses divided into at least six pieces being the most frequently selected. The sub-region also modulated non-corvid abundances ($F_{2,140} = 6.326$, $p = 0.002$), with higher relative numbers in central-western Spain. No significant relationships were found with respect to the season ($F_{3,144} = 1.014$, $p = 0.389$), the scattering level of carrion pieces ($F_{2,143} = 2.069$, $p = 0.130$), the frequency of previous inputs at the

supplementary feeding point ($F_{2,142} = 1.011$, $p = 0.367$) or the provided biomass ($F_{1,141} = 2.304$, $p = 0.131$).

The abundance of corvids was influenced by the season ($F_{3,144} = 4.428$, $p = 0.005$), with a greater number of birds seen during winter inputs. When the carcasses provided were divided, corvids also occurred in greater numbers ($F_{4,143} = 6.225$, $p = 0.001$). The management regime of supplementary feeding points, as well as the supplied biomass, influenced the corvids' presence. Feeding stations with periodic and frequent inputs before the start of this experiment hosted a greater number of corvids ($F_{2,142} = 6.367$, $p = 0.002$), similar to those with a higher biomass provided ($F_{1,141} = 8.039$, $p = 0.005$). In central-western Spain a greater presence of corvids was detected ($F_{2,140} = 11.300$, $p < 0.001$). The effect of the spreading level of carrion pieces was not significant ($F_{2,143} = 1.893$, $p = 0.154$).

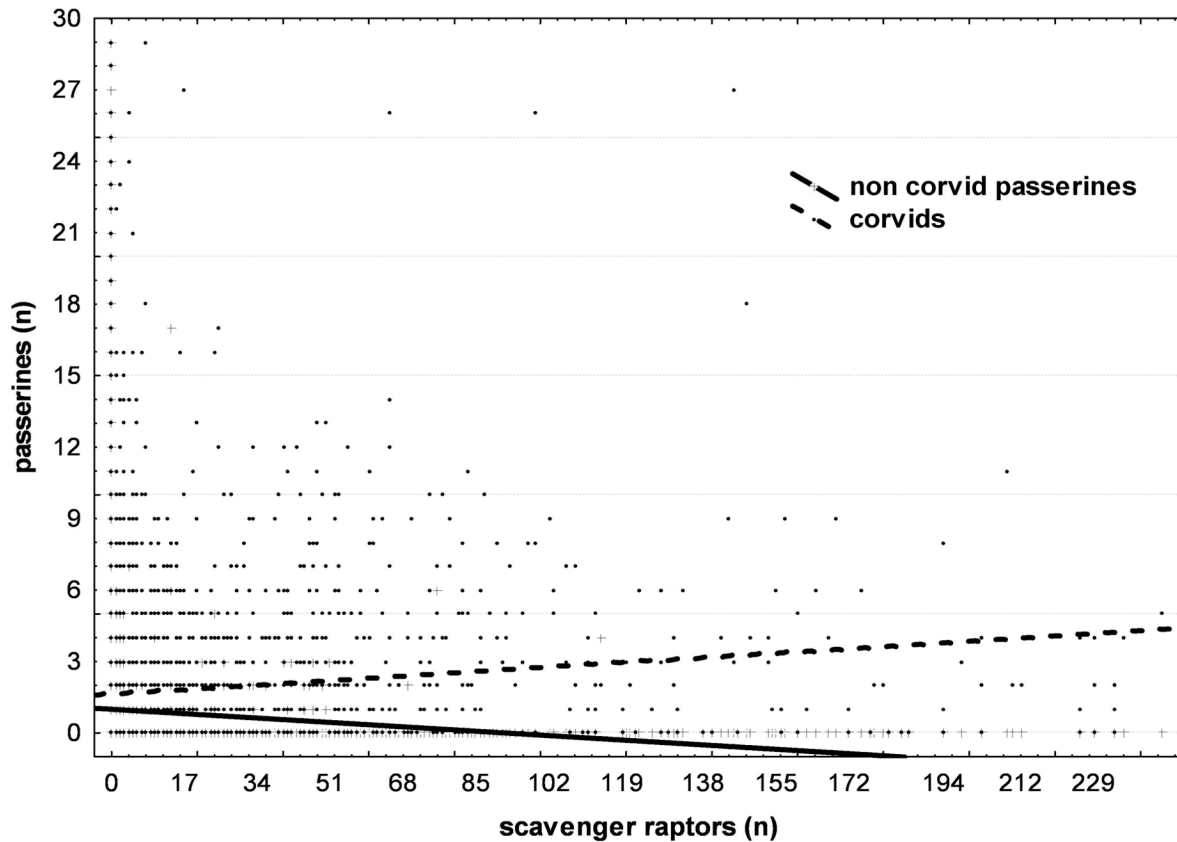


Fig. 2. Relationship between the number of scavenger raptors feeding on experimental inputs of carrion and (1) the number of non-corvid passerines (continuous line, $r = -0.089$), or (2) the number of corvids (dashed line, $r = 0.082$), simultaneously present and feeding on carrion.

Regarding monthly occurrence patterns, passerines were more abundant during the winter and summer inputs ($F_{11,132} = 3.045$, $p = 0.001$, Fig. 4) but with differences between corvids and non-corvids. The former were more abundant in the winter (December to March, $F_{11,115} = 2588$, $p = 0.005$) while non-corvids showed two peak periods, during post-breeding migration season (August to October) and during the winter (December to February, $F_{11,107} = 2.502$, $p = 0.007$, Fig. 4).

DISCUSSION

Factors affecting attendance to carcasses

Factors determining attendance to carrion inputs were different between corvids and the rest of the passerines. The initial discrimination of these two groups within the analysis of this

study, owing to differences in their scavenging performance, allowed an increase in the accuracy of the results as to the display of divergent foraging behaviors. Through observation of the recordings, corvids (except Red-billed Chough *Pyrhacorax pyrrhacorax*) consumed the soft tissues of the carcasses, while non-corvids mainly fed on arthropod larvae, nymphs and adults existing on or around the carrion. Therefore, non-corvids did not exploit the organic biomass in decomposition, but rather benefited from the high levels of arthropod productivity occurring in carrion under certain circumstances (Campobasso et al. 2001). Thus, non-scavenger passerines may be attracted to carrion through invertebrate behaviour, with their attendance to this resource based on the patterns of arthropod presence (Schoenly and Reid 1987, Watson and Carlton 2003, 2005). Other uses of the resources offered

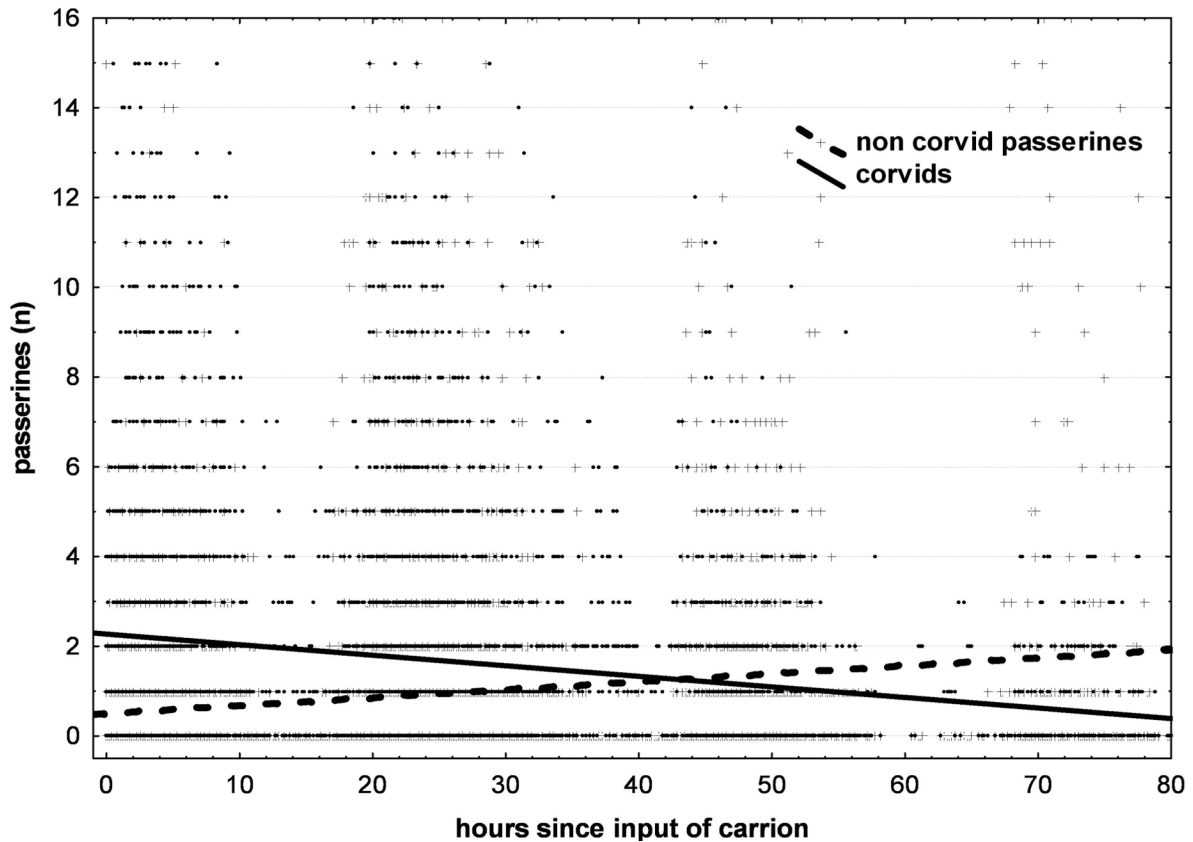


Fig. 3. Number of non-corvid passerines (continuous line, $r = 0.228$) and number of corvids (dashed line, $r = -0.380$) attending to feed on controlled inputs of carrion depending on the time elapsed since the deposit of carrion.

by carrion such as hair or wool for nest building (Riney 1951, Margalida and Bertrán 2000) were also observed. For example, red-billed choughs and ravens harvested wool from sheep carcasses during the pre-breeding period.

Non-passerines therefore showed opportunistic foraging behavior in the exploitation of resources offered by carrion, depending on various factors. The existence of carcasses divided into pieces led to a significant increase in passerine numbers as occurred with other scavenger communities in temperate forests (Selva et al. 2005), which could be due in our case to a greater presence of scavenger invertebrates in this carrion format because of the increased accessibility to soft tissues increasing both egg oviposition and feeding opportunities (Amezquita and Favila 2011, Smith and Merrick 2001). In addition, a greater abundance of passerines in

central-western Spain was noted, possibly due to the influence of the thermo-Mediterranean climate (warmer and less continental than the Pyrenean sub-region), which could lead to greater arthropod richness and abundances and to an increase in the colonization of carrion (DeVault et al. 2004, Matuszewski 2011). Meanwhile, productivity in scavenger arthropods varies between seasons, assuming a similar availability of carcasses (Campobasso et al. 2001, Watson and Carlton 2003, 2005, Battan and Salvo 2012). Non-corvid passerines attended carrion more often in the summer and winter months, coinciding with migratory and wintering periods respectively. In both of these phases of their life history, birds require a high energy intake, due to the physical exertion in both long-distance migration and withstanding harsh winter conditions in temperate climates (Alerstam

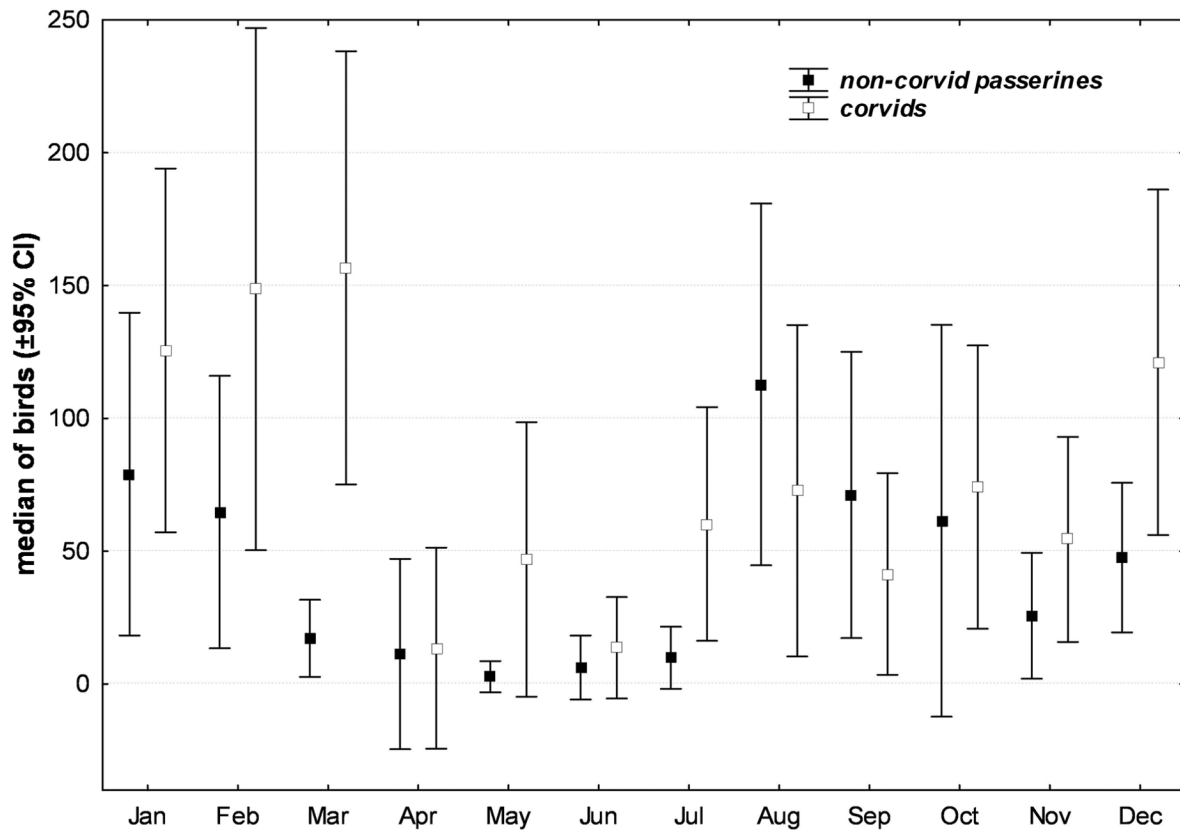


Fig. 4. Monthly distribution of the number of corvids (white) and non-corvid passerines (black) feeding on carrion, expressed as the median of birds ($\pm 95\%$ CI) recorded per input based on the sum of birds in each 10-min interval.

and Hedeström 1998, Klaassen et al. 2012). Passerines may therefore prey on arthropods either because of their occurrence and high abundances during migratory season (mainly summer) or as a resource in periods when the scarcity of other food sources is a constraint factor, as during the winter (Alerstam and Hedeström 1998, Selva et al. 2005).

Predictability of carrion presence did not lead to a greater abundance of non-corvid passerines as opposed to corvids, which more often attended feeding points with more frequent and ongoing inputs. In this sense, greater carrion predictability may lead to the more rapid consumption of carrion by vertebrate scavengers who have learned and become accustomed to the regular presence of food (Deygout et al. 2009, 2010, Donazar et al. 2010), thereby reducing the likelihood of the completion of the scavenger arthropod life cycles at carcasses (Campobasso et

al. 2001). Thus, an important issue for the conservation of endangered avian scavengers, as is the management regime of inputs in supplementary feeding points (Cortés-Avizanda et al. 2010, Moreno-Opo et al. 2010), which seems to have no direct effect on the attendance of non-corvid passerines and, consequently, on the dynamics of arthropod presence (Schoenly and Reid 1987). The continued presence of organic remains at supplementary feeding points may even improve the conservation status of endangered arthropods (Martín-Vega and Baz 2011).

Interspecific relationships

Carrion exploitation has conferred an interlinked feeding and behavioral ecology to scavenger species (Hertel 1994, Selva and Fortuna 2007, Olson et al. 2012), such that they arrange guilds depending on geographical scope. Carrion is energetically cost effective by offering a great

abundance of biomass in the absence of violent predation conflicts, but at the same time involves high competitive costs during exploitation due to its spatial and temporal unpredictability (Ruxton and Houston 2004, Barton et al. 2013). Thus, scavengers perform mutualistic-facilitatory processes for finding carrion (Jackson et al. 2008) such as intra- and inter-specific exclusion and dominance phenomena, depending on the specific hierarchical position and trophic requirements thereof (Wilmers et al. 2003b, DeVault et al. 2011, Kendall et al. 2012). Obligate scavengers with higher energy requirements, usually the larger species, monopolize the greater amount of biomass by displacing and preventing other smaller species from accessing the carrion (Shivik 2006, Blázquez et al. 2009, Cortés-Avizanda et al. 2010). On the other hand, within scavenger guilds, each species is specialized in exploiting different parts of the carcasses, such that their concurrent presence may be complementary as in the case of compatible trophic adaptations (König 1983, Hertel 1994, Olson et al. 2012).

These two issues could lead to differences in the occurrence patterns of corvids and non-corvids in our study. Namely, non-corvid passerines avoided the simultaneous presence with scavenger raptors, due to hoarding of available resources and better hierarchical abilities of raptors (DeVault et al. 2003). Furthermore, when carrion consumption was delayed the number of non-corvid passerines increased, either because of difficulties in its detection by vultures or due to other factors related to the management of the feeding point (human disturbances, presence of other feral species, availability of other alternative food resources, etc.) This might be the result of the existence of decomposing biomass for a longer time and therefore, greater arthropod productivity, which serve as potential prey (DeVault et al. 2004, Bajerlein et al. 2011). On the other hand, corvids were favored by the presence of a greater number of scavenger raptors, mainly vultures, which could indicate commensalism derived from their learning capabilities in carrion exploitation (Seed et al. 2009), as occurs between corvids and top-predators (Stahler et al. 2002, Wilmers et al. 2003a). Corvids usually benefit from small pieces and remains peripheral to carrion, which in many cases is provoked by the active ingestion of vultures and

tearing of tissues (authors' unpublished data). In this sense, after carcass detection and access, vultures quickly consume them and this, in most cases, occurs shortly after its input (Cortés-Avizanda et al. 2012). Corvids also attended to carrion as soon as possible after the input, and consumed it during these early stages, unlike non-corvids, which may have delayed their presence to avoid interfering with avian scavengers because of their lower hierarchical level (Houston 1988).

Role and management of carrion resources

The value of the resources provided by carrion has been increasingly emphasized in recent years (DeVault et al. 2003, Barton et al. 2013). Several studies have analyzed the consequences of alteration in the patterns of occurrence and quality of carcasses in the wild on the demography and behavior of different obligate scavengers (Zuberogoitia et al. 2010, Margalida et al. 2011, Margalida and Colomer 2012, Monsarrat et al. 2013). These issues have been studied mainly in avian scavengers, which are more easily observed and for which adequate basic knowledge on their ecology exists (see Donázar et al. 2009a), but have not been assessed in other species. Moreover, energy flows originating in carrion affect entire food webs, determining the dynamic stability thereof (Melis et al. 2007, Beasley et al. 2012). Such alterations in energy flows can impact the ecological balance of the scavenger communities (Selva and Fortuna 2007, Robb et al. 2008). In this sense, scavenger invertebrates and microorganism communities, or even other species of non-scavenger vertebrates such as passerines, are also dependent on human practices related to carcass management both from wildlife-through hunting, fishing or habitat degradation (Martín-Vega and Baz 2011, Grémillet et al. 2012, Ogada et al. 2012), and livestock species (Bajerlein et al. 2011, Monsarrat et al. 2013).

Carrion management should primarily consider ecological characteristics and patterns of natural occurrence of carcasses: it is a pulsed resource that emerges unpredictably in the landscape depending on wildlife abundances, seasons, human effects or even modulated by the effects of global change (Wilmers and Post 2006, Barton et al. 2013). Hence, imbalances induced on the dynamic equilibrium of carrion appearance,

both by overabundance and depletion, should be reconsidered and redirected towards the implementation of policies addressing the ecological implications of carrion presence (Robb et al. 2008, Donázar et al. 2009b, Margalida et al. 2012). These may include: (1) solving possible negative effects of carrion management on health security, population dynamics and conservation status of scavengers and non-scavengers (Selva and Cortés-Avizanda 2009, Margalida et al. 2010); (2) integrating ecological relationships within the scavengers' guild and other components of ecosystems (Olson et al. 2012); and (3) preventing the possible negative side effects on certain taxa by predation or competition (Cortés-Avizanda et al. 2010, 2012).

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LITERATURE CITED

- Alerstam, T., and A. Hedenström. 1998. The development of bird migration theory. *Journal of Avian Biology* 29:343–369.
- Amezquita, S., and M. E. Favila. 2011. Carrion removal rates and diel activity of necrophagous beetles Coleoptera: Scarabaeinae in a fragmented tropical rain forest. *Environmental Entomology* 40:239–246.
- Bajerlein, D., S. Matuszewski, and S. Konwerski. 2011. Insect succession on carrion: seasonality, habitat preference and residency of histerid beetles Coleoptera: Histeridae visiting pig carrion exposed in various forests Western Poland. *Polish Journal of Ecology* 59:787–797.
- Barton, P. S., S. A. Cunningham, D. B. Lindenmayer, and A. D. Manning. 2013. The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia* 171:761–772.
- Battan, M., and A. Salvo. 2012. Community dynamics of carrion flies and their parasitoids in experimental carcasses in central Argentina. *Journal of Insect Science* 12:8.
- Beasley, J. C., Z. H. Olson, and T. L. DeVault. 2012. Carrion cycling in food webs: comparisons among terrestrial and marine ecosystems. *Oikos* 121:1021–1026.
- Blázquez, M., J. A. Sánchez-Zapata, F. Botella, M. Carrete, and S. Eguía. 2009. Spatio-temporal segregation of facultative avian scavengers at ungulate carcasses. *Acta Oecologica* 35:645–650.
- Campobasso, C. P., G. Di Vella, and F. Introna. 2001. Factors affecting decomposition and Diptera colonization. *Forensic Science International* 120:18–27.
- Carter, D. O., D. Yellowlees, and M. Tibbett. 2007. Cadaver decomposition in terrestrial ecosystems. *Naturwissenschaften* 94:12–24.
- Cortés-Avizanda, A., N. Selva, M. Carrete, and J. A. Donázar. 2009a. Effects of carrion resources on herbivore spatial distribution are mediated by facultative scavengers. *Basic and Applied Ecology* 10:265–272.
- Cortés-Avizanda, A., M. Carrete, D. Serrano, and J. A. Donázar. 2009b. Carcasses increase the probability of predation of ground-nesting birds: a caveat regarding the conservation value of vulture restaurants. *Animal Conservation* 12:85–88.
- Cortés-Avizanda, A., M. Carrete, and J. A. Donázar. 2010. Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. *Biological Conservation* 143:1707–1715.
- Cortés-Avizanda, A., R. Jovani, M. Carrete, and J. A. Donázar. 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology* 93:2570–2579.
- Del Moral, J. C., and R. Martí. 2003. Atlas de las Aves Reproductoras de España. SEO/BirdLife-Ministerio de Medio Ambiente, Madrid, Spain.
- DeVault, T. L., O. E. Rhodes, and J. A. Shivik. 2003. Scavenging by vertebrates: behavioural, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102:225–234.
- DeVault, T. L., I. L. Brisbin, and O. E. Rhodes. 2004. Factors influencing the acquisition of rodent

- carrion by vertebrate scavengers and decomposers. *Canadian Journal of Zoology* 82:502–509.
- DeVault, T. L., Z. H. Olson, J. C. Beasley, and O. E. Rhodes. 2011. Mesopredators dominate competition for carrion in an agricultural landscape. *Basic and Applied Ecology* 12:268–274.
- Deygout, C., A. Gault, F. Sarrazin, and C. Bessa-Gomes. 2009. Modeling the impact of feeding stations on vulture scavenging service efficiency. *Ecological Modelling* 220:1826–1835.
- Deygout, C., A. Gault, O. Duriez, F. Sarrazin, and C. Bessa-Gomes. 2010. Impact of food predictability on social facilitation by foraging scavengers. *Behavioral Ecology* 21:1131–1139.
- Donázar, J. A., A. Margalida, and D. Campión. 2009a. Vultures, feeding stations and sanitary legislation: a conflict and its consequences from the perspective of conservation biology. *Munibe* 29. Sociedad de Ciencias Aranzadi, San Sebastián, Spain.
- Donázar, J. A., A. Margalida, M. Carrete, and J. A. Sánchez-Zapata. 2009b. Too sanitary for vultures. *Science* 326:664.
- Donázar, J. A., A. Cortés-Avizanda, and M. Carrete. 2010. Dietary shifts in two vultures after the demise of supplementary feeding stations: consequences of the EU sanitary legislation. *European Journal of Wildlife Research* 56:613–621.
- European Commission. 2011. Commission Regulation CE 142/2011, of 25th February, implementing Regulation EC No 1069/2009. *Official Journal of the European Union* 54:1–254.
- González-Taboada, F., C. Nores, and M. A. Álvarez. 2007. Breeding bird species richness in Spain: assessing diversity hypothesis at various scales. *Ecography* 30:241–250.
- Grémillet, D., A. Prudor, Y. le Maho, and H. Weimerskirch. 2012. Vultures of the seas: hyper-acidic stomachs in wandering albatrosses as an adaptation to dispersed food resources, including fisheries wastes. *PLoS ONE* 7:e37834.
- Harrel, F. E., K. L. Lee, and D. B. Mark. 1996. Multivariable prognostic models: issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors. *Statistics in Medicine* 15:361–387.
- Heinrich, B. 1998. Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment of the raven, *Corvus corax*. *Behavioural Ecology and Sociobiology* 23:141–156.
- Hertel, F. 1994. Diversity in body size and feeding morphology within past and present vulture assemblages. *Ecology* 75:1074–1084.
- Houston, D. C. 1988. Competition for food between Neotropical vultures in forest. *Ibis* 130:403–417.
- Ives, A. R. 1991. Aggregation and coexistence in a carrion fly community. *Ecological Monographs* 61:75–94.
- Jackson, A. L., G. D. Ruxton, and D. C. Houston. 2008. The effect of social facilitation on foraging success in vultures: a modelling study. *Biology Letters* 4:311–313.
- Jolliffe, I. T. 2002. *Principal component analysis*. Second edition. Springer-Verlag, New York, New York, USA.
- Kendall, C., M. Z. Virani, P. Kirui, S. Thomsett, and M. Githiru. 2012. Mechanisms of coexistence in vultures: understanding the patterns of vulture abundance at carcasses in Masai Mara National Reserve, Kenya. *The Condor* 114:523–531.
- Klaassen, M., B. J. Hoyer, B. A. Nolet, and W. A. Buttemer. 2012. Ecophysiology of avian migration in the face of current hazards. *Philosophical Transactions of the Royal Society B* 367:1719–1732.
- König, C. 1983. Interspecific and intraspecific competition for food among Old World vultures. Pages 153–171 in S. R. Wilbur, editor. *Vulture biology and management*. University of California Press, Berkeley, California, USA.
- Leroux, S. J., and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters* 11:1147–1156.
- Margalida, A., and J. Bertrán. 2000. Nest-building behaviour of the bearded vulture *Gypaetus barbatus*. *Ardea* 88:259–264.
- Margalida, A., D. Campión, and J. A. Donázar. 2011. European vultures' altered behaviour. *Nature* 480:457.
- Margalida, A., M. Carrete, J. A. Sánchez-Zapata, and J. A. Donázar. 2012. Good news for European vultures. *Science* 335:284.
- Margalida, A., and M. A. Colomer. 2012. Modelling the effects of sanitary policies on European vulture conservation. *Scientific Reports* 2:753.
- Margalida, A., M. A. Colomer, and D. Sanuy. 2011. Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. *PLoS ONE* 6:e20248.
- Margalida, A., J. A. Donázar, M. Carrete, and J. A. Sánchez-Zapata. 2010. Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology* 47:931–935.
- Martín-Vega, D., and A. Baz. 2011. Could the 'vulture restaurants' be a lifeboat for the recently rediscovered bone-skippers Diptera: Piophilidae? *Journal of Insect Conservation* 15:747–753.
- Matuszewski, S. 2011. Estimating the pre-appearance interval from temperature in *Necrodes littoralis* L. Coleoptera: Silphidae. *Forensic Science International* 212:180–188.
- Melis, C., N. Selva, I. Turlings, C. Skarpe, J. D. C. Linnell, and R. Andersen. 2007. Soil and vegetation nutrient response to bison carcasses in Bialowieza

- Primeval Forest, Poland. *Ecological Research* 22:807–813.
- Monsarrat, S., S. Benhamou, F. Sarrazin, C. Bessa-Gomes, W. Bouten, and O. Duriez. 2013. How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? *PLoS ONE* 8:e53077.
- Moreno-Opo, R., A. Margalida, A. Arredondo, F. F. Guil, M. Martín, R. Higuero, C. Soria, and J. Guzmán. 2010. Factors influencing the presence of cinereous vulture *Aegypius monachus* at carcasses: food preferences and implications for the management of supplementary feeding sites. *Wildlife Biology* 16:25–34.
- Moreno-Rueda, G., and M. Pizarro. 2009. Relative influence of habitat heterogeneity, climate, human disturbance, and spatial structure on vertebrate species richness in Spain. *Ecological Research* 24:335–344.
- Nowling, W. H. et al. 2008. Comparing resource pulses in aquatic and terrestrial ecosystems. *Ecology* 89:647–659.
- Ogada, D. L., M. E. Torchin, M. F. Kinnaird, and V. O. Ezenwa. 2012. Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conservation Biology* 26:453–460.
- Olson, Z. H., J. C. Beasley, T. L. DeVault, and O. E. Rhodes. 2012. Scavenger community response to the removal of a dominant scavenger. *Oikos* 121:77–84.
- Read, J. L., and D. Wilson. 2004. Scavengers and detritivores of kangaroo harvest offcuts in arid Australia. *Wildlife Research* 31:51–56.
- Riney, T. 1951. Relationships between birds and deers. *Condor* 53:178–185.
- Robb, G. N., R. A. McDonald, D. E. Chamberlain, and S. Bearhop. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in the Ecology and Environment* 6:476–484.
- Ruxton, G. D., and D. C. Houston. 2004. Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology* 228:431–436.
- Schoenly, K. G., and W. Reid. 1987. Dynamics of heterotrophic succession in carrion arthropod assemblages: discrete series or a continuum of change? *Oecologia* 73:192–202.
- Seed, A., N. Emery, and N. Clayton. 2009. Intelligence in corvids and apes: A case of convergent evolution? *Ethology* 115:401–420.
- Selva, N., B. Jedrzejewska, W. Jedrzejewski, and A. Wajrak. 2005. Factors affecting carcass use by a guild of scavengers in European temperate woodland. *Canadian Journal of Zoology* 83:1590–1601.
- Selva, N., and M. A. Fortuna. 2007. The nested structure of a scavenger community. *Proceedings of the Royal Society B* 274:1101–1108.
- Selva, N., and A. Cortés-Avizanda. 2009. The effects of carcasses and carrion dumps on the local environment communities. Pages 464–473. *in* J. A. Donazar, A. Margalida, and D. Campión, editors. *Vultures, feeding stations and sanitary legislation: a conflict and its consequences from the perspective of conservation biology*, Munibe 29 Sociedad de Ciencias Aranzadi, San Sebastián, Spain.
- Shivik, J. A. 2006. Are vultures birds, and do snakes have venom, because of macro-and microscavenger conflict? *BioScience* 56:819–823.
- Smith, R. J., and M. J. Merrick. 2001. Resource availability and population dynamics of *Nicrophorus investigator*, an obligate carrion breeder. *Ecological Entomology* 26:173–180.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. Third edition. W. H. Freeman, New York, New York, USA.
- Soler, M., and J. J. Soler. 1991. Análisis comparado del régimen alimenticio durante el periodo otoño-invierno de tres especies de córvidos en un área de simpatria. *Ardeola* 38:69–89.
- Stahler, D., B. Heinrich, and D. Smith. 2002. Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. *Animal Behaviour* 64:283–290.
- Ulrich, W., K. Komosinski, and M. Zalewski. 2008. Body size and biomass distributions of carrion visiting beetles: Do cities host smaller species? *Ecological Research* 23:241–248.
- Watson, E. J., and C. E. Carlton. 2003. Spring succession of necrophilous insects on wildlife carcasses in Louisiana. *Journal of Medical Entomology* 40:338–347.
- Watson, E. J., and C. E. Carlton. 2005. Insect succession and decomposition of wildlife carcasses during fall and winter in Louisiana. *Journal of Medical Entomology* 42:193–203.
- Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003a. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* 72:909–916.
- Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003b. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecology Letters* 6:996–1003.
- Wilmers, C. C., and E. Post. 2006. Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios. *Global Change Biology* 12:403–409.
- Wilson, E. E., and E. M. Wolkovich. 2011. Scavenging: how carnivores and carrion structure communities. *Trends in Ecology and Evolution* 26:129–135.

- Zuberogoitia, I., J. E. Martínez, A. Margalida, I. Gómez, A. Azkona, and J. A. Martínez. 2010. Reduced food availability induces behavioural changes in Griffon vulture. *Ornis Fennica* 87:52–60.
- Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2009. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14.