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Optimization of supplementary feeding programs for European vultures depends on environmental and management factors

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Abstract. Despite the consensus among ecologists and conservationists of the importance of maintaining scavenger feeding patterns based primarily on natural prey sources, human-mediated feeding remains a widely used management tool for threatened wildlife. Thus, it is important to understand the key factors favoring certain species and age-groups at supplementary feeding sites. Through a detailed videomonitored experiment of carrion inputs at different locations in the Iberian Peninsula (home of >90% of European vultures), we assessed how variables related to weather, time, demography, management and alternative food availability influenced the occurrence patterns of different age-classes of vultures at feeding sites. The most threatened and less gregarious species (bearded vulture *Gypaetus barbatus* and Egyptian vulture *Neophron percnopterus*) attended to earlier inputs, thus reducing interspecific competition with the Eurasian griffon vulture *Gyps fulvus*. The bearded vulture was favored by a larger biomass supply at the feeding sites during the chick-rearing period, while the Egyptian vulture preferred frequent and abundant inputs. Non-adult cinereous vultures *Aegypius monachus* were favored at times of lower abundance of natural resources and in the densest networks of feeding sites, while adults preferentially attended sites with periodic inputs close to breeding colonies in areas with lower availability of other natural prey. Finally, the Eurasian griffon vulture showed a preference for continued and periodic inputs, and for feeding sites with numerous other feeding sites in the surroundings. Our results help to inform the management of supplementing food provision with the aim of enhancing its value to reverse the unfavorable conservation status of endangered species and to mitigate the negative effects of the current global threats impacting them.

Key words: *Aegypius monachus*; carcasses; environmental factors; *Gypaetus barbatus*; *Gyps fulvus*; life-cycle phase; *Neophron percnopterus*; Spain; supplementary feeding management.

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Introduction

Carrion ecology and its role in the feeding of wild scavengers is a field of study that has gained special relevance in recent years (Barton et al. 2013, Oro et al. 2013, Fielding et al. 2014), particularly from the perspective of conservation management in European and African countries

(Cortés-Avizanda et al. 2010, Margalida et al. 2011*a*, Duriez et al. 2012, Kane et al. 2015, Moreno-Opo et al. 2015). In addition, several authors have highlighted the importance of carrion in balancing trophic relationships and cascades, both at small and large scales, influencing carnivore communities, the conservation status of large predators and even the population dynamics of prey species (Wilmers et al. 2003, Selva and Fortuna 2007, Cortés-Avizanda et al. 2009, Wilson and Wolkovich 2011). Therefore, carrion management has important implications in the ecosystem services provided by scavengers (Dupont et al. 2012, Moleón et al. 2014), as well as in the associated economic, health and environmental effects (Margalida and Colomer 2012, Morales-Reyes et al. 2015).

Carrion management with the purpose of supplementary feeding for the scavenger guild is currently an important conservation tool aimed at combating different threat factors (see review in Donázar et al. 2009a). For example, supplementary feeding programs have been implemented to reverse the devastating impact of carcasses from cattle medicated with veterinary drugs such as diclofenac on Asian vultures (Gilbert et al. 2007), to reduce the negative effects of poisoned baits on threatened African vultures (Virani et al. 2011, Ogada et al. 2012) and to alleviate the depletion and alteration of carcasses occurrence due to legislative changes in Europe (Donázar et al. 2009*b*, Margalida and Colomer 2012). Therefore, a general consensus exists among ecologists and conservationists that supplementary feeding should be used as a temporary management option, determined by very specific performance requirements (Gonzalez et al. 2006, Robb et al. 2008, Ewen et al. 2015). In this sense, the relationship between scavengers and food availability should be primarily shaped by natural scenarios regulating the population dynamics of the involved species, which should evolve and interact without human intervention (Oro et al. 2013, Fielding et al. 2014). However, although in several countries some of the above mentioned threats are declining (Margalida et al. 2012, Prakash et al. 2012), there continue to be economic and livestock management schemes with supplementary feeding as an influential and long-term component balancing food availability and ecological requirements for scavenger species.

Supplementary feeding for scavengers can be defined as the set of activities around the provision of carrion by humans for its exploitation by the targeted species through a wide variation of procedures and protocols. These include the management of fenced feeding sites with abundant and predictable carrion inputs from intensive farming, to the non-removal of dead livestock on extensive farms or wild ungulates as a result of hunting activities. This diversity of approaches may continue in Europe since current regulations enable all of these feeding options (European Commission 2011). In this context, it is necessary to improve the use of carrion by target species aiming to optimize its management. This requires knowledge of how the frequency of carcass inputs, time (hour and season), geographic location, weather conditions and the format in which the carrion is presented, impact the occurrence of different scavenger species at feeding points.

The assessment of supplementary feeding for avian scavengers has been the subject of several previous studies, primarily aimed at determining prey selection by species attending feeding sites (Moreno-Opo et al. 2010, 2015), the intra- and interspecific relationships among them (Cortés-Avizanda et al. 2010, 2013, Kendall et al. 2012, Kendall 2013), and both the positive and negative associated effects of supplementary feeding on demographic and behavioral parameters (Carrete et al. 2006, Oro et al. 2008, García-Heras et al. 2013). The effect of time and management on the exploitation patterns of some species have also been analyzed (Bosè and Sarrazin 2007, Duriez et al. 2012). However, these studies have not considered in detail key management aspects of feeding sites such as the frequency of inputs or the amount of provisioned biomass interactively with other influential variables in the feeding ecology of scavengers such as the availability of alternative food sources (of natural or anthropic origin), the life-cycle phase, the proximity to breeding areas or weather conditions during the provision of food. Likewise, the above factors have not been addressed for all European vultures jointly.

This study aims to determine the selection of different factors related to weather, time, demography, management and alternative food avail-

Table 1. European vulture species studied and their breeding population (number of breeding pairs) in a buffer of 25 km, as a surrogate of their relative abundance around the surveyed feeding sites, in the two sub-regions (N-E: northeastern Spain, and C-W: central-western Spain).

Species	Breeding pairs N-E	Breeding pairs C-W
Bearded vulture, *Gypaetus barbatus*	15	0
Cinereous vulture, *Aegypius monachus*	5	148
Egyptian vulture, *Neophron percnopterus*	18	7
Eurasian griffon vulture, *Gyps fulvus*	347	90

ability of carrion inputs experimentally provided at supplementary feeding sites by different age-classes of the four European vulture species. We hypothesized that all vulture species and age-classes would more frequently attend feeding sites during seasons with greater energetic requirements for the individuals (i.e., chick-rearing or winter period) or associated to more favorable flying conditions (benign weather). Similarly, the most endangered species (i.e., Egyptian and bearded vultures) and the less experienced birds (non-adults) should reduce competition by minimizing their overlap with other vultures (adults and cinereous and griffon vultures) at feeding sites. Species and individuals that are more gregarious and abundant at predictable food sources (non adults and griffon vultures) would be expected to attend in higher numbers sites with more frequent inputs and a greater biomass provided. On the contrary, more natural foragers and experienced individuals would not be associated with a greater periodicity of inputs but with a greater abundance of other natural prey.

Methods

Study area

The study was carried out at six locations in Spain, three in the Pyrenean Mountain range (central location 42°25′41″ N, 1°2′54″ E) and three in the central-western Iberian Peninsula (central location 39°10′55″ N, 5°3′19″ W). Experimental sites were chosen at active supplementary feeding points maintained within the framework of official conservation programs for scavenger bird species. The two sampled Spanish regions were selected to include representative populations of the four species of European vultures (Table 1).

Study design and variables considered

Carrion inputs were experimentally provisioned at six supplementary feeding points between May 2009 and April 2011. The provided carrion consisted of cadavers and remains of livestock and wild ungulates. Carrion was supplied during daytime (randomly from 7:00 to 19:15h GMT + 1) on a weekly basis in each sub-region alternating different traits of the inputs (prey species, biomass, scattering) homogeneously among the different points: we provided sequentially carcasses/remains from ovine-caprine (total inputs = 49), porcine-bovine (n = 43) and wild ungulates (n = 47) as prey species, a range of 35–305 kg per feeding event (87.1 kg ± 26.3 kg; mean ± SD) and concentrated (<2 m radius, n = 68) or not concentrated (≥2 m radius, n = 71) regarding scattering (Moreno-Opo et al. 2015). Similarly, several characteristics of the inputs were assessed for their inclusion as explanatory variables (Table 2). These explanatory variables were selected on the basis of their possible influence on species attendance as previously reported (Gavashelishvili and McGrady 2006, Cortés-Avizanda et al. 2010, 2013). Six types of variables were taken into account: location, weather conditions, time, abundance of vultures breeding, management of the feeding site and variables linked to other potential food sources (in total 16 variables; Table 2). Quantitative variables were obtained by direct observation in the field while the considered qualitative variables were issued after training and standardization of field technicians to predetermined values. The number of birds of each species and age-class actively feeding at the sites (see further explanations below) were chosen as response variables (Guisan and Zimmermann 2000).

Birds present at the sampled points were continuously monitored from the time of the

Table 2. Variables analyzed to evaluate attendance at carrion inputs by European vulture species at experimental supplementary provisioning sites (an "a" superscript indicates *time-varying variables*, a "b" in superscript indicates *time-invariant variables*). The environmental or human issue dealt with by each considered variable and its description and categories—when applicable—are shown. A dagger (†) indicates variables included in the analysis after simplification by correlation assessment. Type abbreviations are: cat, categorical; con, continuous.

Variable	Type	Description	Categories	Environmental/ human aspect
Feeding site[b]	cat	Site in which carrion input was provided (random variable, nested in sub-region)	Six experimental sites	location
Sub-region[b]	cat	Sub-region in Spain considered in the study (random variable)	N-E, northeastern; CW, central-western	location
Rainfall[a,]†	cat	Rainfall during the three-day monitoring period after each carrion input	0, no rain; 1, scarce; 2, continuous; 3, hail/snow presence	climate
Wind[a,]†	cat	Wind during the carrion input	0, no wind; 1, light and varying breezes; 2, gusts/gales	climate
Temperature[a,]†	cat	Daytime temperature during the carrion input	0, <0°C; 1, 1–15°C; 2, 15–25°C; 3, >25°C	climate
Cloudiness[a,]†	cat	Coverage of the sky with clouds during the carrion input	0, 0%; 1, 1–33%; 2, 34–66%; 3, >66%	climate
Time[a,]†	con	Hour in which carrion was provisioned during daytime (7:00 to 19:15 GMT+1)		time
Life-cycle phase[a,]†	cat	Season in which carrion was provisioned according to breeding phenology of each species	Non-breeding season, Mating-incubation, Chick-rearing period	time
Breeding pairs other sps[b]	cont	Breeding pairs (n) of other vulture species in a radius of 25 km to feeding site (range 38–380)		demography
Breeding pairs same sps[b,]†	cont	Breeding pairs (n) of the same vulture species in a radius of 25 km to feeding site (range 0–347)		demography
Biomass annually provided[a,]†	cont	Average of the biomass (kg) annually provided to the feeding site during the previous year to the start of the study (2008) (range 4500–106,250 kg)		management
Provisioning frequency[a,]†	cat	Periodicity of carrion inputs at the feeding site during the previous year to the start of the study (2008)	Weekly, 1 input/week; Monthly, ±1 input/ month; Non-periodic inputs, heterogeneous non-sequential inputs	management
Livestock population[b,]†	cont	Population of extensive livestock species (n) in municipalities situated in a 25 km radius (range 31,325–246,905)		other food sources
Ovine-caprine population[b]	cont	Population of sheeps and goats (n) in municipalities situated in a 25 km radius (range 16,541–155,607)		other food sources
Game species abundance[b]	cat	Estimate of relative abundance of ungulate species in the province	1, >3000 ungulates hunted/year; 2, <3000 ungulates hunted/year	other food sources
Other feeding sites[b,]†	cont	Official feeding stations (n) operating in a radius of 50 km from the studied site (range 0–16)		other food sources

provision of food until three days later, during daylight hours. 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 with the 120° display angle of the camera (see further details in Moreno-Opo and Margalida 2013).

The recordings of each three-day event of carrion consumption were visualized by registering vultures present at feeding sites, including those actively feeding. To this end, we considered: (1) bird counts in each 10-minute period (i.e., every 10 minutes a census of all vultures

was carried out), and (2) the maximum number of vultures actively feeding simultaneously recorded in all 10-minute periods. Vultures were assigned to species (bearded vulture, cinereous vulture, Egyptian vulture and griffon vulture) and age level. We divided age classes into "*Adults*" (birds showing typical adult plumage; Forsman 2003) and "*Non-adults*" (birds exhibiting juvenile, immature or sub-adult phases of plumage). As a result, we considered two response variables regarding the abundance of each vulture species: (1) maximum number of adult birds feeding simultaneously during the three-day event, and (2) maximum number of non-adult birds feeding simultaneously during the three-day event. Since the Eurasian griffon vulture exploits the greatest biomass of carrion provided at supplementary feeding sites (Moreno-Opo et al. 2010, 2015, Cortés-Avizanda et al. 2013) the numerical relationships between numbers of each vulture species and the griffon vulture were also considered as response variable to evaluate possible exclusion-competition mechanisms.

Pseudoreplication between subsequent counts of 10 minutes that could lead to the lack of independence of the observations was discarded. Based on the analysis and data gathered from the images, it was observed that the permanence of individuals was dynamic (Cortés-Avizanda et al. 2010, Moreno-Opo et al. 2015). In fact, in most cases, the time spent eating by individuals was less than 10 minutes (Moreno-Opo et al., *unpublished data*). Due to the large distances between sampling points within the same study subregions and to the weekly interval between inputs at different points, spatial autocorrelation therein was dismissed.

Statistical analyses

First, the independent variables to be included in the analyses were examined through Spearman's rank correlation (ρ) index to test their relationship and possible simplification. For variables related to location, *feeding-site* and *subregion* showed strong correlations between them ($\rho = 0.84$) as well as *breeding pairs same sps* and *breeding pairs other sps* ($\rho = -0.89$) regarding abundance of breeding vultures. The variables related to other food sources *livestock population* and *ovine-caprine population* ($\rho = 0.98$) and *other feeding sites* and *game species abundance* ($\rho = 0.99$) were also highly correlated. Therefore, these latter variables were dropped from further modelling. Moreover, the correlation analysis among all the variables led us to remove the *feeding-site* variable since it was correlated ($\rho > 0.75$) with four other variables. Thus, the final number of variables included to explore their influence on the attendance of vultures at feeding sites was 11. The dependent variables were log-transformed to adjust to a normal distribution using a Kolmogorov-Smirnov test (Zuur et al. 2009), except for the Egyptian vulture due to the low number of events with its presence (26.9% from $n = 52$ inputs). Consequently, we transformed the response variables for this species to fit a binomial distribution (presence/absence) allowing for the performance of parametric analyses.

We established competing generalized lineal models (GLM) with a log-link function and normal distribution for bearded, cinereous and griffon vultures and with a logit-link function and binomial distribution for Egyptian vultures, from all possible combinations of explanatory variables aiming to determine the most parsimonious model. Model selection was done using Akaike's Information Criteria (AIC; Burnham and Anderson 2002). The statistical analyses were conducted with *Statistica* 6.1 (StatSoft, Tulsa, Oklahoma, USA).

Results

A total of 139 carrion inputs were supplied and distributed homogeneously among the studied areas and locations. The most parsimonious model determining the attendance patterns of non-adult bearded vultures at feeding sites included variables related to the time: earlier hours of provision during the chick-rearing period were positively related to the number of individuals, as well as those associated with the management, preferring supplementary feeding sites with a greater annual biomass in the previous years during the chick-rearing period (Fig. 1, Table 3). In contrast, the best model explaining the presence of adults at feeding sites included the abundance of extensive livestock around the site and the interaction between the life-cycle phase and the provisioning frequency,

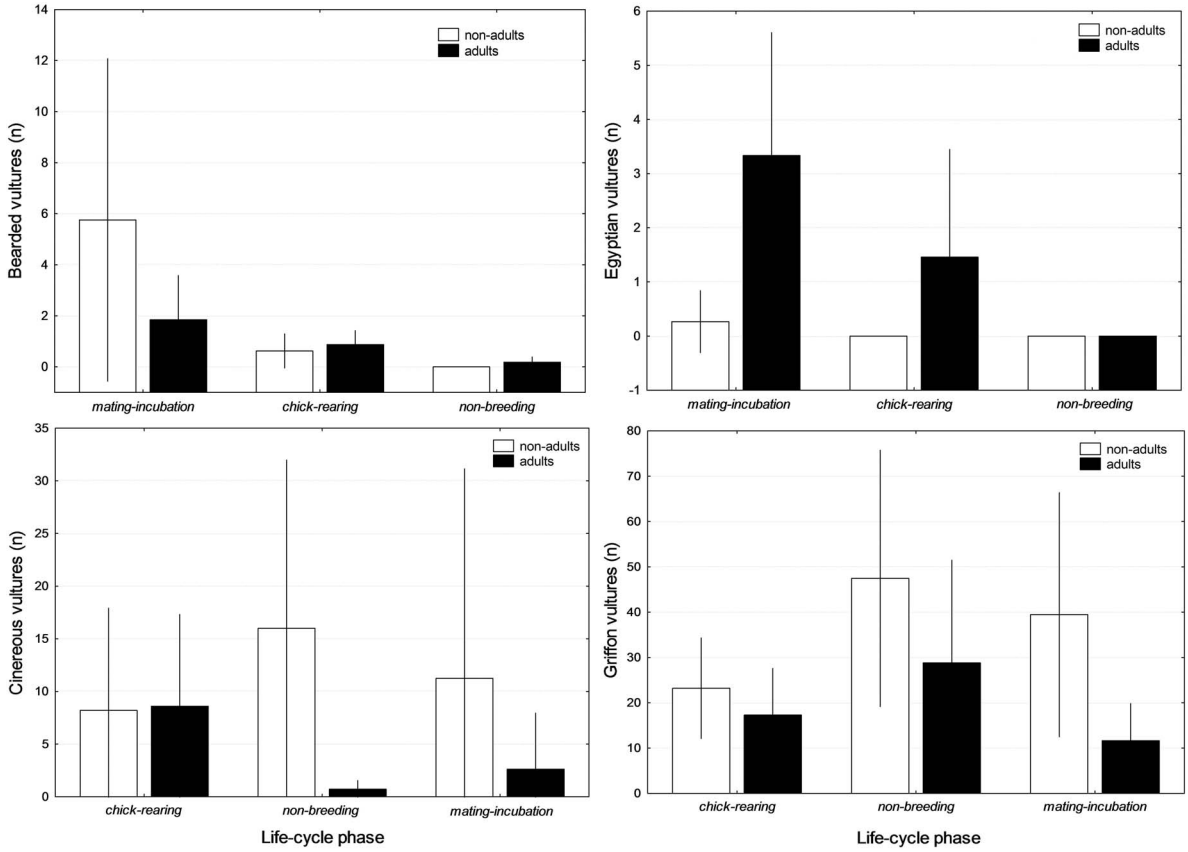

Fig. 1. Mean (columns) ± SD (lines) of the number of individuals observed per feeding input according to their life-cycle phase: bearded vulture (mating-incubation: December–March, chick-rearing: April–July, non-breeding: August–November), Egyptian vulture (M-I: March–15 June, C-R: 16 June–August, N-B: September), cinereous vulture (M-I: January–April, C-R: May–15 September, N-B: 16 September–December), griffon vulture (M-I: December–March, C-R: April–July, N-B: August–November).

with the chick-rearing period and weekly inputs positively related to the number of adult bearded vultures (Table 3).

The model describing a greater presence probability of non-adult Egyptian vultures included the effect of the biomass annually provisioned traditionally in the feeding site and the abundance of other alternative food sources (Table 4): numbers increased with a greater biomass and with lower numbers of extensive livestock in the surroundings of the site (Table 4). The provisioned biomass in previous years, the time and the periodicity of the inputs were the variables included in the most parsimonious model for adult Egyptian vultures (Fig. 2, Table 4): earlier inputs along with a greater biomass provided and weekly periodic inputs positively influenced their numbers during the mating-incubation and chick-rearing periods (Fig. 1).

The variables explaining a greater probability of occurrence of non-adult cinereous vultures were the time of input, preferring provisions as late as possible and during the non-breeding season. The presence of other nearby feeding sites within a radius of 50 km also had a positive effect (Figs. 1 and 2, Table 5). Presence of adult cinereous vultures was positively influenced by the number of alternative feeding sites and weekly inputs of carrion. Besides these variables, more breeding pairs of the species in a radius of 25 km implied a greater number of adults at the feeding site and there was a negative influence of the abundance of livestock in the most parsimonious model (Table 5).

Table 3. Most parsimonious models aimed at assessing the effect of environmental and management factors on bearded vulture *Gypaetus barbatus* maximum numbers feeding at study sites, depending on their age classes and their relationship with griffon vulture *Gyps fulvus* numbers. AICc: Akaike's Information Criterion corrected for small sample size, L-ratio χ^2, scaled deviance and log-likelihood values are shown for the selected models. The estimated value of the variable and its relationship (+/−) to the number of bearded vultures at feeding sites, and the standard error, are also shown.

Model no.	Response parameter and *most parsimonious model*	Variable	Estimate	SE
1	Max. no. non-adults simultaneously feeding	Intercept	8.705	±17.695
	Time + life-cycle phase +biomass annually provisioned	*Time*	−7.212	±1.181
		Life-cycle phase (chick-rearing)	1.663	±0.219
		Life-cycle phase (non-breeding)	−3.392	
		Biomass annually provisioned	0.001	±0.000
2	Max. no. adults simultaneously feeding	Intercept	0.599	±11.990
	Time + life-cycle phase × provisioning frequency + livestock population	*Time*	−3.909	±0.943
		Life-cycle phase × frequency (chick-rearing × weekly)	1.198	±1.190
		Life-cycle phase × frequency (non-breeding × weekly)	−1.401	±2.191
		Livestock population	0.026	
3	Proportion of bearded/griffon vultures	Intercept	−7.467	±140.43
	Time + life-cycle phase × provisioning frequency + biomass annually provisioned	*Time*	−3.272	±2.349
		Life-cycle phase × frequency (chick-rearing× weekly)	1.782	±38.691
		Life-cycle phase× frequency (non-breeding× weekly)	−2.752	±77.331
		Biomass annually provisioned	0.001	±0.001

Note: For model 1, AICc = 68.87, L ratio $\chi^2 = 141.39$, scaled deviance = 90, log-likelihood = −31.33, $P < 0.001$. For model 2, AICc = 131.75, L ratio $\chi^2 = 46.89$, scaled deviance = 90, log-likelihood = −58.93, $P < 0.001$. For model 3, AICc = 9.24, L ratio $\chi^2 = 221.25$, scaled deviance = 68, log-likelihood = 1.42, $P < 0.001$.

The model with a higher predictability of greater numbers for both adult and non-adult griffon vultures included a positive association with the number of other feeding sites in a 50 km radius but was negatively affected by a more abundant breeding population of the species around the study sites (Table 6). For non-adult birds, weekly periodic inputs and a greater biomass annually provided also increased their numbers (Table 6) mainly during the non-breeding season (Fig. 1).

Lastly, the relationships between each of the species with the griffon vulture revealed that inputs provided at earlier hours favored the

Table 4. Most parsimonious models aimed at assessing the effect of environmental and management factors on Egyptian vulture *Neophron percnopterus* presence at feeding sites, depending on their age classes. AICc: Akaike's Information Criterion corrected for small sample size. The estimated value of the variable and its relationship (+/−) to the presence of Egyptian vultures at feeding sites, and the standard error, are shown.

Model no.	Response parameter and *most parsimonious model*	Variable	Estimate	SE
1	Non-adults attending feeding input (presence/absence)	Intercept	−20.544	±1.908
	Biomass annually provisioned + livestock population	*Biomass annually provisioned*	0.0002	±0.000
		Livestock population	−0.008	
2	Adults attending feeding input (presence/absence)	Intercept	5.596	±0.000
	Time + biomass annually provisioned + provisioning frequency	*Time*	−49.897	
		Biomass annually provisioned	0.0001	
		Provisioning frequency (weekly)	0.686	
		Provisioning frequency (non-periodic)	−0.661	±0.634

Note: For model 1, AICc = 273.60, L ratio $\chi^2 = 23.63$, scaled deviance = 52, log-likelihood = −133.05, $P < 0.001$. For model 2, AICc = 866.46, L ratio $\chi^2 = 955.73$, scaled deviance = 90, log-likelihood = −408.39, $P < 0.001$.

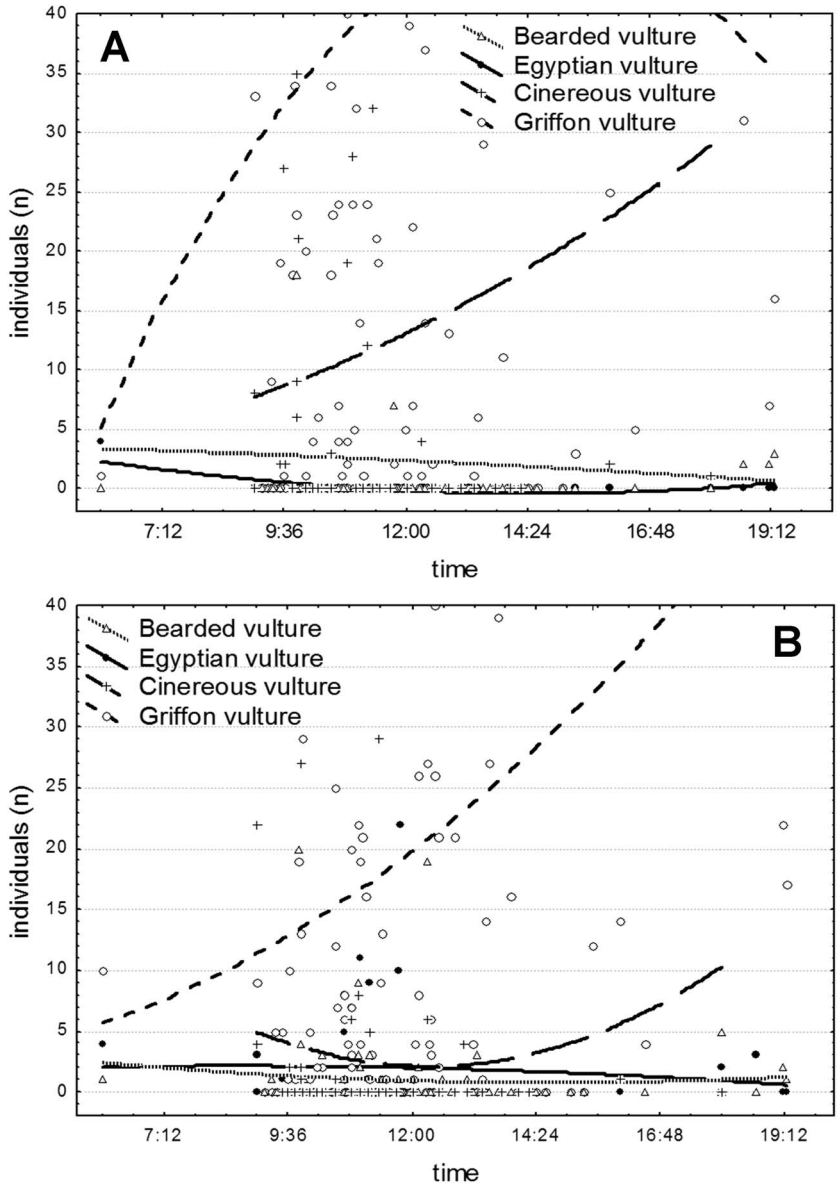

Fig. 2. Line regressions of the number of vultures (expressed as the sum of birds recorded in all 10-minute periods) of bearded, cinereous, Egyptian and griffon vultures at the carcasses provided at supplementary feeding sites according to the time of input, for non-adult (A) and adult (B) age-classes. Y-axis shows the number of individuals registered and time is expressed in hours (GMT + 1).

relative numbers of bearded, cinereous and Egyptian vultures (Fig. 2, Tables 3, 5, and 6). Other variables influencing the relationships of griffon vultures with other species were the annually provided biomass and the interaction between life-cycle phase and provisioning frequency (Fig. 2, Tables 3, 5, and 6).

Discussion

Influence of weather and time conditions

None of the climatic variables analyzed was included among the most simplified models offering a greater explanatory power. This absence contrasts with the known flight and

Table 5. Most parsimonious models aimed at assessing the effect of environmental and management factors on cinereous vulture *Aegypius monachus* maximum numbers feeding at study sites, depending on their age classes and the relationship with griffon vulture *Gyps fulvus* numbers. AICc: Akaike's Information Criterion corrected for small sample size. The estimated value of the variable and its relationship (+/−) to the number of cinereous vultures at feeding sites, and the standard error, are shown.

Model no.	Response parameter and *most parsimonious model*	Variable	Estimate	SE
1	Max no. non-adults simultaneously feeding	Intercept	−8.602	±1134.54
	Time + life-cycle phase + other feeding sites	*Time*	32.480	±14.101
		Life-cycle phase (chick-rearing)	−0.211	±1.304
		Life-cycle phase (non-breeding)	4.011	±1.006
		Biomass annually provisioned	0.707	
2	Max no. adults simultaneously feeding	Intercept	28.381	±2765.09
	Breeding pairs same species + livestock population + other feeding sites + life-cycle phase × provisioning frequency	*Breeding pairs same species*	0.253	
		Livestock population	−0.000	
		Other feeding sites	0.904	
		Life-cycle phase × frequency (chick-rearing × weekly)	3.523	
		Life-cycle phase× frequency (chick-rearing × non-periodic)	−0.890	±1.006
		Life-cycle phase× frequency (non-breeding × weekly)	2.657	
		Life-cycle phase× frequency (non-breeding × non-periodic)	−0.231	
3	Proportion of cinereous/griffon vultures	Intercept	−2.545	±4.229
	Time	*Time*	−0.608	±3.821

Note: For model 1, AICc = 219.77, L ratio $\chi^2 = 38.34$, scaled deviance = 47, log-likelihood = −107.33, $P < 0.001$. For model 2, AICc = 168.01, L ratio $\chi^2 = 20.39$, scaled deviance = 47, log-likelihood = −79.37, $P < 0.001$. For model 3, AICc = 46.70, L ratio $\chi^2 = 0.560$, scaled deviance = 37, log-likelihood = −19.83, $P < 0.001$.

foraging patterns of soaring birds, negatively influenced by adverse weather conditions (rainfall, wind or cold temperatures; Hiraldo and Donázar 1990, Chevallier et al. 2010). The reasons for this lack of significant results may be the low variation in weather conditions across the days of monitoring, or the performed sampling procedure (i.e., scoring weather categories except for rainfall during the time of carrion inputs but not later), which may not be the most accurate for evaluating these conditions.

The time of carrion supply, however, did have a significant effect in the selected models. A preference pattern for earliest food inputs in the most threatened species was observed. Thus, all bearded and adult Egyptian vultures attended in greater numbers when the inputs were supplied early in the morning, contrary to that preferred by cinereous and griffon vultures. In addition, the ratio of griffon vultures, the species monopolizing the highest proportion of food resources at carcasses (Cortés-Avizanda et al. 2010, Moreno-Opo et al. 2015), was less with respect to other vultures when carrion provisions were earlier. This could be related to carrion-segregated use and a subsequent resource partitioning among vulture species, which would minimize their overlap at sites to reduce interspecific competition (Duriez et al. 2012, Kendall et al. 2012, Cortés-Avizanda et al. 2013, Kendall 2014). Likewise, the fact that greater numbers of the larger vultures (cinereous and griffon) attend feeding sites during the midday hours may be explained by the increased need for thermals, which mainly occur around noon, due to their higher wing load (Leshem and Yom-Tov 2008) compared to the Egyptian and bearded vultures, the latter being able to begin foraging flights in less favorable weather and thermal conditions.

Several authors have highlighted the relationship between the use of feeding sites by avian scavengers and the trophic requirements resulting from the life-cycle phase and individual activities (García-Heras et al. 2013, López-López et al. 2013, Monsarrat et al. 2013). Given the considerable parental investment of vultures during their lengthy breeding period (Mundy et al. 1992, Margalida and Bertrán 2000), an optimization of the time spent in searching and obtaining food is expected. In this sense, during the incubation and chick-rearing phases, adult breeders would regularly attend provisioning

Table 6. Most parsimonious models aimed at assessing the effect of environmental and management factors on Eurasian griffon vulture *Gyps fulvus* maximum numbers feeding at study sites, depending on their age classes and their relationship with other vulture species. AICc: Akaike's Information Criterion corrected for small sample size. The estimated value of the variable and its relationship (+/−) to the number of griffon vultures at feeding sites, and the standard error, are shown.

Model no.	Response parameter and *most parsimonious model*	Variable	Estimate	SE
1	Max. no. non-adults simultaneously feeding	Intercept	0.142	±590.36
	Breeding pairs same species + provisioning frequency + other feeding sites + biomass annually provisioned	*Breeding pairs same species*	−0.002	±1.023
		Provisioning frequency (weekly)	1.026	
		Provisioning frequency (non-periodic)	−0.084	±0.290
		Other feeding sites	0.000	
		Biomass annually provisioned	0.006	±0.003
2	Max. no. adults simultaneously feeding	Intercept	−0.851	±536.64
	Breeding pairs same species + other feeding sites + life-cycle phase × provisioning frequency	*Breeding pairs same species*	−0.003	±0.930
		Other feeding sites	0.042	±0.547
		Life-cycle phase × frequency (chick-rearing × weekly)	0.643	±0.460
		Life-cycle phase × frequency (chick-rearing × non-periodic)	0.000	
		Life-cycle phase × frequency (non-breeding × weekly)	−0.016	±0.427
		Life-cycle phase × frequency (non-breeding × non-periodic)	0.000	
3	Proportion other vulture spp./griffon vultures	Intercept	−0.199	±1.308
	Time + biomass annually provisioned	*Time*	−3.422	±2.190
		Biomass annually provisioned	−0.001	±0.000

Note: For model 1, AICc = 99.61, L ratio $\chi^2 = 25.32$, scaled deviance = 80, log-likelihood = −41.88, $P < 0.001$. For model 2, AICc = 79.09, L ratio $\chi^2 = 39.82$, scaled deviance = 81, log-likelihood = −31.29, $P < 0.001$. For model 3, AICc = 91.30, L ratio $\chi^2 = 37.89$, scaled deviance = 82, log-likelihood = −37.08, $P < 0.001$.

sites where the food was more predictable and accessible (Fig. 1; Moreno-Opo et al. 2010, Monsarrat et al. 2013). We found this pattern even in territorial species such as the Egyptian vulture for which the commitment to remain within the territories during breeding season prevents large numbers of birds at feeding sites during this time in non-migrant populations (García-Heras et al. 2013). By contrast, non-adult cinereous vultures show a greater presence at feeding sites in periods different than those selected by adults, possibly to reduce intraspecific competition or to minimize the risk of starvation during the early stages after fledging and emancipation (from September to December; Moreno-Opo et al. 2010). The non-adult bearded vultures did not follow attendance patterns similar to that of adults; they were more frequent and abundant at provisioning sites during the winter period, characterized by adverse weather and reduced food availability (carcasses are hard to find because of snow cover). Non-adult Egyptian and griffon vultures did not show a more pronounced presence at feeding sites in any season.

Effect of feeding site management

The type of management of the feeding site was particularly influential on vultures most dependent on predictable food sources (Donázar et al. 2009*a*, Duriez et al. 2012, Monsarrat et al. 2013). Thus, the occurrence of both adults and especially immature bearded vultures was linked to continued and regular inputs and to a greater overall biomass supplied at the feeding points along the years before and during our field study. This relationship can generate positive effects on survival rates of pre-adult populations (Oro et al. 2008, Margalida et al. 2014) but at the same time may cause the immoderate concentration of individuals around the feeding sites, triggered by predictability and abundance of food resources and conspecific attraction (Margalida et al. 2008, 2011*b*). This entails an increase in intraspecific interactions that would negatively impact productivity of breeding pairs located close

to the feeding sites (Carrete et al. 2006). This same pattern of positive selection for feeding sites with greater amounts of biomass occurred in the Egyptian vulture. The preference of both breeding and non-breeding individuals for these sites with abundant and regular carrion inputs is well documented (Benítez et al. 2009), and has shown to generate the onset of roosting sites (Ceballos and Donázar 1990). A higher frequency of periodic inputs also increased the numbers of non-adult griffon vultures. This pattern is consistent with the widespread and hoarding use of supplementary feeding sites by this species (Cortés-Avizanda et al. 2010), for which survival rates and population growth during the last few decades in Western Europe have been linked to the intensive management of feeding sites (Parra and Tellería 2004).

Other food sources

Our results suggest the existence of asymmetric trends regarding the availability of alternative food sources. On the one hand, adult bearded vultures were more common at provisioning sites close to areas with a greater abundance of extensive livestock, denoting a possible selection towards agro-grazing systems with abundant natural prey and less dependence on predictable food sources (Margalida et al. 2007). On the other hand, non-adult cinereous vultures and all age-classes of griffon vultures more regularly attended sites with a higher number of other feeding points in the immediate surroundings. This indicates that territories with a denser network of supplementary provisioning sites can be an attractant for these groups (Deygout et al. 2009, 2010), according to their more pronounced gregarious behavior and their depedence on the information provided by other vultures to find the carcasses (Cortés-Avizanda et al. 2014).

Management recommendations

If we aim to favor those species with the more unfavorable status, and thus reduce the presence of lower priority species from a conservation perspective (i.e., griffon vulture), measures should be applied primarily to provide carrion at earlier hours and in moderate amounts throughout the year. In the case of the Egyptian vulture whose population trend is the only negative one among vultures in Europe (BirdLife International 2013), it is additionally important to ensure frequent carrion inputs with a greater biomass (Benítez et al. 2009). This would also facilitate the establishment of associated roosts, essential for optimizing recruitment rates of individuals in nearby breeding territories (Ceballos and Donázar 1990, Donázar et al. 1996, Cortés-Avizanda et al. 2010). For the bearded vulture, food should be provided mainly during the chick-rearing period on a periodic and frequent basis so as to improve its breeding performance. Inputs outside of this season should be curbed as they mainly favor the concentration of non-adult birds to concrete locations (Margalida et al. 2011*b*) thus affecting the dispersal behavior and occupation of new territories in peripheral locations to the current range (Margalida et al. 2013). Finally, feeding sites for cinereous vultures should be located next to breeding colonies to encourage their use by adults, benefitting where appropriate from by-products of hunting activities (Moreno-Opo et al. 2010, 2012). These optimized protocols for endangered vultures may also suit the feeding requirements of other avian scavengers exhibiting negative population trends or an unfavourable conservation status at European level, such as the red kite *Milvus milvus* (Knott et al. 2009).

Despite the need to explore best options for managing supplementary feeding for scavengers, it is advisable that conservation policies mimic the natural dynamics of carcasses in the wild for regulating relationships between predator and prey species only under ecological pressures (Wilmers and Post 2006, Barton et al. 2013). These policies may also mitigate influences from ureasonable health guidelines (Donázar et al. 2009*b*, Margalida et al. 2010, Margalida and Colomer 2012). Consequently, managers and policy-makers should prioritize: (1) the proper implementation of current legislation in Europe in the management of animal by-products (European Commission 2011, Margalida et al. 2012), (2) the practical management patterns learnt from this and other similar studies (Cortés-Avizanda et al. 2010, Moreno-Opo et al. 2015), and (3) programs countering threats related to carrion quality, such as poisoning from the illegal use of toxic baits (Virani et al. 2011, Margalida 2012, Ogada et al. 2012), veterinary drugs (Gilbert et al. 2007, Margalida et al. 2014)

or lead intoxication resulting from hunting activities (Gangoso et al. 2009, Hernández and Margalida 2009, Finkelstein et al. 2012) whose use should be banned and replaced with other ammunition made with environmentally friendly materials (Thomas 2013).

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