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Managing supplementary feeding for avian scavengers: Guidelines for optimal design using ecological criteria

Ainara Cortés-Avizanda *, Martina Carrete, José Antonio Donázar

Department of Conservation Biology, Estación Biológica de Doñana, CSIC. c/ Americo Vespucio, s/n, La Cartuja, 41092 Sevilla, Spain

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ABSTRACT

Current European sanitary laws are promoting the concentration of domestic livestock carcasses in limited locations called 'vulture restaurants' or supplementary feeding stations in order to safeguard human health. However, this type of food concentration could lead to monopolization by a few, large dominant species. Management guidelines are urgently needed to ensure that potentially less competitive and more endangered scavengers can also benefit from this resource, considering that once abundant carcasses are now absent from the field. Here, we assess factors affecting the abundance of six avian scavenger species at 17 feeding stations in northern Spain, considering aspects such as carrion availability, physiographic features, humanization, presence of heterospecifics and densities of scavengers during both winter and summer seasons. Results indicate that conditions for interspecific facilitatory processes are possible at low numbers (<100 individuals) of griffon vultures (*Gyps fulvus*). Otherwise, the other avian scavengers are excluded. In a few cases, spatio-temporal patterns of segregation become apparent. Differences in the size of carcasses supplied to feeding stations as well as the local characteristics influence the balance of species at these points and, therefore, how species of conservation concern use feeding stations. Future legislation should encourage the opening of numerous feeding stations supplied with low quantities of food to mimic the original condition of temporal and spatial unpredictability of carcasses and to maintain ecological relationships within the scavenger guild.

1. Introduction

Public health issues and subsequent sanitary laws are increasingly interacting with environmental policies mainly because of the possibility of disease transmission between wildlife and domestic species and humans (Daszak et al., 2000; Cleaveland et al., 2001). One example is the European sanitary laws approved after the outbreak of the Bovine Spongiform Encephalopathy (BSE) in late 1990s that made obligatory the removal and cremation of all livestock carcasses. Traditional practices, especially in remote areas, have included the abandonment of carcasses in the field, which have maintained complex ecological processes affecting the soil, vegetation and consumers, from invertebrate to large vertebrates (DeVault et al., 2003; Selva and Cortés-Avizanda, 2009). Avian scavengers of southern Europe and other warm and temperate Old World regions have positively responded to these practices, and have been historically dependent on livestock carcasses associated with human activities such as traditional agro-grazing practices and transhumance (Mundy et al., 1992; Donázar et al., 1996a; Olea and Mateo-Tomás, 2009).

The onset of generalized collection of carcasses is expected to have consequences for avian scavenger populations (Tella, 2001) and this has led to new regulations (EU1774/2002; EU322/2003; EU830/2005; CE 1069/2009) permitting carcasses to be left in the field to feed scavengers. In any case, legal constraints are still very important and the abandonment of dead animals is only possible in specific locations (Deygout et al., 2009; Donázar et al., 2009a,b). Thus, state and regional governments in Mediterranean countries are following a common strategy, whereby a few sites – commonly termed supplementary feeding stations or "vulture restaurants" – are supplied with carcass remains to feed vultures (Piper, 2006). While waiting for future legislations that will allow scavengers to feed again on extensive livestock carcasses, vulture restaurants currently are an urgency measure. However, in some cases the use of supplementary feeding stations may become permanent in some Mediterranean regions because the current decline of the extensive grazing practices (Donázar et al., 2009b). Because of the strong restrictions imposed by sanitary regulations, the number of these sites is estimated to be less than 20% of the formerly existing feeding places that were traditionally associated with small farms and villages (Donázar et al., 2009a). This new

* Corresponding author. Tel.: +34 954466700; fax: +34 954621125.
E-mail addresses: ainara@ebd.csic.es (A. Cortés-Avizanda), martina@ebd.csic.es (M. Carrete), donazar@ebd.csic.es (J.A. Donázar).

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scenario of food concentration is promoting large aggregations of the largest and most common species, the griffon vulture *Gyps fulvus* (see below), and could be affecting carcass consumption by other less abundant, smaller species of great conservation concern belonging to the same guild or functional group (sensu Blondel, 2003).

The dynamics of scavenging processes, and their role in the function of food webs and ecosystems, are strongly dependent on the concurrence of specialist and facultative scavengers, and on the competitive processes in which they are involved (DeVault et al., 2003). Old World scavengers share a common food resource (i.e., carrion; Hertel, 1994; Hertel and Lehman, 1998) and have evolved particular morphological and/or behavioural skills that allow their coexistence through an ordered resource-partitioning process (König, 1983; Houston, 1988). Facilitatory and/or competitive processes seem to take place according to the species and the number of individuals present at a carcass. In particular, smaller species would benefit from the presence of larger ones (mainly vultures of the *Gyps* genus) that open tough skins and increase the overall availability of resources (facilitatory processes; Kruuk, 1967; König, 1974). However, when larger and dominant species greatly outnumber the others, a monopolization of resources may occur (Mönkkönen et al., 2004). Consequently, guidelines aimed at avoiding these imbalances in the use of supplementary feeding stations are urgently needed to sustain healthy populations of scavengers as well as to maintain ecological and evolutionary processes.

The aim of this paper is to explore some potential ecological consequences of the implementation of the new European sanitary legislation of carcass removal and concentration on the avian scavenger guild. Specifically, we evaluate the use made by six scavenger species (the griffon vulture *G. fulvus*, the Egyptian vulture *Neophron percnopterus*, the bearded vulture *Gypaetus barbatus*, the red kite *Milvus milvus*, the black kite *Milvus migrans*, and the common raven *Corvus corax*) of 17 supplementary feeding stations that differ in their local characteristics and management (mainly in terms of time, quantity, and type of food provided). Taking into account the information available on the guild structure, the population size of scavengers in the study area (see below), and the foraging behaviour of each species, we hypothesize that: (1) large aggregations of griffon vultures, the largest and most abundant scavenger, would inhibit suitable conditions for facilitatory processes, reducing the abundance of other, smaller scavengers at these sites, and (2) features such as geographic location, and availability and type of food supplied to feeding stations would favour their use by some species at the expense of others. Under the first hypothesis, we predict that abundances of griffon vultures should be negatively related to the abundance of the other scavengers consequently reducing the diversity of the guild. Under the second hypothesis, we predict that griffon vultures, a large sized species with well-developed social foraging behaviour (Houston, 1983), would use feeding stations with abundant large carcasses, whereas medium and small sized carrion eaters would use feeding stations supplied with smaller-sized carrion.

2. Materials and methods

2.1. Scavenger species and populations in the study area

The study was performed in a 10,000 km^2 area located in Northern Spain (Fig. 1), where large local densities of scavengers have been reported. The breeding population of griffon vultures (ca. 10,500 g, resident) is around 2400 pairs (ca. 11% of the Iberian population) and, mainly during summer, co-exists with hundreds of immature birds that aggregate at communal roosts (Del Moral and Martí, 2001; authors' unpublished data). Egyptian vultures (ca. 2000 g; migratory) occupy 380 breeding territories (ca. 30% of the Iberian population) and there are six large communal roosts that may attract, during the summer, up to 200 birds from a wide geographic area (Donázar et al., 1996b; author's unpublished data). Bearded vultures (ca. 6000 g; resident) occupy eight breeding territories (ca. 10% of the Iberian population) in the western part of the Pyrenees (Margalida and Heredia, 2005). Finally, there are around 300 breeding pairs (10% of the Iberian population) of red kites (ca. 1000 g; resident), as well as over 3000 wintering individuals (Viñuela et al., 1999; Gorosti, 2007). No reliable information is available for black kites (ca. 800 g, migratory) and common ravens (ca. 1100 g, resident), although they seem to be abundant in the study area and there are probably hundreds of breeding pairs, as well as important winter and summer communal roosts (Campión, 2004; authors' unpublished data).

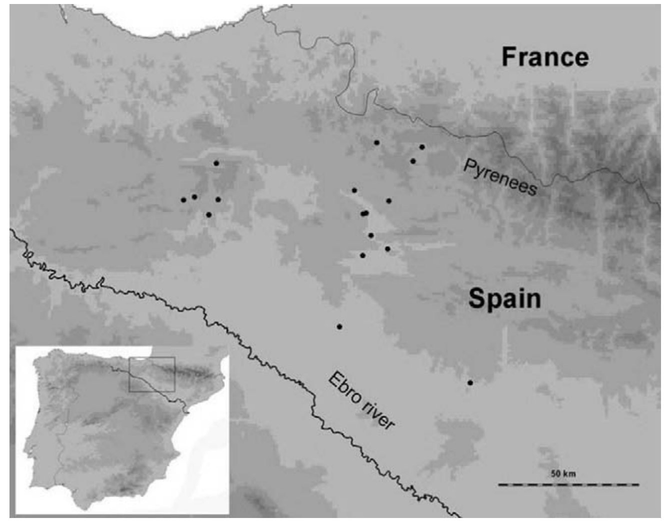

Fig. 1. Study area showing the location of the monitored feeding stations.

2.2. Field procedures

We monitored 17 supplementary feeding stations during the summer of 2005 (n = 16) and winter of 2005–2006 (n = 15). Observations were concentrated during the central months of each season (June–August and December–February) to maximise the presence and abundance of species with marked seasonal changes in abundance (mainly Egyptian vultures and black and red kites, see above). Monitoring length varied between 10–17 days (winter) and 5–24 days (summer). The visits were not simultaneous and were performed from 9 a.m. to 4 p.m. and from 8 a.m. to 8 p.m. during winter and summer, respectively. All the surveys were conducted under good weather conditions permitting foraging activities of the studied species. During each visit, we recorded every 20 min (our sampling unit) individual presence and abundance for each species at the feeding stations and in the immediate surroundings (ca. 200 m). The total numbers of censuses undertaken were 427 in winter and 407 in summer. Although the proximity in time between censuses (20 min) could suggest that the observations were not independent, the activity at feeding stations is very dynamic, with continuous changes in the number of individuals because of the incessant arrivals and departures of birds (authors' unpublished data). To reduce some potential spatial autocorrelation in the data set and to control for this non-independence, we fitted "Date" as a random factor in the analytic procedures (see below).

Data were recorded from a vehicle using binoculars (10× 40) and telescopes (20–60×) fitted to car windows at a minimum distance of 300 m to avoid interfering in the activity of birds.

2.3. Analytical procedures

2.3.1. Prediction 1: abundances of griffon vultures should be negatively related to abundances of the other scavengers and guild diversity

We used Principal Component Analyses (PCA, Digby and Kempton, 1987) to detect association patterns between griffon vultures and the other studied species. Data were previously log (+1) transformed to obtain normality. A Varimax rotation was applied. Additionally, we used Generalized Linear Mixed Models (GLMM, McCullagh and Searle, 2000; SAS Institute Inc., 2009) to assess the effects of the number of griffon vultures on the diversity of species using feeding stations (link function: identity, error distribution: normal). Diversity was calculated using the Shannon index (Magurran, 2003). Subsequently, we explored the relationship between the abundance of griffon vultures and that of the other smaller species (link function: logarithmic, error distribution: Poisson) to detect interspecific differences. We included the time of day at which censuses were performed (morning: <12 a.m.; afternoon: >12 a.m.) to detect temporal segregation between species. "Feeding station" and "Date" were fixed into models as random terms to control for spatial and temporal heterogeneity as well as to reduce non-independence of the data.

2.3.2. Prediction 2: feeding station features may favour their differential use by some species

We used Generalized Linear Models (GLM, McCullagh and Nelder, 1989; SAS Institute Inc., 2009) to identify those characteristics of feeding stations affecting their differential use by scavengers (see below and Table 1). We only considered feeding stations with more than 5 positive surveys (i.e., at least one bird of the study species present; winter $n = 15$; summer $n = 12$). As response variables we considered: (i) the relative presence of each focal species, which was assessed as the proportion of positive surveys out of the total number of surveys performed (link function: logit, error distribution: binomial) (ii) the diversity of small and medium-sized scavengers, excluding griffon vultures (link function: identity, error distribution: normal).

2.3.3. Explanatory variables

Table 1 summarizes all explanatory variables used to model species relationships. The availability of large or small carcasses at each feeding station was estimated by averaging the weight (in kg) of fresh carcasses observed during each census. The mean weight of each species of livestock was determined on the basis of values obtained from local farmers: horse: 300 kg, cow: 350 kg, donkey: 150 kg, calf: 150 kg, sheep and goat: 35 kg, lamb: 10 kg, wild boar: 60 kg, pig: from 10 to 150 kg, according to the size of the animal; dog: 25 kg, chicken and rabbit: 1–2 kg, slaughterhouse remains: from 2 to 20 kg.

Physiographic characteristics (slope) were derived from a digital elevation model (DEM) with a spatial resolution of 100 m. In the study area slope reflects confidently the degree of humanization (villages and infrastructures are concentrated in flat areas; see Campión (2004)). The abundance of scavengers in the area was estimated using information on their population sizes and distributions. We estimated the number of breeding pairs of every studied species within a radius around each feeding station representing the area of average movements of birds during foraging activity (Ceballos and Donázar, 1988; Donázar, 1993; authors' unpublished data). For Egyptian vultures and red kites, we also considered their numbers at communal roosts within a radius of 15 km and 8 km of the feeding stations, respectively. These figures correspond to the movements of radio-tracked individuals of both species (De Pablo, 2004; Gorosti, 2007; authors' unpublished data). Because there is no information on the location of breeding territories of red and black kites we used predictive models of the probability of presence of foraging birds based on landscape features (surface of open areas, proximity to rivers and altitude) determined by the results of previous studies modelling habitat selection by these species in the same study area (Campión, 2004). No information is available on the spatial distribution of breeding pairs or roost sites of common ravens in the study area.

2.3.4. Model fitting

Models were fitted by using a forward stepwise procedure (Donázar et al., 1993) that resulted in multivariate models in which only significant effects ($p < 0.05$) were retained. Final models were those explaining the highest percentages of the initial deviance.

3. Results

3.1. Carcass availability and seasonal use of feeding stations by scavengers

Feeding stations were supplied with more carcasses in winter than in summer (Fig. 2). Large carcasses (>30 kg) dominated

Table 1
Variables used to explain the abundance of avian scavengers in feeding stations in Northern Spain.

Food supply	
Large carcasses	Percentage of large carcasses (items > 30 kg)
Small carcasses	Percentage of small carcasses (items < 30 kg)
Structural features	
Slope	Indicates topographic irregularity as the number of 20 m contour lines cut by a cross of 1 × 1 km, centred on the feeding station
Populations of scavengers potentially exploiting the feeding station	
Colonies GV(20)	Number of breeding pairs of griffon vultures in a radius of 20 km from feeding stations
Territory EV(8)	Number of breeding territories of Egyptian vultures in a radius of 8 km from feeding stations
Roost EV	Maximum number of Egyptian vultures in summer roost sites in a radius of 15 km from feeding stations
Territory BV	Distance to the nearest breeding pair of bearded vulture (m)
Roost RK	Maximum number of red kites in winter roost sites in a radius of 15 km from feeding station
Presence RK	Probability of presence of breeding red kites during breeding season (summer)[a]
Presence BK	Probability of presence of breeding black kites during breeding season (summer)[a]
Abundance of competitors at feeding stations	
Abundance GV	Median abundance of griffon vultures present at the feeding station during census

[a] On the basis of predictive models of the probability of presence of foraging birds based on landscape features (surface of open areas, proximity to rivers and altitude) determined by the results of previous studies modelling habitat selection by these species in the same study area (Campión, 2004).

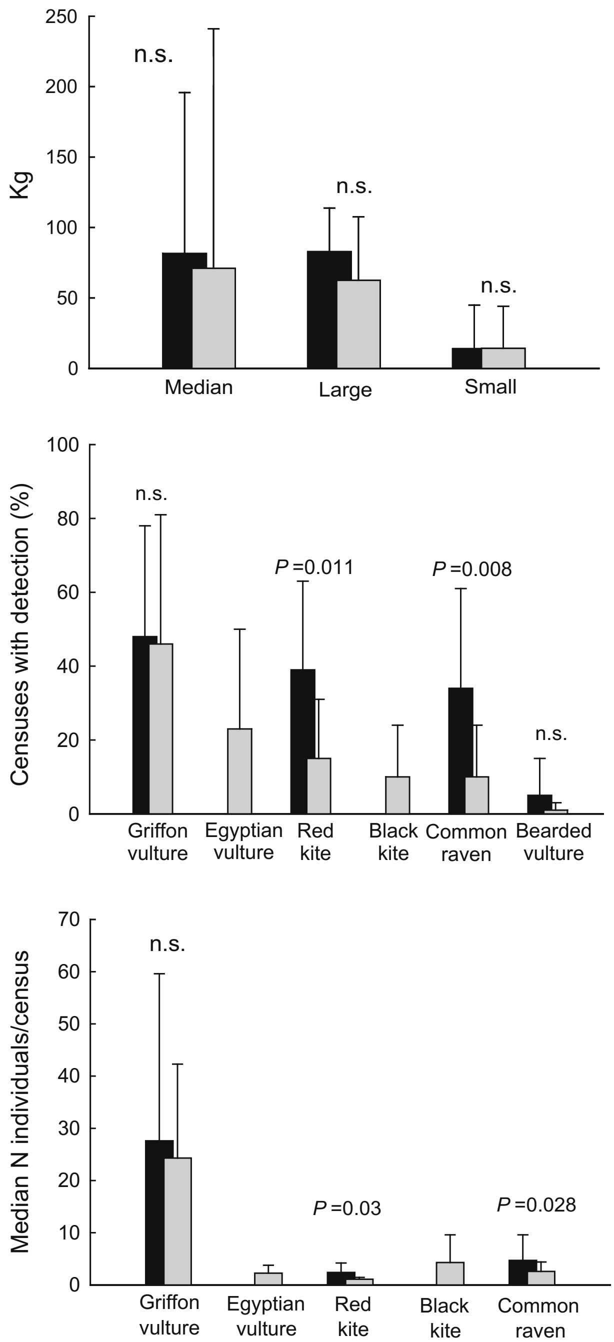

Fig. 2. Seasonal variability in resource availability and scavenger presence in the studied feeding stations (winter: black, $n = 15$ stations; summer: grey, $n = 16$ s.). The means and standard errors shown were calculated on the basis of median values for each station. Significant differences between winter and summer are shown; n.s. = not significant.

(86%) and the relative contribution of large and small items did not change between seasons. Resident scavengers visited a larger proportion of feeding stations during winter (griffon vulture and red kite: 100% vs. 56%; bearded vulture: 26% vs. 12%, and common raven: 87% vs. 62%). Despite these trends, seasonal differences in the frequency of surveys with positive contacts and the median number of individuals were only significant for red kites and common ravens (Fig. 2). Egyptian vultures and black kites, both summer visitors, used a similar proportion of feeding stations (56%).

3.2. Hypothesis 1: large aggregations of the largest and most abundant scavenger would reduce the abundance of the other, smaller scavengers and guild diversity

Field data suggested that at huge concentrations of griffon vultures (e.g. more than 200 individuals), small body size scavengers were almost absent from feeding stations (Fig. 3). This pattern seemed to be the same in the two sampled seasons. Multivariate analyses (PCAs) partially supported this idea. In winter, when the largest abundances of griffon vultures were recorded, we found no association between this species and the other scavengers (Table 2). During this season, Factor I of the PCA (37.7% of variance) reflected that red kites and common ravens were largely associated, while griffon vultures (Factor II, 24.3% of variance) and bearded vultures (Factor III, 23.0% of variance) did not show association with any other species. In summer, however, there was a positive association between griffon and Egyptian vultures (Factor II, 22.8% of variance). Small scavengers such as red and black kites and common ravens were also associated (Factor I, 23.7% of variance) while the bearded vulture remained as a solitary feeder (Factor III, 16.0% of variance).

After controlling for feeding station and date as random terms, wintering abundances of red kites at feeding stations were significantly higher during the afternoon ($F_{1,184} = 12.29$, $p = 0.0006$), whereas griffon vultures visited feeding stations mainly during the morning ($F_{1,206} = 12.16$, $p = 0.0006$). This result supports a negative relationship between both species which is maintained through a temporal segregation pattern. The abundances of medium to small-sized scavengers were not related to the abundance of griffon vultures. However, the overall diversity of the guild at feeding stations was lower when the number of griffon vultures increased (winter: $F_{1,122} = 22{,}26$, $p < .0001$; summer: $F_{1,88} = 43.99$, $p < .0001$, Fig. 4).

3.3. Hypothesis 2: feeding station features may favour their differential use by some species

No significant models were obtained to explain changes in the global diversity of small to medium-sized scavengers at feeding stations. However, the relative presence (frequency of censuses with presence) of each species was largely explained by physiographic characteristics (slope) (Table 3). Feeding stations placed in rugged areas received more visits of bearded vultures whereas common ravens, black kites, griffon and Egyptian vultures used places located in flat areas. The distribution and abundance of these scavenger populations also affect the use of feeding stations. Egyptian and bearded vultures preferentially used feeding stations placed near their breeding territories and communal roosts, while griffon vultures more intensively used feeding stations far from their breeding colonies. During summer (breeding season), red kites used those sites placed in areas with habitat characteristics showing high probabilities of being used in foraging activities significantly more than other sites (Table 3).

Availability of food resources was also related to the use of feeding stations by scavengers. Larger numbers of small scavengers such as red kites and common ravens were observed in feeding stations supplied with small carcasses. Conversely, Egyptian vultures showed a positive association with the availability of large carcasses (Table 3). Finally, the relative presence of red kites was negatively related to the average abundance of griffon vultures at feeding stations.

4. Discussion

Avian scavengers are charismatic birds that have always held a prominent place in public consciousness as a result of their close,

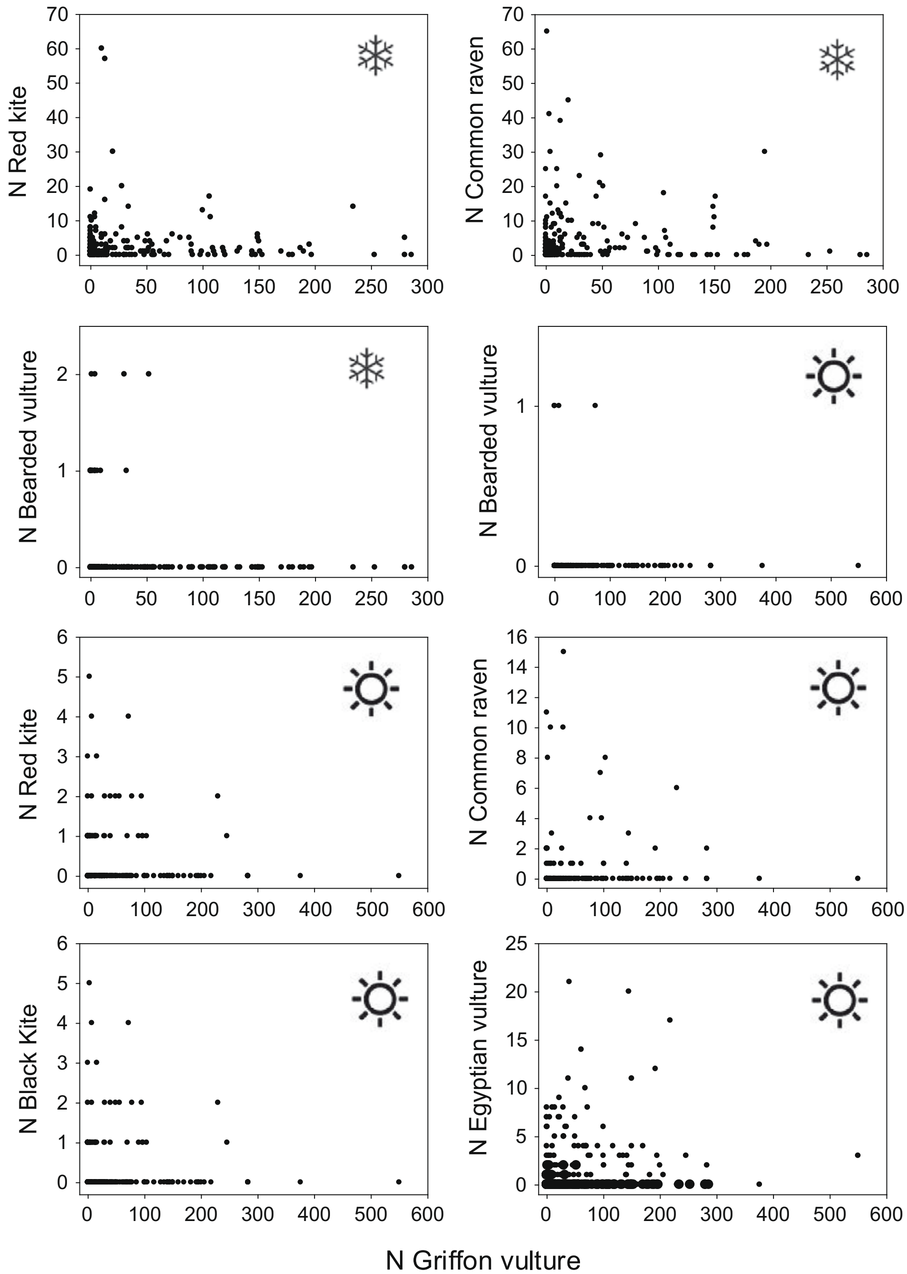

Fig. 3. Abundance of small and medium-sized scavengers in relation to the total number of griffon vultures present at feeding stations in winter and summer.

long-standing relationship with human activities (Houston, 2001) and the interest they engender in developed societies (Becker et al., 2004). Nevertheless, despite the time and money invested by conservation managers and governments, most of the world's avian scavengers are undergoing a serious decline (BirdLife, 2004). The creation of the so-called 'vulture restaurants' is a common feature of many conservation programmes and in Europe now more than ever supplementary feeding may be the only way of providing these birds with sufficient food (Donázar et al., 2009b). Within this context it is important to make sense of the overall situation and here we present a number of guidelines as to how these supplementary feeding stations could be re-designed and managed in order to guarantee the efficiency of the conservation measures that target avian scavengers. These birds interact closely and as such should be treated as a single group and not on a species-by-species basis (Mills et al., 1993; Soulé et al., 2005; Oro et al., 2009).

4.1. Features of supplementary feeding stations and their use by scavengers

Our results show that birds react in a great variety of ways to supplementary feeding stations due to their scattered locations and the complex effects of factors operating on local scales. We tried to capture this variation in our analyses by characterizing the features and other variables associated with management and the species that use feeding stations (see Section 2 for details). As a first step, and because it is well-known that prey-size segregation favours coexistence within carnivorous (Begon et al., 2006) and scavenger guilds (Houston, 1983; König, 1983; but see Margalida, 1997), we aimed to use carcass size as an easily controllable tool that would allow us to focus on the species of greatest conservation concern. However, we found that griffon vultures did not prefer feeding stations supplied with large carcasses, probably because

Table 2
Loadings of the numbers of individuals of each scavenger species on the first three principal components extracted from a correlation matrix. Bold numbers indicate loadings above (below) 0.5 (−0.5).

	Component		
	I	II	III
	Winter		
% Variance	37.7	24.3	23.0
% Cumulative	37.7	62.0	85.0
Griffon vulture	.393	**−.785**	.452
Bearded vulture	−.441	.378	**.809**
Red kite	**.749**	.403	−.017
Common raven	**.772**	.224	.249
	Summer		
% Variance	23.7	22.8	16.0
% Cumulative	23.7	46.5	63.1
Griffon vulture	−.297	**.617**	−.305
Egyptian vulture	.125	**.859**	.059
Bearded vulture	−.052	−.067	**.912**
Black kite	**.660**	.362	.114
Red kite	**.705**	−.200	.065
Common raven	**.615**	−.038	−.302

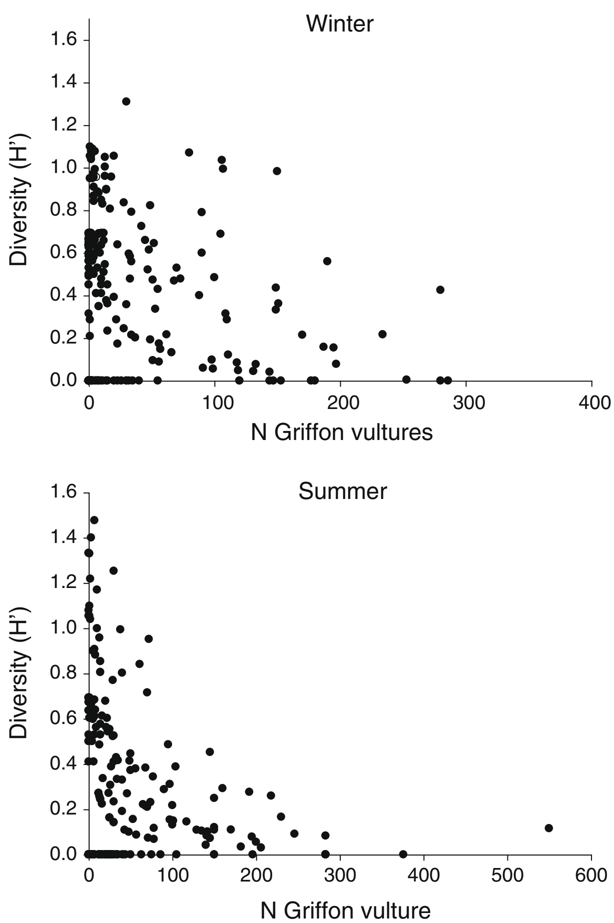

Fig. 4. Diversity of species at feeding stations in relation to the abundance of griffon vultures present both in winter and summer.

of the sheer size of the griffon vulture population in the study area (see Section 2) that causes these birds to consume food items that would otherwise be the exclusive resource of smaller species (Donázar et al., 2010). The remaining scavenger species are much scarcer and are not constrained by population size and show clear preferences for carcasses of different dimensions: Egyptian vultures preferred feeding stations supplied with large carcasses (see also Meretsky and Mannan, 1999), whereas red kites and common ravens relied on much smaller items. Consequently, carcass-size manipulation may be a valuable tool for directing supplementary feeding towards species of interest. The extremely dissimilar sizes of the scavenger populations in the study area, largely dominated by griffon vultures, would preclude the effective use of this type of measure there, although this scenario may be more appropriate in other regions with more balanced scavenger populations.

The spatial position of the feeding station must also be taken into account in any attempt to increase the probabilities of use by breeding threatened species. This is particularly true for bearded vultures and red kites. In our study we found that both species were more commonly detected at feeding stations in areas with favourable characteristics for their foraging activities: in the former this means rugged areas near breeding territories and in the latter mid-altitude areas with landscape mosaics. The consistency of our results regarding the large-scale patterns of habitat selection in these species (Donázar et al., 1993; Campión, 2004) suggests that these preferences are not merely the product of a population response to a new trophic resource, as has been found on other occasions (Carrete et al., 2007; Benítez et al., 2009).

Finally, we found a preference of some scavengers (i.e., griffon and Egyptian vultures, black kites, common ravens) for those feeding stations placed in flat intensively humanized areas that may reflect the indifference of scavengers towards humans derived from the increasing respect for these birds enshrined in the legal protection established in the 1970s (Morillo and Gómez-Campo, 2000). Nonetheless, different results have been found in other region of Europe (Gavashelishvili and McGrady, 2006), which suggests that the response of scavengers to the humanization of the surroundings of feeding stations is probably dependent on historical local factors. Therefore, we encourage the carefully studied of the humanization tolerance of local populations of focal species before conservation programmes are enacted.

4.2. Interspecific relationships determine the use of feeding stations

In their original conception, supplementary feeding stations ('vulture restaurants') were devised as a general tool for the conservation of scavenger populations, being applicable to a number of species with differing feeding and life-history strategies (Wilbur and Jackson, 1983; Houston, 1987; Brown, 1990; Mundy et al., 1992; Piper, 2006; Carrete et al., 2006; Gilbert et al., 2007; Oro et al., 2008). Vultures and associated facultative scavengers, however, are members of guilds composed of strongly interacting species (Hertel, 1994). In particular, the larger species' ability to locate carcasses is improved by the behaviour of smaller scavengers (Buckley, 1996; Jackson et al., 2008), while smaller species benefit from the opening up of carcasses by large vultures (König, 1983). Our results show a negative relationship derived from griffon vulture abundances, demonstrating that the occurrence of the number of species – and thus guild diversity – is only high when there are fewer than 100 griffon vultures present, a similar maximum figure to that found around ungulate carcasses placed experimentally and unpredictably in the wild (authors' unpublished). Consequently, and as has been observed in other interspecific competition scenarios (Petren and Case, 1996; Kieseecker et al., 2001), large aggregations of feeding individuals (up to 600 birds) of the dominant griffon vulture do not provide a framework that will satisfy the requisites of complex interspecific patterns like facilitation processes. When numbers are lower, however, some associations suggesting the maintenance of facilitation appear similar to that observed between griffon and Egyptian vultures (although large groups of Egyptian vultures only occur when there are fewer than 200 griffons present).

Table 3
Effects of characteristics of feeding stations on the frequency of positive counts of focal scavengers.

Response variable	Winter			Summer		
	Explanatory variable	*Chi-square*	*P*	Explanatory variable	*Chi-square*	*P*
Griffon vulture	− Slope	55.70	<.0001	− Slope	44.34	<.0001
				− Colonies GV(20)	9.60	0.019
Red kite	+ Small carcasses	6.88	0.0087	+ Presence RK	17.70	<.0001
	− Abundance GV	4.22	0.0401	+ Small carcasses	19.17	<.0001
Common raven	+ Small carcasses	11.80	<.0001	No model		
	− Slope	28.02	0.0006			
Bearded vulture	+ Slope	17.45	<.0001			
	+ Small carcasses	11.77	0.0006			
	− Territory BV	22.56	0.0001			
Egyptian vulture				− Slope	66.14	<.0001
				+ Large carcasses	5.21	0.0224
				+ Roost EV	4.66	0.0309
Black kites				− Slope	4.76	0.0291

Only significant models ($P < 0.05$) are shown. Symbols indicate the type of response (+: linear and positive; −: linear and negative).

When using these feeding stations small and medium-sized avian scavengers may avoid direct interspecific interaction with griffon vultures by temporal segregation, as has been seen in other pairs of species with similar ecological requirements (Cody, 1974; Carothers and Jaksić, 1984; Moril and Boydl, 2004; Begon et al., 2006; Blázquez et al., 2009). Thus, during winter, when the availability of alternative prey is low, red kites avoid co-occurring temporally with griffon vultures by using feeding stations in the afternoon. During this period soaring conditions are unfavourable for vultures and they return earlier to their breeding or roosting sites. This finding may provide a basis for a guideline: small scavengers may benefit from food supplied when griffon vultures are less active. Thus, we propose that, given the possible disappearance of facilitatory processes, diversifying the time at which carrion is left at feeding sites may be an efficient way of avoiding direct competition.

4.3. Future prospects for management decisions in conservation

In the long term it is desirable that legal dispositions be passed in order to ensure that carcasses generated by extensive livestock production (i.e., those that fulfil all mandatory sanitary requisites) remain in the field. This scenario would recreate the type of carrion availability that occurred up to quite recently in Mediterranean landscapes with traditional agricultural/livestock production (Donázar et al., 1996a; Margalida et al., 2007; Olea and Mateo-Tomás, 2009). The reality, however, is that despite the fact that the restrictive European sanitary legislation that obliges all livestock carcasses to be removed from the wild (EU999/2001) has been complemented by a series of regulations that allow supplementary feeding to be used as a strategy for the conservation of avian scavengers in southern Europe (EU1774/2002; EU322/2003; EU830/2005; CE 1069/2009), the implementation of these policies at the local level is promoting the concentration of carcasses at just a few sites or 'vulture restaurants'. It is logical to assume that this situation is not going to change in the short or mid-term and that feeding stations will remain as a key management tool for endangered scavengers. Therefore, the management of supplementary feeding stations must improve, as much from a sanitary point-of-view (Blanco et al., 2006; Lemus et al., 2008) as from the technical standpoint of how to effectively resolve in situ questions that range from the actual site of the feeding station to the management of the carrion provided.

Our study provides for the first time clear guidelines that will help managers favour species that do not act independently but work as part of a guild that exploits similar resources. Modern conservation premises encourage not only the conservation of single species and populations but also of ecological and evolutionary processes involving complex species interactions (Soulé et al., 2005). Thus, our findings will help to avoid undesirable consequences deriving from strong interspecific hierarchies that can lead to the monopolization of resources by dominant species as a result of its size and degree of sociability and aggressiveness. Management actions should be directed towards the creation of a chain of feeding stations supplied sporadically with food, which would thus avoid the concentration of resources in just a few places (see also Deygout et al., 2009). Other important aspects to take into account include: (a) the need to provide small carcasses, which will benefit the smaller facultative scavengers; (b) the importance of providing food at times at which the dominant species, the griffon vulture, is absent; and (c) that the location of feeding stations be studied carefully in order to maximise the possibility of use by certain species with clear patterns of habitat selection. These kinds of recommendations have begun to be used in the 'vulture restaurants' in Spain that have been specifically created to aid the region's endangered vulture populations (Benítez et al., 2009; Margalida et al., 2009; Moreno-Opo et al., 2010). It is worth noting that our approach may also be applicable to other regions of the world and, in particular, to large areas of Africa, the Middle East and Asia (Green et al., 2004; Shultz et al., 2004; Thiollay, 2006; Koenig, 2006) where scavenger species are in sharp decline and where scavenger guilds have similar species composition and/or structures (gregarious specialists of the genus *Gyps* and a broad range of more facultative species, König (1983), Hertel (1994), Hertel and Lehman (1998)).

The management of 'vulture restaurants' must be regarded as part of a dynamic system whose creation and management must be constantly monitored in order to detect any indications that will give rise to new strategies and techniques that will be of use in the future. Through exhaustive field monitoring managers can learn about the processes occurring at vulture restaurants and thus be in a position to design new conservation measures in accordance with any new conditions and constraints that may arise. It is to be expected that, due to their life strategies, the various species involved will not respond in the same way to management measures, and also that responses will vary over space and time. In our study system, the dominant species, the griffon vulture, has enjoyed populational growth rates of almost 500% in recent decades (Del Moral and Martí, 2001) – way above those of other species – that have not occurred in other areas of Europe (see reviews in Donázar et al. (2009a)). Managers must regard the supplementary feeding of scavengers in 'vulture restaurants' as a valuable conservation tool in cases in which the maintenance of populations purely on the basis of natural resources and carcasses derived from extensive grazing is in jeopardy, and as a management tool that can be aimed at satisfying specific objectives. In this context and in a dynamic environmental and legislative scenario, the active adaptive management of supplementary feeding is essential if we are to learn about the effectiveness of these conservation decisions (McCarthy and Possingham, 2007; Possingham et al., 2001).

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References

Becker, N., Choresh, Y., Inbar, M. 2004. A bio-economic valuation of protecting vultures: estimating the economic benefit of viewing vultures (*Gyps fulvus*) and some policy implications of valuation techniques. In: Paper presented at the Conference ''Economics and the analysis of Biology and Biodiversity'', 2–3 September 2004. Kings College, Cambridge, UK.

Begon, M., Townsend, C.R., Harper, J.L., 2006. Ecology: from Individuals to Ecosystems, fourth ed. Blackwell Publishing, Malden, MA.

Benítez, J.R., Cortés-Avizanda, A., Ávila, E., García, R., 2009. Effects of the creation of a supplementary feeding station for the conservation of Egyptian vulture (*Neophron percnopterus*) population in Andalucia (southern Spain). In: Donázar, J.A., Margalida, A., Campión, D. (Eds.), Vultures Feeding Stations and Sanitary Legislation: a Conflict and its Consequences from the Perspective of Conservation Biology. Sociedad de Ciencias Aranzadi San Sebastián, Spain, pp. 276–291.

BirdLife International, 2004. Birds in the European Union: a Status Assessment. BirdLife International. Wageningen, The Netherlands.

Blanco, G., Lemus, J.A., Grande, J., 2006. Faecal bacteria associated with different diets of wintering red kites: influence of livestock carcass dumps in microflora alteration and pathogen acquisition. Journal of Applied Ecology 43, 990–998. doi:10.1111/j.1365-2664.2006.01200.x.

Blázquez, M., Sánchez-Zapata, J.A., Botella, F., Carrete, M., Eguía, S., 2009. Spatio-temporal segregation of facultative avian scavengers at ungulate carcasses. Acta Oecologica 35, 645–650. doi:10.1016/j.actao.2009.06.002.

Blondel, J., 2003. Guilds or functional groups: does it matter? Oikos 100, 223–231.

Brown, C.J., 1990. An evaluation of supplementary feeding for Bearded Vultures and other avian scavengers in the Natal Drakensberg. Lammergeier 41, 30–36.

Buckley, N.J., 1996. Food finding and the influence of information, local enhancement, and communal roosting on foraging success of North American vultures. Auk 113, 473–488.

Campión, D., 2004. La fragmentación del hábitat mediterráneo y su efecto sobre la distribución, densidad de población y conservación de las poblaciones de aves de presa. PhD thesis, Universidad Autónoma de Madrid, Madrid, Spain.

Carothers, J.H., Jaksić, F.M., 1984. Time as a niche difference: the role of interference competition. Oikos 42, 403–406.

Carrete, M., Donázar, J.A., Margalida, A., 2006. Density-dependent productivity depression in Pyrenean bearded vultures: implications for conservation. Ecological Applications 16, 1674–1682. doi:10.1890/1051-076.

Carrete, M., Grande, J.M., Tella, J.L., Sánchez-Zapata, J.A., Donázar, J.A., Díaz-Delgado, R., Romo, A., 2007. Habitat, human pressure, and social behaviour: partialling out factors affecting large-scale territory extinction in an endangered vulture. Biological Conservation 136, 143–154.. doi:10.1016/j.biocon.2006.11.025.

Ceballos, O., Donázar, J.A., 1988. Actividad, uso de espacio y cuidado parental en una pareja de alimoches (*Neophron percnopterus*) durante el periodo de dependencia de los pollos. Ecología 2, 275–291.

Cleaveland, S., Laurenson, M.K., Taylor, L.H., 2001. Diseases of humans and their domestic mammals: pathogen characteristics, host range and the risk of emergence. Philosophical Transactions of the Royal Society B 356, 991–999. doi:10.1098/rstb.2001.0889.

Cody, M.L., 1974. Competition and Structure of Bird Communities. Princeton University Press, Princeton, NJ.

Daszak, P., Cunningham, A.A., Hyatt, A.D., 2000. Emerging infectious diseases of wildlife, threats to diversity and human health. Science 287, 443–449. doi:10.1126/science.287.5452.443.

De Pablo, F., 2004. Bases ecológicas para la elaboración de un plan de recuperación de milanos reales (*Milvus milvus*) en Menorca. PhD thesis, Universidad de Barcelona, Barcelona, Spain.

Del Moral, J.C., Martí, R., 2001. El Buitre leonado en la Península Ibérica. Monografía n° 7. SEO/BidLife, Madrid, Spain.

DeVault, T.L., Rhodes, O.E., Shivik, J.A., 2003. Scavenging by vertebrates: behavioural, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102, 225–234. doi:10.1034/j.1600-0706.2003.12378.x.

Deygout, C., Gault, A., Sarrazin, F., Bessa-Gomes, C., 2009. Modeling the impact of feeding stations on vulture scavenging service efficiency. Ecological Modelling 220, 1826–1835. doi:10.1016/j.ecolmodel.2009.04.030.

Digby, P.G.N., Kempton, R.A., 1987. Population and Community Biology Series: Multivariate Analysis of Ecological Communities. Chapman and Hall, London, UK.

Donázar, J.A., 1993. Los buitres ibéricos. In: Reyero, J.M. (Ed.), Biología y Conservación. Madrid, Spain.

Donázar, J.A., Hiraldo, F., Bustamante, J., 1993. Factors influencing nest site selection, breeding density and breeding success in the bearded vulture (*Gypaetus barbatus*). Journal of Applied Ecology 30, 500–514.

Donázar, J.A., Naveso, M.A., Tella, J.L., Campión, D., 1996a. Extensive grazing and raptors in Spain. In: Pain, D. (Ed.), Bird Conservation and Farming Policy in Europe. Cambridge University Press, UK, pp. 117–149.

Donázar, J.A., Ceballos, O., Tella, J.L., 1996b. Communal roost of Egyptian vultures (*Neophron percnopterus*): dynamics and implications for the species conservation. In: Muntaner, J., Mayol, J. (Eds.), Biology and Conservation of Mediterranean Raptors (1994) SEO/BirdLife, Monography 4. Madrid, Spain, pp. 189–202.

Donázar, J.A., Margalida, A., Campión, D., 2009a. Vultures, Feeding Stations and Sanitary Legislation: a Conflict and its Consequences from the Perspective of Conservation Biology. Sociedad de Ciencias Aranzadi San Sebastián, Spain.

Donázar, J.A., Margalida, A., Carrete, A., Sánchez-Zapata, J.A., 2009b. Too sanitary for vultures. Science 326, 664.

Donázar, J.A., Cortés-Avizanda, A., Carrete, M., 2010. Dietary shifts in two vultures after the demise of supplementary feeding stations: consequences of the EU sanitary legislation. European Journal of Wildlife Research. doi:10.1007/s10344-009-0358-0.

Gavashelishvili, A., McGrady, M.J., 2006. Geographic information system-based modelling of vulture response to carcass appearance in the Caucasus. Journal of Zoology 269, 365–372. doi:10.1111/j.1469-7998.2006.00062.x.

Gilbert, M., Watson, R.T., Ahmed, S., Asim, M., Johnson, J.A., 2007. Vulture restaurants and their role in reducing diclofenac exposure in Asian vultures. Bird Conservation International 17, 63–77. doi:10.1017/S0959270906000621.

Gorosti, 2007. El milano real en Navarra. <http://www.gorosti.org/proyectosornitologia/milano_real_proy/mr_marco>.

Green, R.S., Newton, I., Schultz, S., Cunningham, A.A., Gilbert, M., Pain, D.J., Prakash, V., 2004. Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. Journal of Applied Ecology 41, 793–800. doi:10.1111/j.0021-8901.2004.00954.x.

Hertel, F., 1994. Diversity in body size and feeding morphology within past and present vulture assemblages. Ecology 75, 1074–1084. doi:10.2307/1939431.

Hertel, F., Lehman, N., 1998. A randomized nearest neighbor approach for assessment of character displacement: the vulture guild as a model. Journal of Theoretical Biology 190, 51–61. doi:10.1006/jtbi.1997.0531.

Houston, D.C., 1983. The adaptive radiation of the griffon vulture. In: Wilbur, S.R., Jackson, J.A. (Eds.), Vulture Biology and Management. University of California Press, Berkeley, CA, pp. 135–152.

Houston, D.C., 1987. Management techniques for vultures – feeding and releases. In: Hill, D.J. (Ed.), Breeding and Management of Birds of Prey. University of Bristol, Bristol, pp. 15–29.

Houston, D.C., 1988. Competition for food between neotropical vultures in forest. Ibis 130, 402–417. doi:10.1111/j.1474-919X.1988.tb00998.x.

Houston, D.C., 2001. Vultures and Condors. Colin Baxter Ltd., Grantown on Spey. Scotland.

Jackson, A.L., Ruxton, G.D., Houston, D.C., 2008. The effect of social facilitation on foraging success in vultures: a modelling study. Biology Letters 4, 311–313. doi:10.1098/rsbl.2008.0038.

Kieseecker, J.M., Blaustein, A.R., Miller, C.L., 2001. Potential mechanisms underlying the displacement of native red-legged frogs by introduced bullfrogs. Ecology 82, 1964–1970.

Koenig, R., 2006. Vulture research soars as the scavengers' numbers decline. Science 312, 1591–1592. doi:10.1126/science.312.5780.1591.

König, C., 1974. Zum verhalten spanischer Geier an Kadavern. Journal für Ornithologie 115, 289–320.

König, C., 1983. Interspecific and Intraspecific Competition for Food Among Old World Vultures. In: Vulture Biology and Management. University of California Press, Berkeley, CA, pp. 153–171.

Kruuk, H., 1967. Competition for food between vultures in east Africa. Ardea 55, 171–193.

Lemus, J.A., Blanco, G., Grande, J., Arroyo, B., García-Montijano, M., Martínez, F., 2008. Antibiotics threaten wildlife: circulating quinolone residues and disease in avian scavengers. PLoS ONE 3, e 1444. doi:10.1371/journal.pone.0001444.

Magurran, A.E., 2003. Measuring Biological Diversity. Blackwell Publishing, Oxford, UK.

Margalida, A., 1997. Consumición de pequeños cadáveres por parte de buitres leonados (*Gyps fulvus*) en Cataluña (NE España). Butlletí del Grup Català d'Anellament 14, 55–57.

Margalida, A., Heredia, R., 2005. Biología de la conservación del quebrantahuesos (*Gypaetus barbatus*) en España. Organismo Autónomo Parques Nacionales. Madrid, Spain.
Margalida, A., García, D., Cortés-Avizanda, A., 2007. Factors influencing the breeding density of bearded vultures, Egyptian vultures and Eurasian griffon vultures in Catalonia (NE Spain): management implications. Animal Biodiversity and Conservation 30, 189–300.
Margalida, A., Bertrán, J., Heredia, R., 2009. Diet and food preferences of the endangered bearded vulture *Gypaetus barbatus*: a basis for their conservation. Ibis 151, 235–243.
McCarthy, M.A., Possingham, H.P., 2007. Active adaptive management for conservation. Conservation Biology 21, 956–963. doi:10.1111/j.1523-1739.2007.00677.x.
McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models. Chapman and Hall, London, UK.
McCullagh, P., Searle, S.R., 2000. Generalized Linear and Mixed Models. Wiley-Interscience, New York, NY, USA.
Meretsky, V.J., Mannan, R.W., 1999. Supplemental feeding regimes for Egyptian vultures in the Negev desert, Israel. Journal of Wildlife Management 63, 107–115.
Mills, L.S., Soulé, M.E., Doak, D., 1993. The keystone species concept in ecology and conservation. BioScience 43, 219–224.
Mönkkönen, M., Forsman, J.T., Thomson, R.L., 2004. Qualitative geographical variation in interspecific interactions. Ecography 27, 112–118. doi:10.1111/j.0906-7590.2004.03705.x.
Moreno-Opo, R., Margalida, A., Arredondo, A., Guil, F., Martín, M., Higuero, R., Soria, C., Guzmán, J., 2010. Factors influencing the presence of the cinereous vulture *Aegypius monachus* at carcasses: food preferences and implications for the management of supplementary feeding sites. Widlife Biology 16, 1–10. doi:10.2981/09-037.
Moril, Y., Boydl, I.L., 2004. Segregation of foraging between two sympatric penguin species: does rate maximisation make the difference? Marine Ecology Progress Series 275, 241–249.
Morillo, C., Gómez-Campo, C., 2000. Conservation in Spain, 1980–2000. Biological Conservation 95, 165–174. doi:10.1016/S0006-3207(00)00031-8.
Mundy, P., Butchart, D., Ledger, J., Piper, S., 1992. The Vultures of Africa. Academy Press, San Diego, CA.
Olea, P.P., Mateo-Tomás, P., 2009. The role of traditional farming practices in ecosystem conservation: the case of transhumance and vultures. Biological Conservation 142, 1844–1853.. doi:10.1016/j.biocon.2009.03.024.
Oro, D., Margalida, A., Carrete, M., Heredia, R., Donázar, J.A., 2008. Testing the goodness of supplementary feeding to enhance population viability of an endangered vulture. PLoS ONE 3 (12), e4084. doi:10.1371/journal.pone.0004084.
Oro, D., Pérez-Rodríguez, A., Martínez-Vilalta, A., Bertolero, A.VidalF., Genovart, M., 2009. Interference competition in a threatened seabird community: a paradox for a successful conservation. Biological Conservation 142, 1830–1835. doi:10.1016/j.biocon.2009.03.023.
Petren, K., Case, T.J., 1996. An experimental demonstration of exploitation competition in an ongoing invasion. Ecology 77, 118–132.
Piper, S.E., 2006. Supplementary feeding programs: how necessary are they for the maintenance of numerous and healthy vultures populations? In: Houston, D.C., Piper, S.E., (Eds.), Proceedings of the international conference on conservation and management of vulture populations. Natural History Museum of Crete WWF Greece, pp. 41–50.
Possingham, H.P., Andelman, S.J., Noon, B.R., Trombulak, S., Pulliam, H.R., 2001. Making smart conservation decisions. In: Orians, G., Soulé, M. (Eds.), Research Priorities for Conservation Biology. Island Press, Washington, DC, pp. 225–244.
SAS Institute Inc., 2009. SAS /STAT 9.2., Language Reference: Concepts. SAS Institute Inc. Cary NC.
Selva, N., Cortés-Avizanda, A., 2009. The effects of carcasses and carrion dumps sites on communities and ecosystems. In: Donázar, J.A., Margalida, A., Campión, D. (Eds.), Vultures, Feeding Stations and Sanitary Legislation: a Conflict and its Consequences from the Perspective of Conservation Biology. Sociedad de Ciencias Aranzadi San Sebastián, Spain, pp. 452–473.
Shultz, S., Baral, H.S., Charman, S., Cunningham, A.A., Das, D., Ghalsasi, G.R., Goudar, M.S., Green, R.E., Jones, A., Nighot, P., Pain, D.J., Prakash, V., 2004. Diclofenac poisoning is widespread in declining vulture populations across the Indian subcontinent. Proceedings of the Royal Society of London B 271, 458–460. doi:10.1098/rsbl.2004.0223.
Soulé, M.E., Estes, J.A., Miller, B., Honnold, D.L., 2005. Strongly interacting species: conservation policy, management, and ethics. Bioscience 55, 168–176. doi:10.1641/0006-3568(2005)055.
Tella, J.L., 2001. Action is needed now, or BSE crisis could wipe out endangered birds of prey. Nature 410, 408. doi:10.1038/35068717.
Thiollay, J.M., 2006. The decline of raptors in West Africa: long-tem assessment and the role of protected areas. Ibis 148, 240–254. doi:10.1111/j.1474-919X.2006.00531.x.
Viñuela, J., Martí, R., Ruiz, A., 1999. El milano real en España. Monografía n° 6. SEO/BidLife. Madrid, Spain.
Wilbur, S.R., Jackson, J.A., 1983. Vulture Biology and Management. Univ. of California Press, Berkeley.