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Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures

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ABSTRACT

Supplementary feeding is one of the most common techniques used to alleviate threats to scavengers species related to the quality and availability of food resources. Because supplementary feeding may have undesired effects, the management of supplementary sites should be optimized from an ecological and conservation perspective. We installed high-resolution videocameras at six Spanish feeding stations recording more that 7500 h of observations at 105 feeding events. We analyzed food preferences in the four European vulture species (Eurasian griffon vulture *Gyps fulvus*, Egyptian vulture *Neophron percnopterus*, bearded vulture *Gypaetus barbatus* and cinereous vulture *Aegypius monachus*) as they relate to the characteristics of the food remains and carcasses provided at feeding sites. Our results suggest that carrion features (format, scattering, prey species, biomass and items) influence differential selection between species and age-classes. At a species level, large inputs of unscattered carrion increased the abundance of actively feeding griffon vultures. The ratio of the abundance of bearded vultures, Egyptian vultures and cinereous vultures with respect to griffon vultures was favored when less biomass was supplied and when the food provided was not presented as whole carcasses. Thus, using medium-size ungulates (i.e. sheep and goats) presented as small, abundant and scattered pieces favors the consumption of the resource by the most endangered species. Our findings can be used to optimize the supplementary provisioning of vultures in cases where this conservation tool is considered essential for managing targeted species or population groups.

1. Introduction

The application of sound and effective conservation measures based on scientific evidence requires an analysis of the characteristics of the threat and an assessment of the impact and ecological effects of proposed conservation actions (Arlettaz et al., 2010). Supplementary feeding is a common management tool consisting of the provision of safe and high quality food to particular populations to mitigate anthropogenic impacts that cannot be otherwise eliminated in the short term and that may affect the conservation status of a species (González et al., 2006; Oro et al., 2008; Robb et al., 2008). It aims to increase survival rates, reduce the risk of ingestion of contaminated food (Oro et al., 2008), and improve breeding performance, even contributing to the settlement of new breeding territories (González et al., 2006; Schoech et al., 2008). In addition to these positive effects, undesired impacts on non-target species may occur (Cortés-Avizanda et al., 2009). Similarly, unintended impacts on demographic and behavioral parameters of the target species may occur when applied protocols do not integrate all of the appropriate variables (Carrete et al., 2006; Robb et al., 2008; García-Heras et al., 2013).

Vultures play a key role in temperate ecosystems due to their consumption of carrion, a trophic resource with an unpredictable occurrence in the wild but of great importance given its high energy transfer (Wilson and Wolkovich, 2011, Moleón et al., 2014). Four vulture species occur in Europe: the bearded vulture (*Gypaetus barbatus*), the cinereous vulture (*Aegypius monachus*), the Egyptian vulture (*Neophron percnopterus*) and the Eurasian griffon vulture (*Gyps fulvus*; Table 1). In Europe, the conservation

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status of these species differs: while the first three are considered threatened, the griffon vulture exhibits larger and unthreatened populations (Table 1). Spain is the greatest vulture stronghold in the Western Palearctic hosting 67%, 96%, 70% and 91% of the European breeding pairs of the bearded, cinereous, Egyptian and griffon vultures, respectively (BirdLife International, 2013; Deinet et al., 2013). One of the main limiting factors for these birds is food due to changes in its geographic occurrence, quality and unavailability as a result of changes in agro-grazing systems and repeated poisoning events (Donázar et al., 2009a; Margalida and Colomer, 2012; Ogada et al., 2012; BirdLife International, 2013). To counter these threats, there are several official ongoing conservation programs in different European countries with supplementary provisioning constituting one of the primary activities (see review in Donázar et al., 2009a; Margalida et al., 2010). This occurs primarily through the provision of carrion at specific locations close to breeding sites, in accordance with requirements of sanitary regulations for the management of animal by-products not intended for human consumption (Donázar et al., 2009b; Margalida et al., 2010). This supplementary provisioning has partly mitigated the negative effects of widespread and compulsory removal of livestock carcasses from the wild, though it has been shown to be insufficient in meeting the ecological requirements of scavenger species, populations and age-classes at a global scale (Donázar et al., 2009b; Margalida et al., 2012a).

Despite the fact that vultures share a common food source, there are ecological, morphological and behavioral adaptations that have led to specialization in the consumption of carrion and evolutionary resource-partitioning by the different species (König, 1983; Houston, 1988; Hertel, 1994). This includes interspecific co-existence and facilitation processes in the exploitation of geographically and temporally limited resources (Jackson et al., 2008; Moleón et al., 2014), generating intra- and interspecific competition and hierarchical relationships (Wilmers et al., 2003; Kendall et al., 2012). This is particularly relevant in European vulture species of which one, the griffon vulture, monopolizes the largest quantity of biomass at carcasses due to its competitiveness, larger population size and morphological features allowing it to feed from the inner parts of cadavers (Hertel, 1994; Cortés-Avizanda et al., 2010). This has meant that, due a the lack of detailed knowledge about patterns of resource consumption, most supplementary provisioning programs (mainly in Spain) have primarily favored the species of least conservation interest (Parra and Tellería, 2004; Cortés-Avizanda et al., 2010).

Outside of the aforementioned knowledge on adaptations to scavenging, there are few studies in which the type and format of carrion selected by each species have been experimentally assessed within controlled observational conditions (Moreno-Opo et al., 2010). Moreover, no previous studies provide accurate information on the four vulture species together in sampling areas with sufficiently abundant populations (Cortés-Avizanda et al., 2010; Duriez et al., 2012). Detailed information on the prey typology selected by different age-classes and species should be considered in supplementary provisioning initiatives, considering the relevance of this management technique in a global scenario with ongoing changes in landscape characteristics, sanitary policies, illegal poisoning, veterinary drugs and lead poisoning (see reviews in Donázar et al., 2009a; Ogada et al., 2012).

This paper aims to determine the selection patterns of different types and formats of carrion provided at supplementary feeding sites by different age-classes of European vultures. Through an accurate and detailed observational process in which a variety of carrion characteristics such as the size, amount and appearance were experimentally manipulated, we hypothesized that according to the different scavenging adaptations, vulture species and ages should diverge in their feeding performance. Thus, feeding patterns of vultures with regards to their relative abundance and their relationship to the main monopolizing species (i.e. the griffon vulture) were expected to vary according to the food characteristics in supplementary feeding sites. Accordingly, we hypothesized that the most endangered species (i.e. Egyptian and bearded vultures), being the most specialized for particular carrion characteristics, should reduce competition with other vultures selecting more specific, small and dispersed food remains. On the contrary, the most abundant and behaviorally dominant vultures (i.e. cinereous and griffon vultures) should adapt their feeding to inputs with a greater biomass. Based on our findings, we provide recommendations to facilitate the implementation of management protocols in supplementary provisioning programs.

2. Methods

2.1. Study area

The study was carried out at six sites in the Iberian Peninsula (Spain), three in the northeast (Pyrenean Mountain range) and three in the central-west (Sierra Morena, Montes de Toledo-Sierra de San Pedro ranges, Fig. 1). Active supplementary feeding points

Table 1
Population and main biological traits of the four vulture species inhabiting Europe.

Species	Breeding pairs (n) in Europe[a]	Trend of European populations[b]	Breeding behaviour[c]	Social behaviour[c]	Nesting habitat selection[c]	Morphological specialization for feeding[c,d]	Migratory status[c]
Bearded vulture	200	+	Territorial	Individualists except non-breeders	Caves in mountain cliffs	Gulper (bones, small pieces of meat)	Sedentary
Cinereous vulture	2147	+	Colonial and territories within colonies	Partially gregarious	Trees in mature forests	Ripper (tendons, muscle)	Sedentary
Egyptian vulture	~2000	–	Territorial	Individualists except non-breeders	Caves in cliffs and gorges	Scrapper (small pieces)	Long-distance migrant
Eurasian griffon vulture	28 088	+	Colonial	Gregarious	Ledges in cliffs and gorges	Gulper (all meat parts)	Long-distance -only ~20-30% of juveniles- and sedentary

Main sources.
[a] Deinet et al. (2013).
[b] BirdLife International (2013).
[c] Cramp (1998).
[d] Hertel (1994).

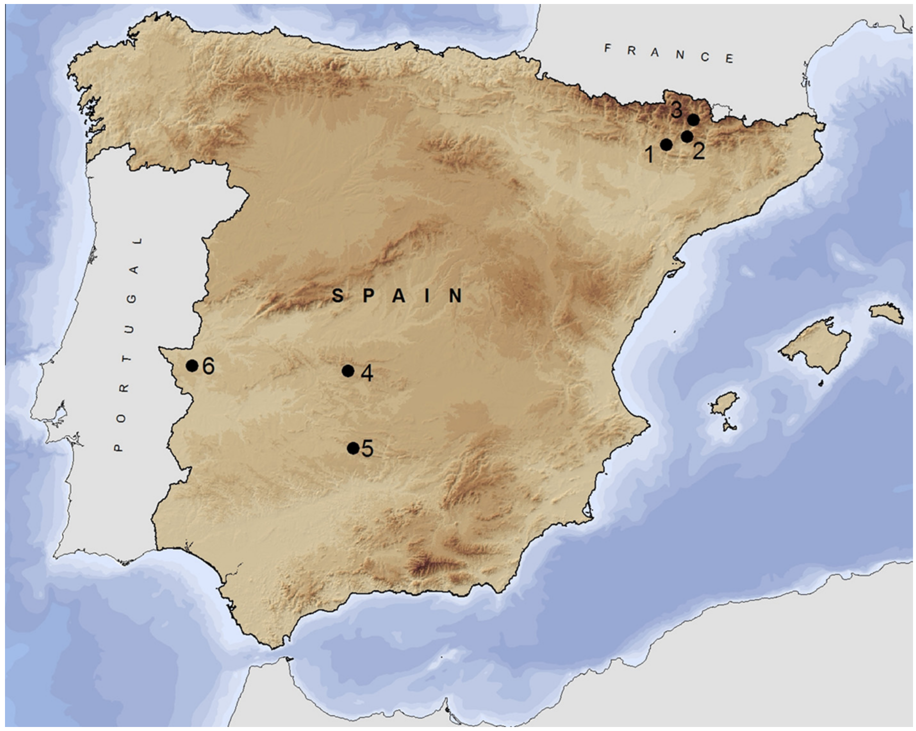


Fig. 1. Study area in the Iberian Peninsula. The locations (dots) where experimental carrion inputs were controlled are shown, in northeastern (1 = Tremp; 2 = Buseu; 3 = Alt Pirineu Natural Park) and central-western (4 = Cabañeros National Park; 5 = Alcudia-Sierra Madrona Natural Park; 6 = Sierra de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

maintained within the framework of official conservation programs were chosen as experimental sites. We selected one site per sub-region with each of the following characteristics: weekly abundant provisions (>100 kg/input; sites 2, 4; Fig. 1); approximately fortnightly and less abundant inputs (<100 kg/input; sites 1, 6; Fig. 1); and non-periodic light inputs (<100 kg/input; sites 3, 4; Fig. 1). These various site selections were made to include a variety of different management scenarios previous to the start of the study. In this way, we aimed to reduce heterogeneity and conditioning in the site-specific responses of avian scavengers between sub-regions due to different previous management approaches at the experimental study sites.

The two Iberian regions, of varying climate, vegetation, altitude and land use, were selected to include representative populations of the four European vultures. Within the northeastern sub-region (sites 1, 2, 3; Fig. 1), 347 breeding pairs of griffon vultures, five pairs of cinereous vultures, 18 pairs of Egyptian vultures and 15 pairs of bearded vultures were present in a 25 km radius around the locations of carrion inputs. For the central-western sub-region (sites 4, 5, 6; Fig. 1) the numbers of breeding vulture pairs were, respectively, 90, 148, 7 and 0 (authorś unpublished data). No changes in their status were detected after the development of the supplementary provisioning and monitoring program.

The northeastern area is situated between the Mediterranean continental and the high-altitude mountain climatic sub-regions. Mean temperature in winter (January) is 2.9 °C and 20.3 °C in summer (July). The altitude of the study locations ranged between 1045 and 1330 m asl. The vegetation of the surroundings was mainly formed by scot pine (*Pinus sylvestris*) forests, subalpine grasslands and a series of shrub-tree developments. The main socioeconomic land uses are extensive grazing, ecotourism and, to a lesser extent, big game harvesting. The central-western subregion exhibits a continental Mediterranean climate with hot summers, with an altitude ranging from 521 to 686 m asl. Mean temperature in winter (January) is 5.7 °C and 25.4 °C in summer (July). The prevailing vegetation is holm oak (*Quercus rotundifolia*) and cork oak (*Quercus suber*) accompanied by other Mediterranean species, in the form of pasturelands (dehesas) or unmanaged forests. Big game hunting, logging activities mainly for cork exploitation, and extensive grazing represent the main income for the local population.

2.2. Study design and data collection

Between May 2009 and March 2011 an experimental program of carrion inputs at six supplementary feeding sites was carried out. The provided carrion consisted of cadavers and remains of livestock and wild ungulates (Table 2). Carrion was supplied periodically at each point, by alternating inputs approximately on a weekly basis at the three sites of each sub-region. We controlled the characteristics of the carrion provided (Table 2) and combined the different kinds of inputs periodically. Thus, at the end of the two-year experiment, a similar number of inputs for each combination of the studied variables had been implemented (Table 2).

Carrion exploitation was continuously monitored during the day, from the time of its provision until three days later. 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. The recording quality was controlled so that images occurred in a sequence of 20 frames per second with a resolution of 5 megapixels. This high resolution allowed zoom images to capture accurate data on the studied variables (see sections below). Images were stored for subsequent visualization using the AV program v.5.1.4.239 Application Manager.

2.3. Response and explanatory variables

The recordings of each three-day event of carrion consumption were visualized by registering different response and independent

Table 2
Independent variables regarding the characteristics of the carrion in experimental inputs, considered to assess their influence on the presence and relative abundance of vulture species with feeding activity. The number of inputs in which each category was provided is shown in brackets.

Variable	Type	Description	Categories
Format	Categorical	Type/characteristics of the provided carrion	Whole carcass (one or more) (25) Carcass/es divided into at least six pieces (12) Remains (guts, legs and various pieces) including meat and bones (54) Bone remains (legs, backbones, etc.) (14)
Scattering	Categorical	Radius of dispersion of the carrion parts/remains from a central point	Concentrated (<2 m radius) (35) Not concentrated (⩾2 m radius) (70)
Prey species	Categorical	Species of the provided carrion	Ovine/caprine (sheep *Ovis aries* or goat *Capra hircus*) (29) Porcine/bovine (pork *Sus scrofa* var. dom. and cow *Bos taurus*) (39) Wild ungulates (red deer *Cervus elaphus* or wild boar *Sus scrofa*) (23)
Biomass	Continuous	Weight (kg) of the carrion measured with a digital scale or a visual assessment by trained technicians	
Items	Continuous	Number of pieces/items in which the divided carcass was delivered	

variables. The first were to determine the number of actively feeding vultures, discarding those perched or landing but not eating. To this end, we considered: (1) bird counts in each 10-min period (i.e., every 10 min a census of all feeding vultures was carried out); and (2) the estimated total number of vultures that fed on the carrion after each input, expressed as the sum of birds recorded in all 10-min periods. Vultures were assigned to the species and age-class considered. We divided age classes into "*Adults*" (birds showing typical adult plumage; i.e. Forsman, 2003), "*Non-adults*" (birds exhibiting juvenile or sub-adult phases of plumage) and "*All*" (all present, active feeding birds independent of age). As a result, we considered six variables regarding prey preferences for each vulture species: (1) maximum simultaneous number of individuals (from each 10-min period count), (2) maximum simultaneous number of adult individuals, (3) maximum simultaneous number of non-adult individuals, (4) estimated total number of individuals (summing the counts of all 10-min periods), (5) estimated total number of adult individuals, and (6) estimated total number of non-adult individuals.

Since the griffon vulture monopolizes and exploits the greatest biomass of carrion provided at supplementary provisioning sites (Moreno-Opo et al., 2010; Cortés-Avizanda et al., 2010) the ratio between the occurrence of each vulture species and the griffon vulture was considered as a response variable to evaluate possible exclusion-competition mechanisms that may occur between the two groups in relation to explanatory variables.

The carrion characteristics (Table 2) were assumed to be independent variables. To consider the influence of the management regime of each feeding site previous to the start of our experiment, we included the sub-region and the provisioning site (nested in the sub-region) as random variables. Despite its importance in the attendance patterns of vultures (Cortés-Avizanda et al., 2010; Moreno-Opo et al., 2010) we did not consider time circumstances (hours, seasons and life-cycle phases) as covariables since the proportion of the different types of provisions were similarly distributed. As a consequence of the scarcity or absence of different vulture species in some regions (i.e. bearded vulture in the Mediterranean region and cinereous vulture in the Pyrenees) or periods (Egyptian vulture from September to February), we built specific subsets of the general database aimed at fitting the analyses of prey selection to the spatio-temporal presence of each species. In this regard, we did not provide the categories "bone remains" and "divided carcass/es" in the Mediterranean and Pyrenean regions, respectively, in our experimental trial.

Pseudoreplication between subsequent counts of 10 min that could lead to the lack of independence of the observations was discarded. Based on the analysis and data gathered from the images, it was observed that vulture presence was dynamic and continuously changing (Cortés-Avizanda et al., 2010, Moreno-Opo and Margalida, 2013). In most cases, the time spent eating by individuals was less than 10 min (authorś unpublished data). To avoid time autocorrelation among experimental sites we provided carrion on a weekly basis alternating inputs at different sites of the same sub-region. Inputs were never supplied on the same day at different study sites.

2.4. Analytical procedures

The response variables to be included in the analyses were examined through Spearman's rank correlation (ρ) index to test their relationships and identify possible areas of simplification. The response variables regarding the total number of vultures attending carrion input were highly correlated with those response variables related to the maximum simultaneous number of birds ($\rho > 0.75$, for all studied species and all age categories). Thus we only included in the models the three variables related to the total number of vultures (adult birds, non-adult birds and all birds).

The dependent variables were log-transformed to adjust to a normal distribution using a Kolmogorov-Smirnov test (Zuur et al., 2009). Nevertheless, the Egyptian vulture variables do not follow a normal distribution due to the low number of input events with its presence (27.2%, $n = 44$). Consequently, we transformed the response variables for this species to fit a binomial distribution (presence/absence) allowing for the performance of parametric analyses for attendance patterns. The ratio between Egyptian and griffon vulture numbers was analyzed through non-parametric tests, by comparing the mean ranks of categorical variables with a Kruskall-Wallis test, and for continuous variables through a Spearman's rank correlation and *t*-test.

Generalized Linear Mixed Models (GLIMMIX, 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 vulture) were performed to determine the effect of different characteristics of the carrion inputs on the number of vultures feeding. The independent variables included in these multivariate analyses were the categorical *format*, *scattering*, *prey species*, and the continuous *biomass* and *items* (Table 1). All of these were included individually in each model along with the feeding site (nested in sub-region) as random variables. We performed this procedure because the number of independent variables exceeded one-tenth of the studied events (Harrel et al., 1996) for all vulture species except the griffon vulture. Model building was based on the Akaike Information Criterion corrected for sample size (AICc) aiming at selecting the most parsimonious subset of variables (that with the lower AIC, Burnham and Anderson, 2002). Subsequently, to estimate the effects of each studied variable included in the most parsimonious models we applied the Likelihood Type 1 test. We also performed a frequency analysis (Chi-square test with Yates correction) to compare the relation between the number of individuals present at carrion inputs and their populations in the study area. We used the software Statistica 6.1 (StatSoft, Tulsa) for the statistical analyses.

3. Results

From 174 performed inputs, we used 105 for the analyses with all considered variables correctly monitored and with 8990 kg of biomass supplied. Subsets of the number of inputs aimed at analyzing the food preferences of each species were distributed as follows: 74 inputs for bearded vultures, 31 for cinereous vultures, 54 for Egyptian vultures and 105 for griffon vultures. Over 7500 h of video-recordings were registered, which allowed the counting of 24 520 observed individuals (not necessarily different birds): griffon vultures (20 544), cinereous vultures (2773), bearded vultures (903) and Egyptian vultures (300) (Appendices 1 and 2). The species most frequently attending carrion inputs was the griffon vulture (91.4%), followed by the cinereous vulture (87.1%), the bearded vulture (55.4%) and the Egyptian vulture (27.2%). There were differences in attendance patterns (observed) in relation to the breeding numbers (expected) at the local (<25 km radius around selected sites; $\chi^2_1 = 90.14$; $p < 0.001$) and at the country level ($\chi^2_1 = 246.81$; $p < 0.001$). The bearded vulture exhibited the highest proportional occurrence locally (0.81 and 0.15), expressed as the ratio between total numbers and the number of adults feeding on carrion inputs vs. the breeding population, divided by the number of carrion inputs, followed by the cinereous (0.60 and 0.15), griffon (0.44 and 0.12), and Egyptian (0.27 and 0.25) vultures. According to age-classes, most individuals feeding at the provided carcasses were *Non-adults* (73.3%, 74.5%, 79.9% for griffon, cinereous and bearded vultures respectively), except for the Egyptian vultures which were mainly *Adults* (91.3%).

The attendance of non-adult bearded vultures at carrion inputs was not significantly correlated to any of the variables considered. However, adults fed on carcasses when they were not concentrated, consisted of bones or meat and bone remains and when the number of pieces into which the carcass/es was divided was higher, and preferably from sheeps/goats (Table 3 and Fig. 2). Similarly, the ratio of all bearded vultures with respect to griffon vultures was greater at carrion inputs made up of scattered bone remains or of less biomass (Table 3 and Fig. 3).

Adult Egyptian vultures selected carrion inputs with a greater biomass of ovine-caprine species and mixed meat and bone pieces (Tables 3 and 4). Prey species and carrion format also determined a positive relationship between Egyptian and griffon vultures (Table 3).

The numbers of all age-classes of cinereous vultures were positively related to a higher biomass presented as carcasses divided into at least six pieces and scattered in the field (Table 3 and Fig. 2). Moreover, non-adult cinereous vultures preferred carcasses from ovine and caprine species (Tables 3 and 4).

Lastly, griffon vultures were more abundant at piled and unscattered carrion pieces or carcasses and at those with a greater biomass (Table 3 and Fig. 2). Both whole carcasses and meat remains favored griffon vultures over other species (Fig. 3).

4. Discussion

Although the assessment of the feeding patterns in vultures has developed over several decades (i.e. König, 1983; Houston, 1988; Hertel, 1994), there are no previous case studies using monitoring techniques allowing the precise and continuous analysis of abundances of actively feeding individuals (i.e. not just the presence of birds), controlling the characteristics of the provided carcasses and across a wide geographic scale. Our study allowed us to evaluate the joint feeding patterns of the four European vulture species in areas with abundant populations to illustrate interspecific relationships with the categories of the carrion provided (Table 4).

4.1. Species-specific food choice

The bearded vulture consumes different carrion parts, both meat (especially selected by adults during the chick-rearing period) as well as bone remains (Brown and Plug, 1990; Margalida et al., 2009). It is the only species able to obtain most of its energetic requirements through the ingestion of medium and small bone remains (Houston and Copsey, 1994), mainly from those parts with higher nutritive content (Margalida, 2008). Therefore, adult bearded vultures showed a higher efficiency of food intake when inputs included bones and a larger number of items.

With respect to the cinereous vultures, prey selection of carcasses divided into several pieces, mainly from sheep and goats, and with a high biomass and number of pieces attracted a greater number of individuals of all age classes (Moreno-Opo et al., 2010). These features allow birds to optimize their provisioning performance given their ability to take pieces of muscle, tendons and midsized viscera scattered over a wide area (König, 1983).

The Egyptian vulture fed on inputs consisting of greater quantities of mixed scraps of meat and bones from sheep and goats. This reflects the specieś adaptation to the consumption of small and scattered remains due to its pecking behavior, peripheral to the central points of feeding activity by other vulture species (König, 1983; Meretsky, 1995). Its attendance pattern was less frequent and more irregular than the other vulture species, possibly due to (1) a greater preference for other food sources of natural and wild origin (Donázar et al., 2010; Margalida et al., 2012b); (2) a better prospecting aptitude given the patchy/random distribution of the breeding territories (García-Heras et al., 2013); and/or (3) the preference for particular vulture restaurants with constant and abundant evening inputs of carrion pieces attracting a greater number of birds (Donázar et al., 2009a; Cortés-Avizanda et al., 2010) located at a few points, essential to the information exchange between individuals (Ceballos and Donázar, 1990; Donázar et al., 2009a).

Finally, the griffon vulture responded to carrion inputs according to its ability to better exploit large carcasses from which it tears and consumes internal parts (Bosé et al., 2012; Duriez et al., 2012).

4.2. Age differences

With the exception of the Egyptian vulture, the juvenile and subadult ratio was four to five times greater than that of adults in all the studied species. This suggests a higher feeding rate and consequently, a possibly greater dependence on predictable food sources by the non-breeding individuals (Oro et al., 2008; Donázar et al., 2009a; Moreno-Opo et al., 2010). Adults may take advantage of their experience and skills in finding other food items with less predictable occurrence (Margalida et al., 2009). Otherwise, the greater proportion of non-adults could reflect the age ratio in the local population but due to the lack of global age ratio estimates in wild populations of our study areas, this hypothesis could not be tested.

Non-adult vultures showed carrion selection patterns that were less specialized than adults. This was particularly apparent in the bearded vulture, in which no carrion characteristics were significantly selected by non-adults, thus highlighting plasticity and a greater dependence on the use of all resources provided at the

Table 3
Statistically significant relationships of numbers of European vulture species (top to bottom, bearded, Egyptian, cinereous and griffon vulture) actively feeding with the explanatory studied variables, from the GLIMMIX analysis. The relationship between the variables is also shown, positive (+) or negative (−) for continuous variables, and the category/categories more positively correlated with the response variable.

Species	Response parameter	Explanatory variable	χ^2	*df*	*p*	Relation
Bearded vulture	All birds actively feeding (n)	Format of carcass	12.51	2,73	0.001	Bones > others
		Scattering	4.67	1,74	0.030	Not concentrated > concentr.
		Prey species	8.41	2,26	0.014	Ovine-caprine > others
	Adults (n) actively feeding	Format of carcass	14.70	2,70	<0.001	Bones > remains > others
		Scattering	5.22	1,38	0.022	Not concentrated > concentr.
		Items-pieces (n)	8.49	1,21	0.003	+
	Ratio bearded/griffon	Format of carcass	25.93	2,31	<0.001	Bones > others
		Scattering	6.79	1,67	0.009	Not concentrated > concentr.
		Biomass delivered	7.01	1,25	0.029	−
Egyptian vulture	All birds actively feeding (n)	Format of carcass	6.56	3,44	0.014	Remains > others
		Prey species	4.70	2,41	0.045	Ovine-caprine > others
		Biomass delivered	5.70	1.44	0.016	+
	Ratio Egyptian/griffon	Format of carcass	9.26[a]	4,42	0.054	Remains > others
		Prey species	10.71[a]	3,42	0.013	Ovine-caprine > others
Cinereous vulture	All birds actively feeding (n)	Prey species	4.56	2,23	0.003	Ovine-caprine > others
		Biomass delivered	4.49	1,24	0.033	+
	Non-adults (n) actively feeding	Format of carcass	7.94	2,21	0.018	Divided carcass > others
		Scattering	8.21	1,22	0.004	Not concentrated > concentr.
		Prey species	4.48	2,26	0.034	Ovine-caprine > others
		Biomass delivered	5.45	1,23	0.019	+
	Adults (n) actively feeding	Format of carcass	16.36	2,21	<0.001	Divided carcass > others
		Scattering	16.15.	1,25	<0.001	Not concentrated > concentr.
		Biomass delivered	15.56	1,18	0.037	+
Eurasian griffon vulture	All birds actively feeding (n)	Biomass delivered	19.66	1,90	<0.001	+
	Non-adults (n) actively feeding	Scattering	8.81	1,84	0.002	Concentrated > not concentr.
		Biomass delivered	8.64	1,85	0.003	+
	Adults (n) actively feeding	Biomass delivered	11.41	1,102	<0.001	+
	Ratio griffon/other vulture species	Format of carcass	8.59	2,63	0.035	Whole carcass > others

[a] Kruskal-Wallis test.

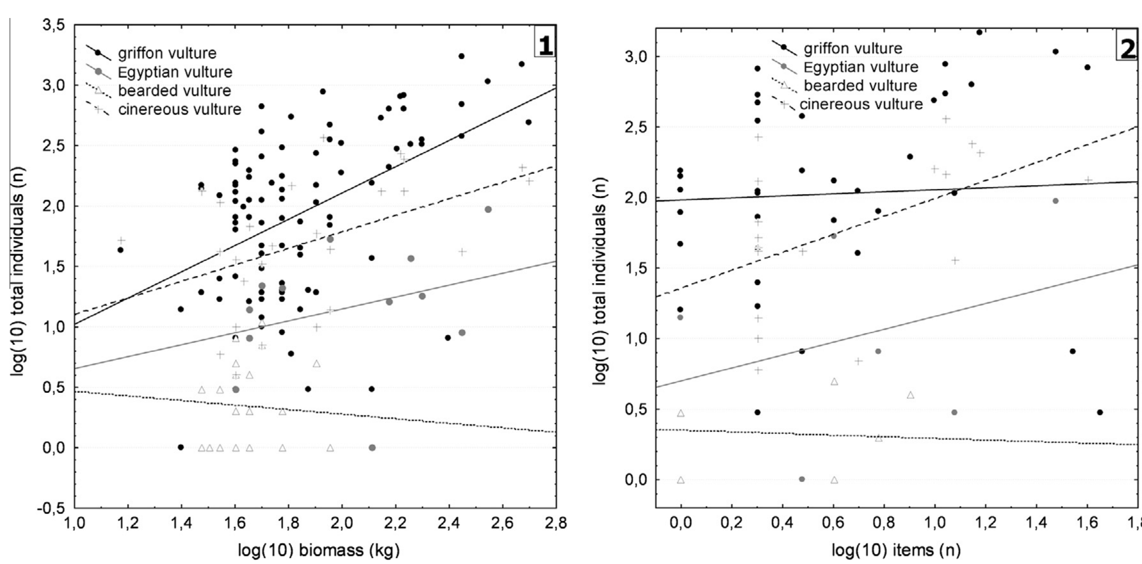


Fig. 2. Linear regression of the number of individuals – without distinguishing age-classes-of the four European vulture species actively feeding with (1) the biomass (kg) of provided carrion, and (2) the number of items in which the carrion was delivered. These figures show general relationships for all of the studied species being statistically significant only for the Egyptian, cinereous and griffon vultures in 1 and none in 2.

feeding points (Carrete et al., 2006). However, an additional explanation may be related to the characteristics of bone remains, that can accumulate in the feeding site and be consumed several weeks after provisioning (Brown and Plug, 1990), provoking the regular presence of non-territorial individuals. Conversely, in the cinereous vulture intraspecific hierarchical phenomena could mean that non-adults were favored by carcasses from sheep and goats, which could contribute to the decrease in the likelihood of aggressive interactions with other adults (Wallace and Temple, 1987). Selection patterns in the griffon vulture were similar between adults and non-adults as was previously shown in other European populations (Duriez et al., 2012).

Egyptian vultures observed at supplementary feeding sites were mainly adults, likely due to a number of reasons. Juvenile individuals remain in African wintering grounds and do not return to European breeding areas until their second calendar year or later (Ceballos and Donázar, 1990; Meyburg et al., 2004). Non-adult individuals present during the breeding–migration seasons tend

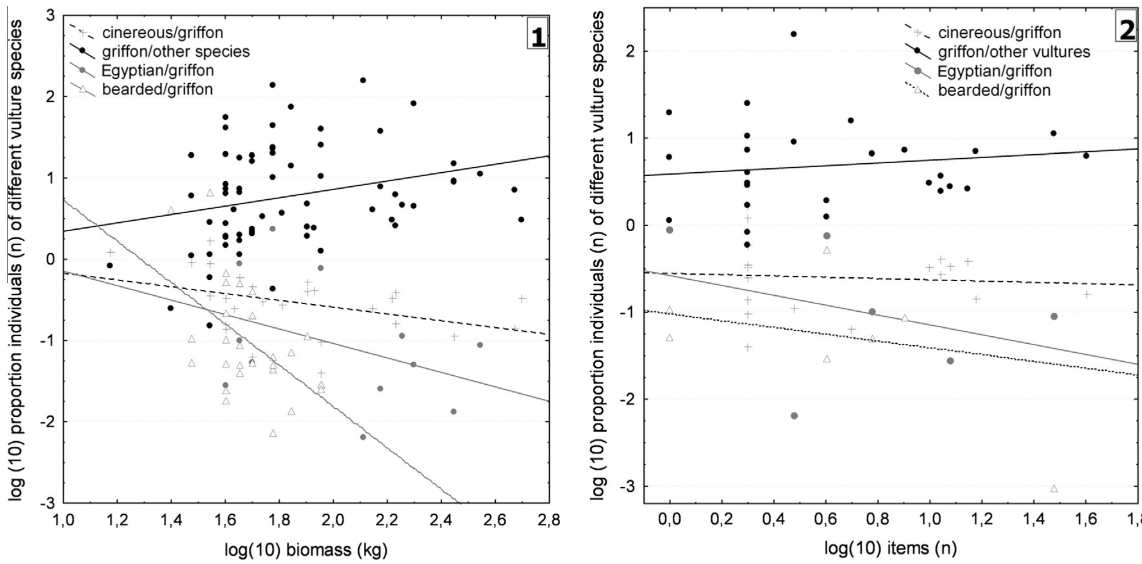
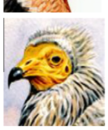
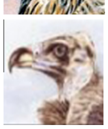
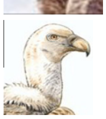


Fig. 3. Linear regression of the ratio between individuals actively feeding of bearded, cinereous and Egyptian vulture species with respect to griffon vultures, and (1) the biomass (kg) of carrion, and (2) the number of items in which the divided carrion was delivered. These figures show general relationships for all of the studied species being statistically significant only for the bearded vulture in 1.

Table 4
Positive selection of different characteristics of the carrion provided at experimental feeding sites (from categorical variables, see a detailed description in Table 1) by the four European vulture species (up to bottom, bearded, Egyptian, cinereous and griffon vulture). Tick-marks show statistically significant relationships, being their size related to p-values (greater size = $p < 0.001$; medium size = $0.001 \leqslant p < 0.01$; smaller size = $0.01 \leqslant p \leqslant 0.05$).

	Format				Scattering		Prey species		
	Whole carcass	Divided carcass	Meat/bone remains	Bones	Concentrated	Dispersed	Ovine-caprine	Porcine-bovine	Wild ungulates
				√		√	√		
			√				√		
		√				√	√		
	√				√				

to congregate in certain locations (roosting sites), usually associated with predictable food sources (Ceballos and Donázar, 1990). In this regard, our feeding sites were not associated with roosting sites, which are located close to other vulture restaurants in the studied regions.

4.3. Interspecific relationships

Our results showed species-specific segregation for several of the studied variables, highlighting the role of scavenging as driver of morphological and behavioral specialization (Hertel, 1994; Kendall, 2013). Thus, the griffon vulture, whose selection patterns match values related to a greater amount of food (Donázar et al., 2010, Duriez et al., 2012), has been the most abundant both at carcasses and at a global population level. In contrast, vultures that are more specialized in categories offering less overall biomass exhibit an unfavorable conservation status in Europe (BirdLife International, 2013). This is the case of the bearded and Egyptian vultures, both of which significantly preferred parts that provide much less biomass such as leg bones or the remains of entrails and meat. The fact that this study was performed at fixed feeding locations could enhance this effect and partially bias the conclusions with regards to unmanaged situations (Monsarrat et al., 2013). In this sense, the most specialist and territorial vultures balance this negative situation and optimize carrion ingestion with improved detection capabilities of small carcasses from a wider range of wildlife species randomly distributed in the field (Ceballos and Donázar, 1990; Margalida et al., 2009; Donázar et al., 2010).

In relation to interspecific competition, when carrion is available in greater and piled-up quantities and as whole carcasses, the ratio of griffon vultures significantly increased, with this species monopolizing most of the biomass and displacing other avian scavengers (Cortés-Avizanda et al., 2010, 2012; Bosé et al., 2012).

Cinereous vultures negatively selected the above variables and preferred divided carcasses presented as scattered and abundant pieces. This species will be outcompeted due to the increased number of griffon vultures (König, 1983) reducing its competitive efficiency and performance despite being dominant at the individual level due to its greater body size and a higher hierarchical position than the griffon vultures (Wallace and Temple, 1987).

The selection of bearded vultures for bones bestows exclusivity as an advantage in scavenging since this trait is not found in other species (Houston and Copsey, 1994). This preference could also be related to the selection of carcasses with less overall biomass and unconcentrated pieces by the bearded vulture, given that large carrion inputs are usually made up of meat scraps and larger carcasses. Finally, the Egyptian vulture optimized intake efficiency when the input consisted of remains formed by meat, entrails and bones. Due to its soft texture, this type of input would lead to small pieces and scraps not initially hoarded by the griffon vulture (Ceballos and Donázar, 1990; Donázar et al., 2010).

4.4. Management recommendations

Supplementary food provisioning to vultures is only effective when tailored to the feeding ecology of all species involved, particularly because differences in diet and behavioral dominance leads to unequal benefits between species and age classes. Thus, it is necessary to prioritize actions aimed at increasing the feeding rate of targeted species according to their ecological and conservation status. In the European case, managers should not present the food supply as whole carcasses which mainly favor the unthreatened griffon vulture (BirdLife International, 2013) but rather as small and abundant pieces of sheeps and goats scattered around the feeding area. This specially suits the preferences of bearded, cinereous and Egyptian vultures, which may benefit from a greater amount of pieces allowing more rapid access to the provided food (Cortés-Avizanda et al., 2010) and reducing competition with griffon vultures. This recommendation implies managing supplementary feeding programs in a way opposite to that of 1980s to 2000s, which led to the increase in the population of the griffon vultures, mainly in northern Spain (Donázar and Fernández, 1990; Margalida et al., 2010).

It is also important to consider other management options for optimizing supplementary feeding. In general, it is desirable to substitute the wide use of vulture restaurants with the promotion of light supplementary feeding in extensive livestock exploitations, as is being incipiently implemented in Spain or France according to the new legal framework (European Commission, 2011; Moreno-Opo et al., 2012). These new management options allow access to food in natural agro-grazing systems without the prior collection of the carcasses and are more sustainable in economic, ecological and social terms (Donázar et al., 2009a; Margalida et al., 2012a), and lead to a lower temporal predictability of food (Margalida et al., 2010).

Nonetheless, supplementary feeding sites will continue to play an important role in addressing and managing several current conservation issues. In the case of the bearded vulture, juvenile and adult survival may be strengthened by continuing inputs of legs and bones (Oro et al., 2008; Margalida et al., 2014). These inputs could promote the settlement of new breeding units and prevent the lack of juvenile dispersal if feeding points are distributed in a more sparse and widespread manner, even in areas peripheral to the main population nuclei (Margalida et al., 2013). Likewise, it is desirable to test the effect of food inputs in situations other than predictable feeding locations, especially in territorial species like the Egyptian vulture. This can be achieved through procedures of prey delivery within breeding territories, whose effectiveness has been demonstrated for endangered raptors such as the Spanish imperial eagle (*Aquila adalberti*) (González et al., 2006).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.10.022.

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