

# Foraging movements of Eurasian griffon vultures (*Gyps fulvus*): implications for supplementary feeding management

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**Abstract** The outbreak of bovine spongiform encephalopathy provoked restrictive European sanitary legislation that forced farmers to remove livestock carcasses from the wild. This had serious repercussions for the scavenger raptor guild. Against this background, we developed a study to analyse the foraging movements of Eurasian griffon vultures (*Gyps fulvus*) in northern Spain. We ringed 241 griffon vultures with alphanumeric plastic rings in Biscay between 2000 and 2011 and set experimental feeding stations in 24 sites over an area of 10,614 km<sup>2</sup>; recording re-sightings of the ringed vultures between 2005 and 2012. Using these re-sighting records, we tested whether birds randomly moved

long distances whilst searching for food, or if vulture re-sightings were restricted to a few feeding sites within a limited area. We summarised 329 field-work days, with an average of 2.06 ringed vultures re-sighted per day, accounting for 1,017 re-sightings. Adult vultures were detected in three separate foraging nuclei within the study area. Movements out of the main foraging nuclei were statistically less frequent than would be expected if adult vultures accessed all resources at a similar rate. Once established at breeding areas, subadult vultures behaved in the same way as adults. Our results suggest that vultures' home ranges are largely restricted to zones close to breeding areas. This has important consequences from a conservation point of view, suggesting that management decisions should take into consideration spatial scale effects.

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## Introduction

Vultures are long-lived scavenger birds that depend on the availability of medium and large carcasses. Shortages in food resources, direct persecution, poisoning, electrocution, diseases and collision with power lines and wind turbines have been the main causative factors leading to the decline of scavengers in Europe over the last hundred years and are still hazards for their conservation today (Cramp and Simmons 1980; Sarrazin et al. 1994; Carrete et al. 2009, 2011; Olea and Mateo-Tomás 2009; Tellería 2009; García-Ripollés and López-López 2011). In fact, long-term changes in livestock husbandry and management have occurred in many parts of Europe and Asia, and the decline in numbers of wild herbivores has diminished the extent and carrying

capacity of habitats that can support vultures (Gavashelishvili and McGrady 2006).

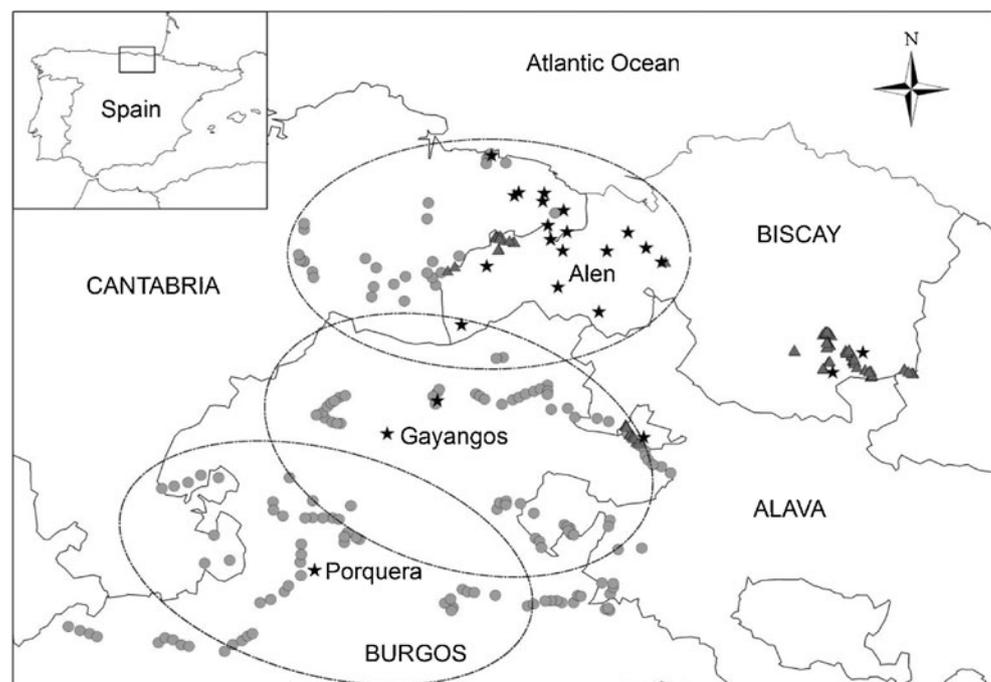
During the last decades, thanks to both legal protection and high food availability, griffon vulture (*Gyps fulvus*) populations have increased in the Mediterranean basin, especially in Spain, where the largest population of the species in the Western Palearctic is found (ca. 25,000 breeding pairs; Del Moral 2009). However, the outbreak of bovine spongiform encephalopathy in 2000, and the consequent sanitary legislation, caused restrictions in the traditional use of animal products to feed scavengers because state and regional administrations reinforced measures requiring farmers to remove or destroy the remains of dead livestock (Iñigo and Atienza 2007; Donázar et al. 2009a). The effects of this policy caused a halt in griffon vulture population growth, a decrease in breeding success, changes in foraging behaviour and an apparent increase in mortality amongst younger age groups (Donázar et al. 2009b; Zuberogoitia et al. 2009; Martínez-Abraín et al. 2012). However, these phenomena, and the magnitude to which they occurred, were not equally distributed throughout the breeding range of the species (Del Moral 2009).

The current, restrictive European sanitary legislation that requires all livestock carcasses to be removed from the wild (European Union Directive EU999/2011) 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). However, the implementation of these policies at a local level is promoting the concentration of carcasses at just a few sites called “vulture

restaurants” or “supplementary feeding stations” (Cortés-Avizanda et al. 2010; Margalida et al. 2010). Recently new legislation has been brought in which allows livestock carcasses to be left in the field, outside of the “vulture restaurant” areas (CE 142/2011, see Margalida et al. 2012). Additionally, because of the current decline in extensive grazing practises, some of the supplementary feeding stations in Mediterranean regions may become permanent (Donázar et al. 2009b).

In this dynamic scenario of changing regulations, scientists and managers have been trying to adopt the best solutions for the management of vulture populations. The “habitat-matching rule” states that all individuals will access resources at a similar rate, wherever they are, so that the final patterning of densities ought to reflect the distribution of resources (Pulliam and Caraco 1984). This rule might be applied to population dynamics of griffon vultures, since vultures are able to track food resources across traditional and new feeding grounds by establishing breeding colonies near highly productive spots (Parra and Tellería 2004). This ability for tracking food is reinforced by the capability of individuals to move long distances away from the breeding colonies in the search for food (c. 50–70 km; Donázar 1993 for review). However, previous studies suggest a strong effect of the availability of nesting sites in limiting the range of the species (Parra and Tellería 2004). In fact, the scarcity of suitable nesting sites in some areas prevents an efficient spatial tracking of changes in livestock biomass. Usually the breeding individuals from these colonies patrol the surrounding areas in search for food but are unable to access faraway regions. The available carcasses in these distant zones are

**Fig. 1** Study area within the Iberian Peninsula (*inset map*). Griffon vulture breeding colonies are shown as *grey circles* (whole study area) and *grey triangles* (for the long-term intensive monitoring programme in Biscay). Experimental feeding points (*black stars*) were separated into three main areas (*circles with discontinuous lines*): Alen (*northern area*), Gayangos (*central area*) and Porquera (*southern area*)



hence underutilised or used by non-breeding floaters (Parra and Tellería 2004; García-Ripollés et al. 2011).

We developed a long-term monitoring programme in Spain in order to improve our current knowledge about griffon vulture spatial behaviour. We particularly tested the null hypothesis for which, taking into account the displacement ability of griffon vultures, birds would access resources at similar rate wherever they were situated. The alternative hypothesis was that vulture movements would be restricted within a limited area and resources outside this range would not be available to them.

## Methods

### Study area

The study area encompasses 10,614 km<sup>2</sup> (Fig. 1), along a north–south axis, ranging between the Eurosiberian and the temperate–Mediterranean bioregions. The area includes the following Spanish administrative units: Biscay province, with 101 griffon vulture breeding pairs (hereafter, bp); the western region of Álava, where there are 410 bp; the eastern area of Cantabria, with 279 bp; and the northern extremities of Burgos, with 538 bp in 2008 (Del Moral 2009). Cantabria and Biscay (altitudinal range: 0–1,450 m a.s.l.) have a typical Eurosiberian climate, and the region is mountainous and densely populated, with extensive urban and industrial areas. Even so, extensive livestock, mostly consisting of cows and horses, is still present in mountainous areas. By contrast, Álava and Burgos (altitudinal range: 400–1,450 m a.s.l.) have a Mediterranean climate. The landscape is dominated by crops and scrubland, with extensive cereal-growing plains. As above, bovine and equine livestock is abundant in mountainous areas, whereas herds of sheep are generally found close to flat, arable areas. Medium and large-sized wild ungulates such as roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) are very abundant, and red deer (*Cervus elaphus*) reach high densities in some mountainous areas.

In 1986, the first and only vulture restaurant in the study area was opened in the western part of Biscay (Fig. 1). Traditionally, any livestock that died in the field was left there, so that it could be consumed by scavengers. In addition, there were sites for dumping the remains of animals that died in their stables or in other surrounding areas. In the 1990s, the situation began to change, due to the appearance of transmissible spongiform encephalopathies, more specifically bovine spongiform encephalopathy (commonly known as “mad cow” disease). This resulted in restrictions involving the obligation to remove any carcasses that were declared specific risk material (SRM) (Spanish Royal Decree 2224/1993 relating to the public health regulations on

removal and transformation of dead animals or remains of animal origin, and Spanish Law 10/1998 on waste). Nevertheless, food continued to be left at the vulture restaurant without interruption, with adaptations being made to conform to mandatory regulations and, in addition, dead animals continued to appear in the field until 2006. Following the Royal Decrees 1911/2000, 3454/2000 and 4/2001, bovine, ovine, caprine, equine, porcine and avian carcasses also began to be considered SRM and hence, in line with these laws, they had to be eliminated through incineration or inhumation and were never left out in the field or at vulture restaurants that were controlled or legal to any degree. Hence, in 2006, the vulture restaurant was closed. Besides this, a policy involving greater control of dead livestock in the field was applied across the whole study area. Some vulture restaurants, at both previous and new sites, were opened after 2008, but the frequency and amount of food supplied was greatly reduced in comparison with previous levels.

### Capturing and ringing vultures

From 2000 to 2011, we ringed 241 griffon vultures in Biscay with official metallic rings and alphanumeric yellow plastic rings as follows: 55 nestlings; 113 griffon vultures rehabilitated in the Wildlife Rehabilitation Centre of Biscay; and 73 vultures that were trapped using cage traps (25 m square × 2 m in height) or remote control system nooses. Apart from the 55 above-mentioned nestlings, the numbers of griffon vultures ringed per age class (in calendar year (cy)) were: first, 85; second, 15; third, 4; fourth, 4; fifth, 3; sixth, 1; seventh, 1; ninth, 1; and >tenth, 72. We considered subadults those vultures from first to ninth cy and adults those older than tenth cy (Zuberogoitia et al. 2012). In Biscay, we only detected one subadult (i.e. fourth cy) breeding out of 92–102 breeding pairs monitored over 5 years (2006–2011; see Zuberogoitia et al. 2010, 2012). Therefore, we considered all subadult individuals as non-breeders. We could not guarantee the breeding status of all the adults since we trapped them at feeding sites and, moreover, it was extremely difficult to read alphanumeric coloured rings at the breeding colonies, which were located in remote areas. In fact, only eight individuals were recorded at their respective nests.

### Experimental feeding points

From 2005 onwards, we established feeding points spread over the study area in order to monitor the displacements of ringed vultures in search of food. We established three permanent experimental feeding areas in which we placed different feeding points: (1) “Alen”, located in the north of the study area, partly in western Biscay and partly in eastern

Cantabria (Fig. 1), where one researcher placed food (approximately 100 kg of waste meat from butchers' shops) at two different feeding points every Saturday morning from May 2008 to December 2011 (sampling effort = 62 and 12 positive days respectively, considering only days with positive re-sightings; i.e. days on which at least one ringed vulture was re-sighted); (2) "Gayangos", located in the central area, northern Burgos, where another researcher placed the same quantity of food at one feeding point every Wednesday morning from January 2009 to December 2011 (sampling effort = 153 positive days) and also at a second neighbouring feeding point every Thursday morning from January 2011 to December 2011 (sampling effort = 4 positive days, since vultures did not land at this site); and (3) "Porquera", located in the south-western part of the study area, where a third researcher irregularly placed approximately 50 kg of food at a single feeding point on Sunday mornings, from July 2009 to December 2011 (sampling effort = 38 positive days). We also developed the same methodology at 19 additional feeding points across the study area during irregular periods from August 2008 onwards (Fig. 1). Sample effort for these 19 sites was 2.4 positive days on average (S.D. = 2.38;  $n=60$ ). In total, we accumulated 329 positive days at the 24 feeding points located within the study area (Fig. 1).

### Statistical analyses

In order to study the spatial movements of griffon vultures, we first assembled a null model describing the set of expected observations if the movements of birds from the centroid of all sampling points followed a random distribution. Following the rationale of Korner-Nievergelt et al. (2010), we compared the sightings of marked birds with the expected pattern assuming free movement. Taking into account that the maximum distance between the south-westernmost and the north-westernmost point is 73 km, and between the first and the easternmost point 90 km (Fig. 1), we expected that, if birds randomly moved long distances in the search for food (ca. 50–70 km, Donázar 1993; 37–120 km, García-Ripollés et al. 2011), the probability that a marked animal was re-sighted at any one of the 24 feeding points distributed throughout the study area would be merely a function of the sampling effort carried out at that site.

To create the null model, we used the  $x$ ,  $y$  UTM coordinates of each sampling site to describe the set of all possible observations based on the spatial distribution of the sampling effort. To achieve this, we obtained the location of the centroid of all sampling sites, after multiplying coordinates by the corresponding sampling effort. For instance, if a site A, with  $x_A$ ,  $y_A$  coordinates, was sampled  $m$  times and a site B, with  $x_B$ ,  $y_B$  coordinates, was sampled  $n$

times, the  $x$  and  $y$  values from A were included  $m$  times and those from B  $n$  times before computing the total centroid. We then computed the Euclidean distance from each location to the global centroid and bootstrapped ( $n=1,000$  times, with replacement) this set of values to obtain the bootstrapped distribution of frequencies that describe the free movement of birds in the study area. On the other hand, we used capture–mark–re-encounter data (Korner-Nievergelt et al. 2010) to compute the frequency distribution of real, observed bird movements. For each individual, we used the location of all re-encounter data to compute the corresponding centroid, then we computed the Euclidean distance from each re-encounter point to the corresponding centroid. Finally, we bootstrapped ( $n=1,000$  times, with replacement) the set of individual Euclidean distances to the corresponding centroids and used these data to describe the location of the actual observations of ringed griffon vultures. These analyses were carried out on both adults and subadults with a minimum of five data per individual. We used *PopTools* 3.1 (Hood 2009) to perform all re-sampling analyses. After correcting for sampling effort, two predictions were tested: (1) if vultures move freely within the study area, the frequency distribution of distances from study sites to their centroid should be similar to the frequency distribution of individual distances from re-encounter data to their centroids, and (2) if both adult and subadult vultures move around in the same way, the frequency distributions of individual distances from re-encounter data to their centroids should also be similar between the two age classes.

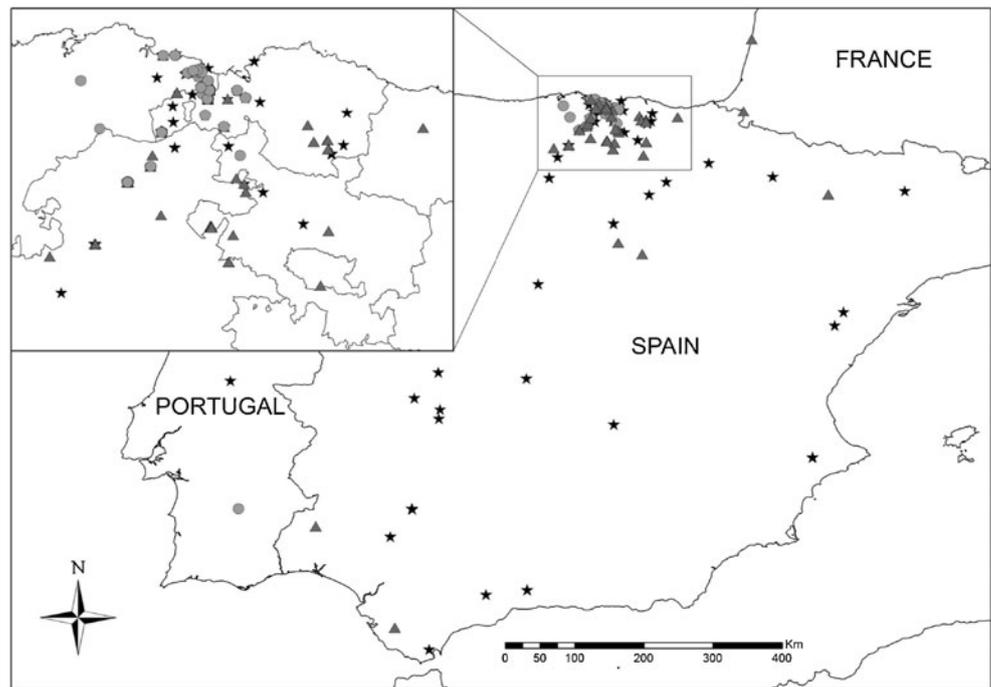
## Results

### Re-sightings

During the study period, we ringed 241 griffon vultures and obtained 765 re-sightings at experimental feeding points (average=8.32 re-sightings/re-sighted vulture, SD=12.52). Additionally, 60 different griffon vultures that had been ringed outside the study area were re-sighted 288 times at the experimental feeding points (average=4.65 re-sightings/vulture, SD=8.84).

Those griffon vultures ringed as nestlings or recently fledged were first detected in the study area after 3.23 years on average (SD=1.01, range=2–6 years,  $n=13$  re-sightings). Thirteen of them were re-sighted outside the study area, throughout the Iberian Peninsula, during these initial years (Fig. 2). None of the griffon vultures ringed as adults were recorded outside our study area except for one individual, which was found dead in Portugal. Subadults were detected all over Spain, Portugal and France (area=

**Fig. 2** Re-sightings of Eurasian griffon vultures ringed in Biscay during three life stages: (1) nestlings (*black stars*); (2) subadults (from one to nine calendar year (cy), *grey triangles*); and (3) adults (> 10 cy, *grey circles*) and those of the griffon vultures ringed elsewhere and re-sighted in the study area



361,500 km<sup>2</sup>), whilst adults were detected within an area encompassing 1,802 km<sup>2</sup> (Fig. 2).

**Foraging movements of adults**

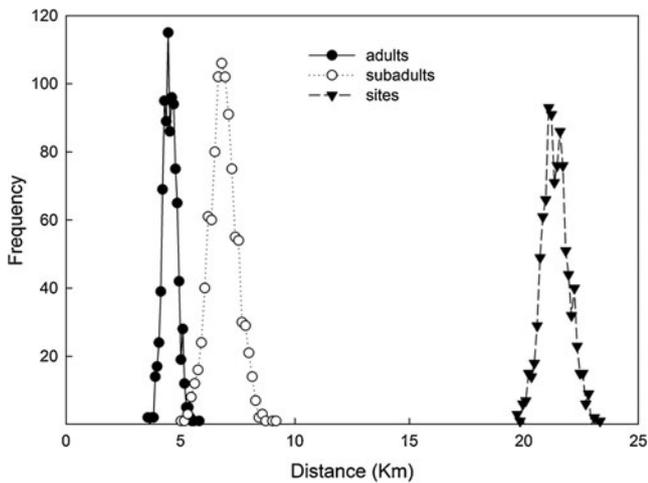
Altogether, we summarised 329 field-work days on which at least one ringed vulture was recorded at the experimental feeding points. On average, 2.06 ringed vultures (SD=1.36) were re-sighted per day, summarising 1,017 records. We distinguished three different nuclei considering the foraging range of adult vultures and field effort, i.e. “Alen” (northern area), “Gayangos” (central area) and “Porquera” (south-western area) (Fig. 1). Twenty-three adults were observed

239 times in Alen’s area (average=10.4 re-sightings, SD=10.2, range=1–35, Table 1), and five of these were also detected six times in the area of Gayangos (2.5 % of the re-sightings, Table 1). Considering Gayangos’s area itself, 27 adults were registered 418 times (average=15.5 re-sightings, SD=15.6, range=1–55, Table 1), and eight of these were also detected nine times in Alen’s area (2.4 % of the re-sightings, Table 1). These figures clearly show that there was minimum interchange between the two areas. The movements out of the principal areas were statistically less frequent than would be expected if adult griffon vultures accessed resources at a similar rate regardless of location ( $X^2_1=612.09, P<0.001$ ). Distances between the control

**Table 1** Contingency table outlining the number of vultures marked and re-sightings at the three main regions into which the study area was divided. Note the high number of observations at the site of capture indicating that this is the habitual foraging area. For example, in the

“Gayangos” area, 27 adult vultures were re-sighted 418 times, eight of them were re-sighted nine times in “Alen”, and none was re-sighted in “Porquera”

	Alen		Gayangos		Porquera	
	Vultures	Re-sightings	Vultures	Re-sightings	Vultures	Re-sightings
<b>Adults</b>						
Alen	23	239	8	9	0	0
Gayangos	5	6	27	418	0	0
Porquera	0	0	0	0	12	51
<b>Subadults</b>						
Alen	16	114	5	14	0	0
Gayangos	7	18	6	142	0	0
Porquera	0	0	0	0	2	20
Sampling effort/days with positive re-sightings		74		157		38



**Fig. 3** Frequency distributions of Monte Carlo simulations for the mean distance between the location of the experimental feeding points (sites) and individuals' re-sightings to their corresponding centroid for both subadult and adult griffion vultures. In each case, data were bootstrapped  $n=1,000$  times with replacement (see details in "Methods")

feeding stations and their central point were shorter than those exhibited by vultures considering only random movements (Monte Carlo simulations,  $P<0.001$ , Fig. 3).

Moreover, the monthly distribution of adult griffion flights out of the habitual foraging nuclei was not homogeneous throughout the year ( $\chi^2_{11}=23.06$ ,  $P=0.018$ , Table 2) there being no extra-nuclei visits recorded during the pre-laying or incubation periods or during the initial months of chick rearing.

Finally, none of the Alen's or Gayangos's adults were detected within the Porquera area (Table 1). In this third area, 12 vultures that had not been ringed inside our study zone were recorded 51 times. Three of these birds were ringed elsewhere at the beginning of the 90s, so they were considered as adults. These three vultures were detected 30 times in Porquera's area (average=10 re-sightings,  $SD=4.35$ , range=7–15) and were not sighted outside this area.

#### Foraging movements of subadults

A total of 22 subadults were detected 276 times in the whole study area (average=8.6 re-sightings,  $SD=12.8$ , range=1–51), and two of these birds were detected in Porquera's area nine and 11 times, respectively. In addition, 16 subadults

were detected 114 times in Alen's area (average=6.4 re-sightings,  $SD=9.8$ , range=1–39), and seven of these were also registered a total of 18 times in Gayangos's area (13.64 % of the re-sightings, Table 1). Six subadults were observed 142 times in Gayangos's area (average=21.9,  $SD=20.9$ , range=3–51), and five of these individuals were also detected 14 times in Alen's area (9.0 % of the re-sightings). These movements out of the foraging nuclei were statistically less frequent than would be expected if subadult griffion vultures accessed resources at similar rates and location was not a factor ( $\chi^2_1=173.43$ ,  $P<0.001$ ). Distances between the control feeding stations and their central point were significantly shorter than those considering only random movements of subadult griffions (Monte Carlo simulations,  $P<0.001$ ; Fig. 3). The movements of the subadults between foraging nuclei were regularly distributed throughout the year ( $\chi^2_{11}=19.228$ ,  $P=0.06$ , Table 2).

## Discussion

In this study we show the results of a long-term monitoring programme of griffion vultures in northern Spain, which has allowed us to gain insight into their spatial ecology. Studies based on field observations may lead to underestimation of spatial parameters and ranging behaviour (García-Ripollés et al. 2011). Nevertheless, the results presented here can help managers to make decisions regarding the administration of supplementary feeding for conservation of this scavenger species. Our results show that, after being ringed as nestlings in the study area, juvenile birds were re-sighted for the first time in the study (natal) area only three or more years later. During these initial years, juveniles wandered around vast areas of the Iberian Peninsula. These birds tend to be attracted by or associated with an aggregation of feeders at regular feeding places (Dermoddy et al. 2011; Bosè et al. 2012; Duriez et al. 2012). In accordance with this, most of the records of juveniles outside the study area were restricted to vulture restaurants, where large concentrations of immature vultures are regularly detected (García-Ripollés et al. 2004, 2011; Gil et al. 2009; Cortés-Avizanda et al. 2010; Margalida et al. 2011a). Once subadults became temporarily or definitively established in the study area, they seemed to behave as resident adults. Thereby, subadults

**Table 2** Monthly distribution (as a percentage of the total) of adult and subadult griffion vulture records from the habitual foraging nuclei. Sample effort is the monthly distribution of the 329 positive days at the 24 feeding points (see details in "Methods")

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Adults					18.7	12.5	12.5	31.3		18.7	6.3	
Subadults	4.3		17.4	13.0	21.7	17.4	8.7		13.0			4.3
Sampling effort	14	19	25	28	35	42	41	32	28	25	22	18

were taking advantage of transference of information from conspecific, experienced adults, in order to increase their foraging success (Dermody et al. 2011; Mateo-Tomás and Olea 2011). Nevertheless, according to García-Ripollés et al. (2011), movements of subadult birds are less site-dependent than those of adults, i.e. they patrol longer distances than the latter. Moreover, we found that large movements of immature vultures were not seasonally dependent, probably because they are not breeders and are not totally linked to a colony or roosting site.

Adult griffon vultures ranged through a relatively small foraging area. Adults were located almost exclusively within a zone of only 30 km in radius (ca. 2,800 km<sup>2</sup>, considering the distribution of the experimental feeding points). This pattern of movements is close to the 25–30-km radius described by Arroyo and Garza (1995), Van Beest et al. (2008) and Xirouchakis and Andreou (2009), and within the average daily distance (3–48 km) of non-breeding adult and subadult individuals reported in García-Ripollés et al. (2011) by means of GPS satellite telemetry. Moreover, preliminary results of a GPS monitoring project of two breeder males and two breeder females in Navarra (close to our study area) reported home ranges ranging from 4,737 to 8,369 km<sup>2</sup>, although 75 % of the kernel areas was restricted between 291 and 1,551 km<sup>2</sup> (Fernández and Azkona 2011, [www.pirineosostenible.eu](http://www.pirineosostenible.eu)). Other papers based on field observations and conventional radio-tracking reported larger distances (75–100 km) in other regions or with related species (Elosegui and Elosegui 1977; Donázar 1993; Ruxton and Houston 2002; Gilbert et al. 2007). Nevertheless, these variations are due to the combination of age, breeding status, availability of adequate sites for nesting and of livestock and ungulate carcasses in the field, as well as distance to regular feeding stations and individual differences. For example, in our case, one adult which was found dead in Portugal, 688 km away, which may be in agreement with vagrant movements out of the breeding season (see Fernández and Azkona 2011; [www.pirineosostenible.eu](http://www.pirineosostenible.eu)). Individual variation may even be due to biases related to the methodology (García-Ripollés et al. 2011). Our results showed that adult movements out of the main foraging areas were scarce and restricted to the non-breeding period, mainly during summer and mid-autumn, according to the preliminary results of Fernández and Azkona (2011; [www.pirineosostenible.eu](http://www.pirineosostenible.eu)). These occasional and seasonally-related movements tie in with the large distance ranges described above. In fact, during mating, nest building and laying periods, vultures usually remain within nesting areas for extended periods, in order to prevent extra pair copulation (i.e. they exhibit mate-guarding behaviour) and to avoid competition for nesting sites and predation (Xirouchakis and Mylonas 2007; Margalida and Bertran 2010). This behaviour reduces the time devoted to foraging and thus adults

necessarily concentrate their activities around nesting sites (Mundy 1982; Bamford et al. 2007; Murn and Anderson 2008). This would explain why adults have never been recorded in neighbouring areas albeit the intense monitoring effort carried out during recent years.

In summary, our results suggest rejecting the null hypothesis by which griffon vultures would access resources at a similar rate regardless of where they are situated, since vultures' home ranges are largely restricted to zones close to their breeding areas. In other words, adult griffon vultures behave as typical central-place foragers (Rosenberg and McKelvey 1999), being obligated to return to their breeding colony. This has important consequences from a conservation point of view, suggesting that management decisions should take into consideration the spatial scale of vulture movements.

#### Supplementary feeding: management implications

The sole vulture restaurant in Biscay was closed in 2006 following the implementation of European sanitary legislation. We were already monitoring vulture populations in the area when this occurred. Most of the monitored vultures had previously been trapped at that location, since up to ca. 400 vultures gathered there regularly (see Zuberogoitia et al. 2010). The immediate effect of the closure was a decrease in the breeding success of the species and an increase in the mortality rate of juveniles, but there were no short-term changes in the number of breeding pairs (Zuberogoitia et al. 2009). Other studies showed that fluctuations in the number of breeding pairs were positively correlated with changes in livestock abundance, supporting a functional relationship between food availability and population density (Parra and Tellería 2004). Similarly, Van Beest et al. (2008) found that a 50 % decrease in available food biomass resulted in a rapid decrease in vulture numbers, 11 % over 5 years (see also Margalida et al. 2011c). However, although we did not detect changes in local population size, we observed short-term changes in two proxies of foraging behaviour (i.e. reaction time and flight initiation distance), which reduced the negative effects of food restriction on the breeding population (Zuberogoitia et al. 2010).

Controlled artificial feeding can alleviate problems of food shortage and has been used for conservation when food has been in short supply (Zuberogoitia et al. 2010; Martínez-Abraín et al. 2012). Nevertheless, our results show that artificial feeding may only be a valid method of improving breeding parameters when the feeding station is placed within the foraging area of adults. By contrast, feeding would not have clearly positive effects on more distant colonies, if the main goals were the improvement of breeding success or the maintenance of breeding numbers. Vulture restaurants attract non-territorial subadults in large

numbers and this is the root of several current problems: large flocks concentrated in small areas, conflicts with farmers, competition with other endangered species for food resources and alteration of social behaviour (Selva and Cortés-Avizanda 2009; Margalida and Campión 2009; Xirouchakis and Andreou 2009). Therefore, supplementary feeding should only be considered in those areas where no other food resources are available and thus vulture populations are dependent on the provision of artificial feeding. In other areas, such as our study zone, where wild ungulates and extensive livestock are abundant resources, conservation strategies should encourage leaving livestock carcasses in the field rather than at “vulture restaurants”, as recommended in the latest legislation (CE 142/2011, see Margalida et al. 2012). Hence, the vulture population would be naturally regulated by density-dependent effects (Carrete et al. 2006) and by annual fluctuations in the availability of carcasses (e.g. birth periods of domestic and wild ungulates, high mortality rates of ungulates during hard winters or dry seasons and occasional peaks of diseases in wild ungulates). Moreover, since food availability would not be a temporarily and/or spatially predictable resource, large flock concentrations would be notably scarcer, thus limiting the local population density. Finally, this reduction in flock size would have positive effects for local farmers and would help to relieve the stress accumulated over previous years due to presumed and demonstrated vulture attacks on livestock (Margalida and Campión 2009), as well as avoiding detrimental practises such as illegal poisoning (Margalida et al. 2011b).

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