Distribution of avian scavengers inside and outside of protected areas: contrasting patterns between two areas of Spain and South Africa

Marcos Moleón[1,2,3,4,*], Ainara Cortés-Avizanda[3,5], Juan M. Pérez-García[2,6], Jesús Bautista[7], Claire Geoghegan[8], Martina Carrete[9], Arjun Amar[10], José A. Sánchez-Zapata[2] & José A. Donázar[3]

[1]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, 2050, South Africa

[2]Department of Applied Biology, University Miguel Hernández, Avda. de La Universidad, s/n, 03202, Elche, Alicante, Spain

[3]Department of Conservation Biology, Doñana Biological Station-CSIC.C/Américo Vespucio, 26, 41092, Seville, Spain

[4]Present address: Department of Zoology, University of Granada, Avda. de Fuentenueva, s/n, 18071, Granada, Spain

[5]Animal Demography and Ecology Group, IMEDEA CSIC-UIB, C/Miquel Marqués, 21, 07190, Esporles, Spain

[6]Department of Animal Sciences, Faculty of Life Sciences and Engineering, University of Lleida, 25198, Lleida, Spain

[7]Agencia de Medio Ambiente Y Agua, Consejería de Medio Ambiente Y Ordenación del Territorio, Junta de Andalucía, C/Minerva, 7, Edificio Zeus III, 18014, Granada, Spain

[8]Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Pretoria, 0002, South Africa

[9]Departamento de Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, Ctra. de Utrera, km 1, 41013, Seville, Spain

[10]FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, Department of Biological Sciences, University of Cape Town, Rondebosch, Cape Town, 7701, South Africa

*Correspondence to Marcos Moleón. mmoleonpaiz@hotmail.com

Abstract

Protected areas are central to the conservation of biodiversity across the globe. However, their performance, especially in relation to highly mobile species, is largely dependent on the socio-ecological characteristics of the landscape that surrounds them. Here, we assess the patterns of avian scavenger distribution, including both obligate (i.e., vultures) and facultative (corvids and other raptors) scavenger species, inside and outside of protected areas. We contrast the situation between an African area, which has protected areas surrounded by mostly subsistence stockbreeding (KwaZulu-Natal Province, South Africa) and a European area, which has protected areas surrounded by commercial farming (Ebro Valley, Spain). We found large differences between the two areas. In the South African area, the richness and abundance of vultures, but not of facultative scavengers, were higher inside than outside of protected areas; as a result, the richness and abundance of vultures were negatively related to the distance to the nearest protected area in South Africa. In contrast, the richness and abundance of vultures in the Spanish area were similar inside and outside of protected areas. We obtained similar results when focusing solely on presence and abundance of *Gyps* vultures. The contrasting effects of protected areas in the distribution of avian scavengers, especially vultures, in the studied areas may be due to differences in agro-systems and socio-economical models that lead to differential availability of ungulate carcasses. We suggest that carrion shortage in the subsistence farming systems in the South African area, whereby domestic livestock carcasses are generally used by householders and thus rarely become available to vultures, should be considered alongside poisoning prevention to help conserve African vulture populations.

Introduction

Since the late nineteenth-century, protected areas (PAs) have become a central component in the conservation of biodiversity across the globe. Currently, PAs represent ca. 12.5% of terrestrial ecosystems globally, and the PA network continues to expand (Watson et al. 2014). However, whilst PAs have been efficient in achieving certain biodiversity conservation targets (Gaston et al. 2008), they are not without weaknesses, and many species continue to decrease within their boundaries (e.g., Brashares et al. 2001). These concerns extend to the role of PAs in maintaining ecosystem functions and services (DeFries et al. 2007; Fynn and Bonyongo 2011; Xu et al. 2017). Importantly, the performance of PAs, especially small reserves, is highly dependent on the habitat matrix that surrounds them, since threats to wildlife outside of PAs can permeate through borders (Newmark et al. 1994; Woodrofe and Ginsberg 1998; Brashares et al. 2001; Loveridge et al. 2007). Understanding how species occurrence may be shaped by the distribution and locational setting of PAs is, therefore, a fundamental question in biodiversity conservation (Parrish et al. 2003).

The socio-ecological context around PAs may vary widely among regions. For instance, Europe has suffered a generalized rural depopulation and abandonment of traditional farming lands in recent decades (Sirami et al. 2008; Mateo-Tomás and Olea 2010; Bernués et al. 2011; Cocca et al. 2012; Plieninger et al. 2014), which has led to subsequent passive "rewilding" (Soulé and Noss 1998; Navarro and Pereira 2015; Corlett 2016). In contrast, in Africa, human population is increasing at a greater rate than anywhere in the world and is expected to double in the next 35 years (United Nations 2015). Human populations in Africa are increasing in both rural and urban areas (Tusting et al. 2019; especially around protected areas; Wittemyer et al. 2008), with the corresponding increment in the demands on natural resources and land for agriculture and farm intensification that threats wildlife (Ogutu et al. 2011). These patterns have had considerable influence on the distribution of African wildlife, which is increasingly being confined to protected areas (Thiollay 2006a; Newmark 2008; Amar and Cloete 2018).

How species respond to the landscape configuration of protected and unprotected areas may be dependent on the ecological characteristics of the focal species or guilds. Within terrestrial vertebrate scavenging communities, vultures are obligate scavengers that can efficiently exploit vast areas thanks to extraordinary soaring (Ruxton and Houston 2004) and social information transmission abilities (Cortés-Avizanda et al. 2014). Vultures, especially those within the genus *Gyps*, are specialized in the consumption of ungulate carcasses from either wild species or extensive livestock (Houston 1979; Mateo-Tomás et al. 2017). In recent decades, Old-World vulture populations have undergone catastrophic declines (McClure et al. 2018). These declines will likely compromise the important functions these birds play within ecosystems, including the provision of multiple services to humans (Ogada et al. 2012; Moleón et al. 2014; Cortés-Avizanda et al. 2015a; Buechley and Sekercioglu 2016; DeVault et al. 2016). This is of special concern in Africa, which supports the richest community of vultures in the world, including ten resident and one wintering species, eight of which are endemic or near-endemic (del Hoyo et al. 1994; Anderson 2007). Most species on this continent are currently threatened (Ogada et al. 2016a; see also IUCN Red List: https://www.iucnredlist.org/) and large areas have been devoid of vultures within a few decades, particularly outside of protected reserves (e.g., Thiollay 2006b, 2007; Virani et al. 2011; Ogada and Buij 2011). Although many and varied threats to vultures have been identified in Africa (e.g. Nikolaus 2001; Monadjem and Garcelon 2005; Thiollay 2007; Virani et al. 2011; Ogada et al. 2012; Garbett et al. 2018), poisoning is viewed as the main cause of vulture population decline and range contraction on this continent (e.g., Virani et al. 2011; Ogada et al. 2012a, 2016b). Shortage of food is also another potential threat to vulture populations, for which there is some evidence, although this topic has received relatively little attention (Kruger et al. 2015; Schabo et al. 2017). In contrast to Africa and many other regions around the globe, European vulture populations have maintained stable or even increased in numbers in recent decades (e.g., del Moral and Molina 2018). However, European vultures are highly vulnerable to sanitary measures that compromise the supply of domestic (Margalida et al. 2010; Morales-Reyes et al. 2017) and wild ungulate carcasses (Margalida and Moleón 2016).

Besides vultures, many other birds feed on carrion, such as other raptors and corvids (e.g., Mateo-Tomás et al. 2015). These species are considered to be facultative scavengers, in that they do not rely on carrion to survive and reproduce because they are able to exploit other trophic resources, but opportunistically use carrion when available (DeVault et al. 2003), including small carcasses that are less attractive to vultures (Moleón et al. 2015). Thus, unlike vultures, the distribution of these ubiquitous facultative scavengers may be less constrained by the availability of carcasses, especially of ungulates. However, poisoning is an important risk for not only vultures, but also avian facultative scavengers (Márquez et al. 2013; Cano et al. 2016).

In this study, we assess the patterns of avian scavenger distribution, including both obligate and facultative scavenger species, in relation to protected areas and the agro-system matrix adjacent in two globally important areas for vulture conservation: the KwaZulu-Natal Province of South Africa (Africa) and the Ebro Valley of Spain (Europe). Both areas consist of a mosaic of protected and unprotected areas, and both areas suffer from the presence of poisoning (e.g., Margalida et al. 2014; Ogada et al. 2016b). However, the two areas likely differ in the availability of carrion due to the prevailing agro-grazing systems and the spatial distribution of wild ungulates (see Study areas). Thus, we expect to find differential effects on the scavenger guilds depending on the asymmetric socio-ecological context around protected areas in both areas. The results may be useful to define site-dependent strategies aimed to preserve endangered populations of obligate and facultative scavengers, as well as ecosystem processes and services.

Methods

Study areas

Our South African study area was mainly focused on the uMkhanyakude District, KwaZulu-Natal Province (28.15º S; 32.08º E; Fig. 1). This area comprises six main public protected reserves and several private reserves within a matrix of unprotected land that is mainly devoted to subsistence gathering and agriculture, with scattered *Pinus* spp. and *Eucalyptus* spp. plantations. The district covers an area of 12,821 km^2, and in 2011 held a human population of 630,926 people (49.21 people/km^2), mainly restricted to unprotected areas. The climate is warm to hot, humid sub-tropical with two distinct seasons: a rainy, hot summer from October to May and a dry, cooler winter from April to September. Natural vegetation is dominated by grassland-forest mosaics, thickets and thorn savannas (Balme et al. 2010; Weladji and Laflamme-Mayer 2011; Grange et al. 2012). We focused on two protected reserves: Hluhluwe-iMfolozi Park (HiP) and Mkhuze Game Reserve (Mkhuze). In these reserves, three species of vultures are present all year round (white-backed *Gyps africanus*, the most abundant vulture species in the area, lappet-faced *Torgos tracheliotos*, and white-headed vultures *Trigonoceps occipitalis*) and three species are occasional visitors (Cape *G. coprotheres*, hooded *Necrosyrtes monachus*, and palm-nut vultures *Gypohierax angolensis*; authors, pers. observ.). In 2010, ungulate density in HiP and Mkhuze was, respectively, 36.47 (35,010 ungulates in 960 km^2) and 54.58 ungulates/km^2 (19,647 ungulates in 360 km^2; Grange et al. 2012; D. Druce, G. Clinning, D. Kelly and T. Bodasing, pers. comm.). The main ungulate species within the reserves included impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*), Burchell's zebra (*Equus quagga*), African buffalo (*Syncerus caffer*), blue wildebeest (*Connochaetes taurinus*), warthog (*Phacochoerus africanus*), white (*Ceratotherium simum*) and black rhinoceroses (*Diceros bicornis*), greater kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellipsiprymmus*), giraffe (*Giraffa camelopardalis*) and elephant (*Loxodonta africana*). In the whole district (excluding the Mtubatuba municipality, where data are unavailable), ungulate livestock (mainly cattle and goat) numbers were 239,924 animals (21.65 individuals/km^2) in 2009 (South African Department of Agriculture, Forestry and Fisheries, Directorate of Food and Veterinary Services, Regional District of uMkhanyakude).

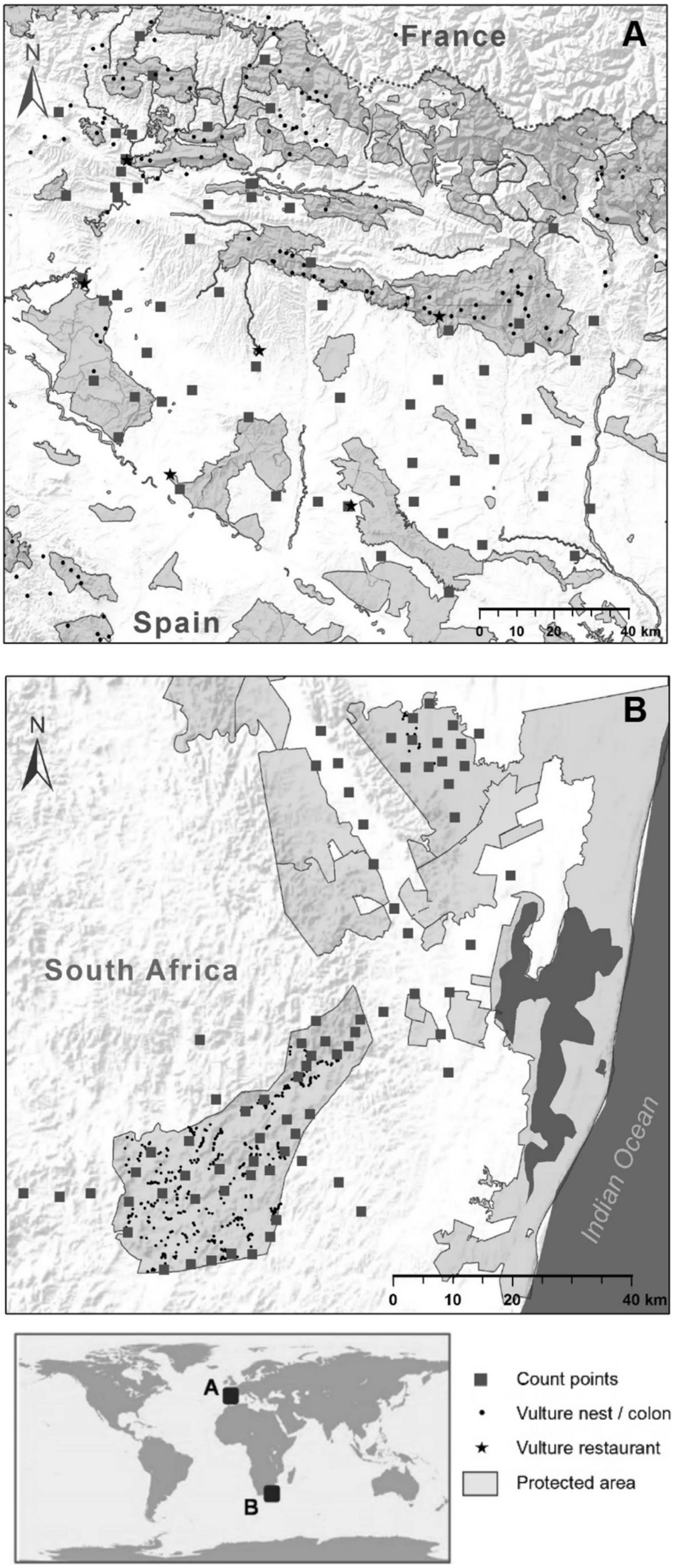


Fig. 1. Study areas: Ebro Valley in Spain (a) and KwaZulu-Natal Province in South Africa (b)

Our European study area was focused on the Ebro Valley (42.57º N; 0.18º W northern Spain), a 10,000 km^2-area lying between the Pyrenees and the Iberian mountains (Fig. 1). The human population is concentrated in the main valleys (< 10 people/km^2 in the mountains and > 200 people/km^2 in the valleys; Cortés-Avizanda et al. 2011). The area comprises eight main protected areas, plus several smaller protected areas, mostly surrounded by non-irrigated crops. Extensive livestock rearing is common both outside and inside of the protected areas. The climate is typically Mediterranean, with a mild winter, a hot, dry summer, and precipitation mainly concentrated in spring and autumn. Natural vegetation is characterized by Mediterranean shrub and steppe (Rivas-Martínez 1986). The Ebro Valley holds populations of three species of vultures: Eurasian griffon (*Gyps fulvus*; the most abundant vulture species in the area), Egyptian (*Neophron percnopterus*) and bearded vulture (*Gypaetus barbatus*; Cortés-Avizanda et al. 2011, 2012). Wild ungulates (red deer *Cervus elaphus* and, especially, wild boar *Sus scrofa*) are common (no density data are available for these species at the regional scale, though wild boar normally reaches densities between c. 50 and > 150 individuals/km^2 in the study area; Acevedo et al. 2014), while domestic ungulates (mainly cattle, sheep and goat) reach approximate densities of 40.00 individuals/km^2 (ca. 400,000 heads; Cortés-Avizanda et al. 2014).

Regarding carrion resources, commercial livestock farming (under both intensive and extensive regimes) dominates in the European area, producing abundant carcasses inside and outside of protected areas that are available to avian scavengers at vulture restaurants or freely in the wild (Olea and Mateo-Tomás 2009; Cortés-Avizanda et al. 2011, 2012; Morales-Reyes et al. 2017). Livestock carcasses, especially in remote areas, were available even during the most restrictive sanitary regulations established in Europe after the outbreak of bovine spongiform encephalopathy (Olea and Mateo-Tomás 2009). Within this area, wild ungulates are widely distributed even in unprotected areas (Palomo et al. 2007). In contrast, within the African system, the areas outside of protected areas are largely characterized by subsistence stockbreeding, in which domestic livestock carcasses are mostly consumed by people and only a small fraction of the dead animal becomes available to wild scavengers (see Discussion below). In contrast to the European scenario, African wild ungulates are largely depleted outside of the studied protected reserves (as occurs in other African areas; e.g., Kinnaird and O'Brien 2012), and no active vulture restaurants were found within the study area during the study period.

Avian scavenger survey

We surveyed the abundance of avian scavengers, both obligate and facultative, by means of 30 min point counts (Sánchez-Zapata et al. 2007) in the South African (n = 50 in December 2010 and n = 24 in October 2011, 50 inside and 24 outside protected areas) and the Spanish (n = 63 in May 2005, 13 inside and 50 outside protected areas) areas (Cortés Avizanda et al. 2011; see Fig. 1). Both flying and perched birds were recorded with the help of binoculars (10×) and field scopes (20–60×). We estimate that these point counts covered birds within a 3 km radius, based on our fields of view. Points were randomly distributed across both study areas, always in places with high visibility such as hills and wildlife observation towers, and were separated by > 6 km to increase independence. When possible, nearby points were consecutively surveyed within a day to minimize the chance of double-counting. Two observers were normally involved in each point count. For each observation within a point count, we recorded the number of birds and the lowest taxonomic level identified (usually, the species). The surveys were conducted in the mornings (since 1 h after the sunrise to 13:00 h), avoiding adverse weather conditions such as intense heat, wind, rain or fog.

For each point count, we determined the richness (no. of species) of obligate and facultative scavengers, and the abundance (no. of individuals) of each species. We also recorded the distance to the nearest protected area (either public or private in South Africa and 'Natura 2000' network in Spain), the distance to the nearest vulture nest or colony (*Gyps* spp.: white-backed vulture in South Africa and griffon vulture in Spain), and the distance to the nearest vulture restaurant (only for Spain). For all points located within protected areas, the distance to the nearest protected area was 0. Data on the spatial distribution of protected areas were provided by EKZN Wildlife technical staff in HiP and the Spanish governmental spatial data web-repository (https://www.idee.es). Vulture nest locations were obtained from aerial surveys performed in 2011 in South Africa (Howells et al. 2011) and from the Spanish national census conducted in 2008 (del Moral and Molina 2018). Distances were calculated using Quantum GIS 2.2 software (QGIS; https://www.qgis.org/).

Statistical analyses

We conducted the following two analyses. First, we used Generalized Linear Models (GLMs; McCullagh and Searle 2000) to relate richness and abundance of avian scavengers (response variables; negative binomial error distribution and log link function) to the distance to the nearest protected area (explanatory variable). Analyses were done separately for obligate and facultative scavengers and for the South African and Spanish areas.

Second, we undertook an analysis focusing on just the *Gyps* spp. vultures. We used GLMs to model the presence (binomial error distribution and logit link function) and abundance (negative binomial error distribution and log link function) of *Gyps* spp. (response variables) as a function of their distance to the nearest protected area, conspecific nest and, when present, vulture restaurant (explanatory variables). Analyses were done separately for the South African and Spanish areas. To control for the spatial autocorrelation of our *Gyps* observations, we included a third variable describing the spatial pattern of the points, obtained as the combination of the linear, quadratic and cubic distributions of their spatial coordinates (x, y, x^2, y^2, x^3, y^3, xy, x^2y, xy^2; Legendre and Legendre 1998). To assess the pure and joint contribution of each variable, we performed a deviance partitioning analysis (Cushman and McGarigal 2002). In this analysis, we did not consider the effect of the distance to the nearest vulture restaurant to allow direct comparisons between the South African and Spanish areas.

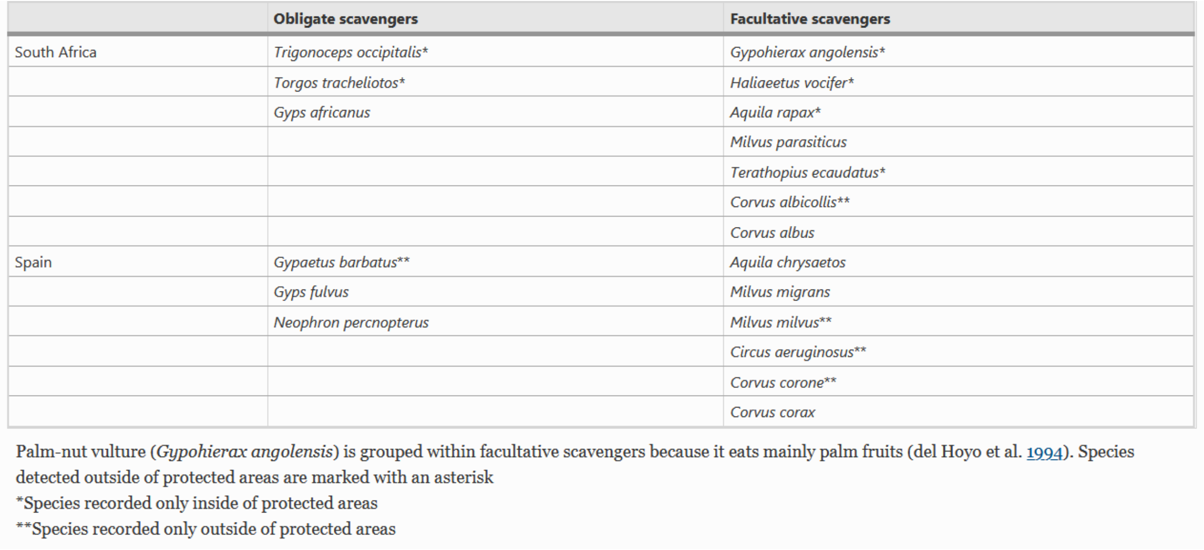
All analyses were done with R statistical software (R Core Team 2013), using the MASS package (Venables and Ripley 2002) for the GLM analyses.

Results

Distribution of obligate and facultative scavengers

We observed 3533 individuals (939 in the South African area, 843 inside and 96 outside of protected areas; 2594 in the Spanish area, 226 inside and 2368 outside of protected areas) of avian scavengers, belonging to three species of obligate scavengers and seven species of facultative scavengers in South Africa and to three species of obligate scavengers and six species of facultative scavengers in Spain (Table 1). Other observed raptors and corvids (see Table S1) were excluded from the analyses because they only scavenge occasionally. Obligate scavengers were less frequently seen at point counts in the South African (52.7%) than in the Spanish area (90.5%), while facultative scavengers were recorded in similar frequencies (South Africa: 89.2%; Spain: 90.5%). In the South African area, the species richness of obligate scavengers and their abundance were ca. 5 and 50 times higher, respectively, inside than outside of protected areas (richness: $\chi^2 = 18.25$, df = 1, $p < 0.001$; abundance: $\chi^2 = 21.11$, df = 1, $p < 0.001$), while species richness and abundance of facultative scavengers were similar inside and outside of protected areas (richness: $\chi^2 = 0.16$, df = 1, $p = 0.686$; abundance: $\chi^2 = 2.49$, df = 1, $p = 0.114$; Fig. 2). In the Spanish area, we found a different pattern: obligate scavenger richness and abundance were similar inside and outside of protected areas (richness: $\chi^2 = 0.117$, df = 1, $p = 0.732$; abundance: $\chi^2 = 0.009$, df = 1, p = 0. 925), while facultative scavenger species richness and abundance were lower inside than outside of protected areas (richness: $\chi^2 = 8.15$, df = 1, $p < 0.01$; abundance: $\chi^2 = 4.02$, df = 1, $p < 0.05$; Fig. 2).

Table 1. List of species recorded in the avian scavenger surveys of KwaZulu-Natal Province (South Africa) and Ebro Valley (Spain)



	Obligate scavengers	**Facultative scavengers**
South Africa	*Trigonoceps occipitalis**	*Gypohierax angolensis**
	*Torgos tracheliotos**	*Haliaeetus vocifer**
	Gyps africanus	*Aquila rapax**
		Milvus parasiticus
		*Terathopius ecaudatus**
		*Corvus albicollis***
		Corvus albus
Spain	*Gypaetus barbatus***	*Aquila chrysaetos*
	Gyps fulvus	*Milvus migrans*
	Neophron percnopterus	*Milvus milvus***
		*Circus aeruginosus***
		*Corvus corone***
		Corvus corax

Palm-nut vulture (*Gypohierax angolensis*) is grouped within facultative scavengers because it eats mainly palm fruits (del Hoyo et al. 1994). Species detected outside of protected areas are marked with an asterisk

*Species recorded only inside of protected areas

**Species recorded only outside of protected areas

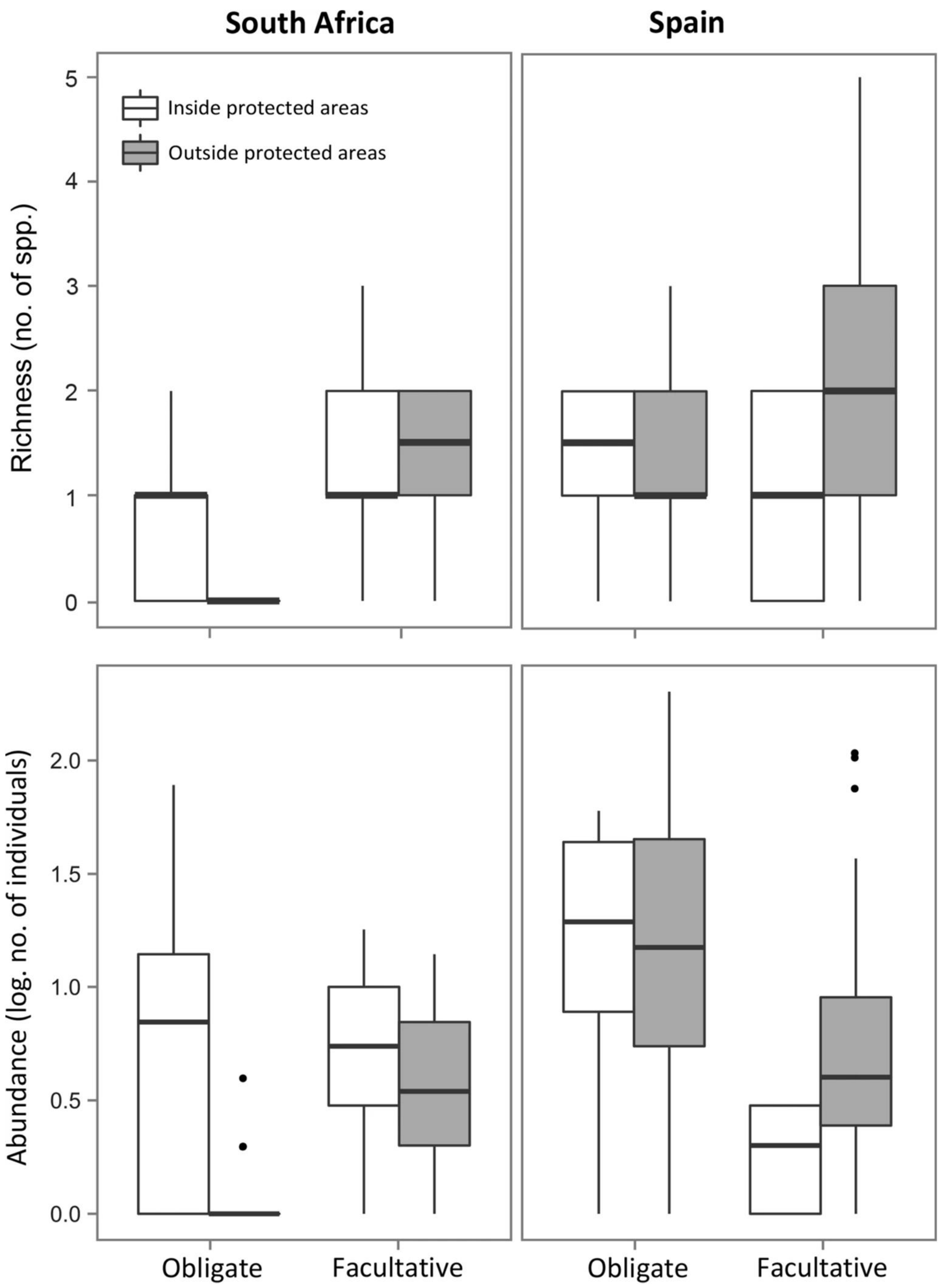


Fig. 2.Richness and abundance (log-transformed) of obligate and facultative avian scavengers inside and outside of protected areas at KwaZulu-Natal Province (South Africa) and Ebro Valley (Spain)

Species richness and abundance of obligate scavengers were negatively related to the distance to the nearest protected area in the South African area ($p < 0.05$ in both cases), but not in the Spanish area ($p > 0.05$ in both cases). In South Africa, all vulture observations outside of protected areas ($n = 5$) were made at less than 3 km from the border of protected reserves (Fig. 3). The richness of facultative scavenger species was, however, unrelated to the distance to the nearest protected area in both study areas ($p > 0.05$ in both cases). In contrast, the abundance of facultative scavengers was significantly related to the distance to the nearest protected area in both study areas, with a negative relationship (although the estimate of the slope was very shallow) in South Africa and a positive one in Spain ($p < 0.05$ in both cases; Fig. 3).

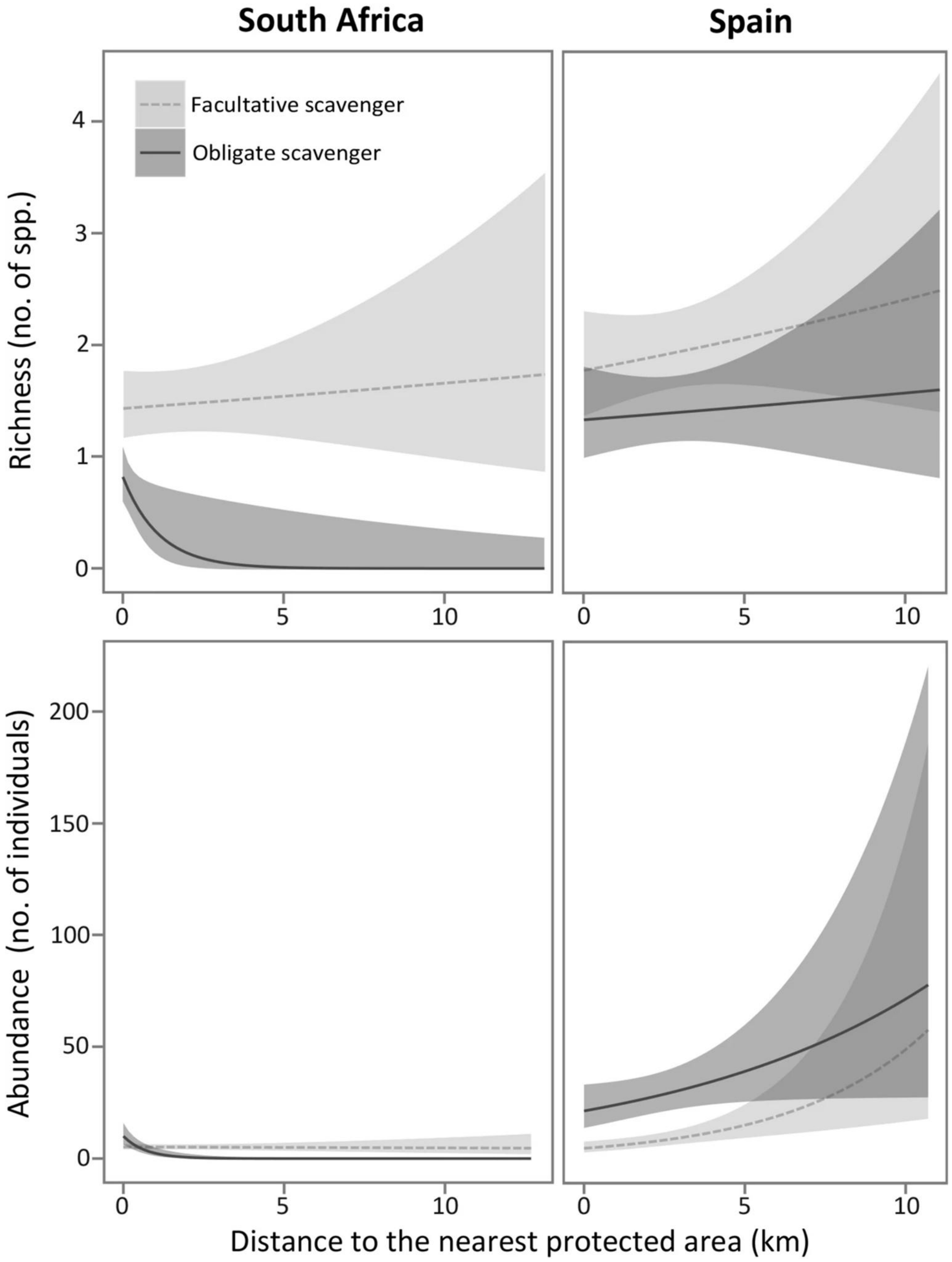
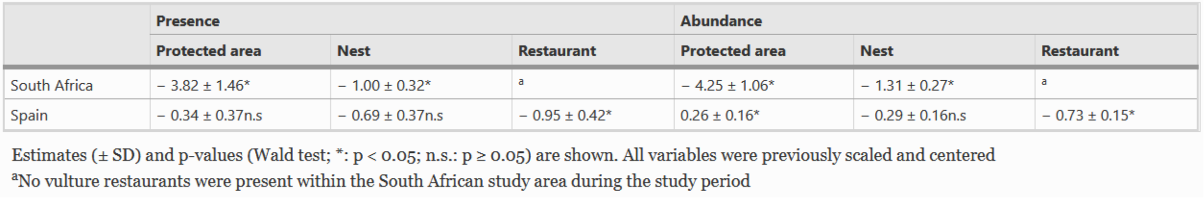


Fig. 3. Generalized Lineal Models to relate species richness and abundance of obligate and facultative avian scavengers to distance to the nearest protected area in KwaZulu-Natal Province (South Africa) and Ebro Valley (Spain)

Distribution of *Gyps* spp.

We observed 2360 *Gyps* vultures (549 in the South Africa area, 543 inside and 6 outside of protected areas; 1811 in the Spanish area, 193 inside and 1618 outside of protected areas). GLMs showed that, in South Africa, both the presence and abundance of *G. africanus* were negatively related to the distance to the nearest protected area and to the nearest conspecific nest (see Table 2). In Spain, however, the presence and abundance of *G. fulvus* were negatively related to the distance to the nearest vulture restaurant, while the abundance was also related (positively) to the distance to the nearest protected area (see Table 2), indicating that *G. fulvus* were seen in greater numbers further away from protected areas.

Table 2. Relationships between the presence and abundance of *Gyps* spp. and the distance to the nearest protected area, *Gyps* nest and vulture restaurant in the study areas obtained from Generalized Linear Models



	Presence			**Abundance**		
	Protected area	**Nest**	**Restaurant**	**Protected area**	**Nest**	**Restaurant**
South Africa	− 3.82 ± 1.46*	− 1.00 ± 0.32*	[a]	− 4.25 ± 1.06*	− 1.31 ± 0.27*	[a]
Spain	− 0.34 ± 0.37n.s	− 0.69 ± 0.37n.s	− 0.95 ± 0.42*	0.26 ± 0.16*	− 0.29 ± 0.16n.s	− 0.73 ± 0.15*

Estimates (± SD) and p-values (Wald test; *: $p < 0.05$; n.s.: $p \geq 0.05$) are shown. All variables were previously scaled and centered

[a] No vulture restaurants were present within the South African study area during the study period

Within each study area, the results from deviance partitioning were similar for both presence and abundance data. In the South African area, the presence and abundance of *G. africanus* were mainly explained by the pure effect of the distance to the nearest protected area. The interaction between this variable and the distance to the nearest nest also explained an important part of the deviance, especially for abundance data (Fig. 4). Conversely, in the Spanish area, most of the variation in the presence and abundance of *G. fulvus* was explained by the variable describing the spatial autocorrelation of the data (Fig. 4), i.e., by factors with the capacity to create a spatial pattern, other than the distances to the nearest protected area and the nearest conspecific nest. Models explained between 27.4 and 43.5% of the variability in the presence and abundance of *Gyps* spp. in both areas (Fig. 4).

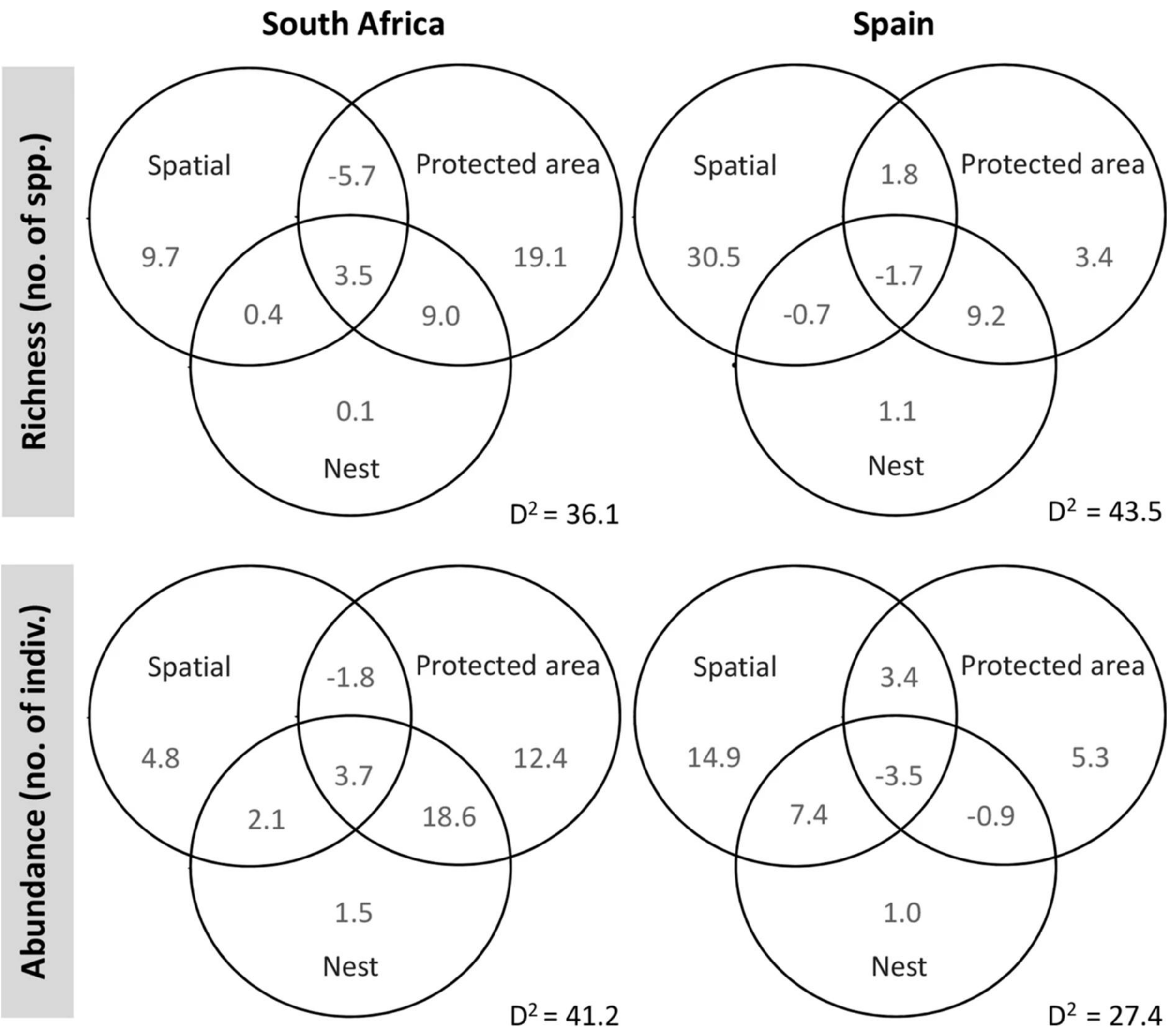


Fig. 4. Deviance partitioning analysis obtained to assess the relative importance of the spatial autocorrelation, the distance to the nearest protected area and the distance to the nearest conspecific nest/colony on the richness and abundance of *Gyps* vultures in KwaZulu-Natal Province (South Africa) and Ebro Valley (Spain). D^2 = total percentage of deviance explained by the models

Discussion

Avian scavenger occurrence patterns

Our findings, based on regional-scale avian scavenger surveys conducted on two continents, showed contrasting effects of protected areas in the distribution of different guilds of avian scavengers between the Spanish and South African study areas. The richness and abundance of African vultures were substantially higher inside than outside of protected areas in the South African area. Indeed, African vultures were never observed at distances greater than 3 km from protected reserves during counts. This pattern was not seen for vultures in the Spanish area, which were widely observed outside of protected areas, nor by facultative scavengers, which were commonly recorded both inside and outside of protected reserves in both study areas.

Factors affecting avian scavenger occurrence patterns

The observed pattern in scavenger occurrence must be largely due to a factor that operates only in the African system and affects mostly obligate scavengers. Poisoning is not likely because this threat also operates in Spain, where it also kills many avian scavengers and other wildlife every year (Villafuerte et al. 1998; Margalida 2012; Márquez et al. 2013; Cano et al. 2016), including within our study area in the Ebro Valley (Grande et al. 2009; Margalida et al. 2014; Cortés-Avizanda et al. 2015b). In addition, high levels of poisoning are not consistent with the fact that facultative scavengers were frequently observed outside of protected areas. Moreover, vultures are highly mobile organisms that can perform long-distance movements during foraging trips (usually > 100 km; Phipps et al. 2013; Spiegel et al. 2015; Arrondo et al. 2018; for comparison, see the scale of our study areas in Fig. 1). Therefore, poison would affect vulture population size, and thus vulture distribution, at a regional rather than a local scale. In regions such as our study areas, where protected reserves are relatively small, avian scavengers nesting inside of protected areas are largely sensitive to practices performed in their surroundings (Sergio et al. 2005; Cortés-Avizanda et al. 2015b). Thus, threats that mainly operate by increasing mortality rates, such as poisoning, should impact vulture occurrence not only outside but also inside of protected areas (Virani et al. 2011).

The sharp reduction in the occurrence of the highly mobile vultures outside of the studied African protected reserves suggests that the main cause of vulture distribution is most likely related to vulture foraging movements rather than to mortality (see Arrondo et al. 2018). Low (or no) availability of carrion resources outside of protected reserves results in reduced and inconsistent feeding opportunities for vultures in these areas, thus skewing their foraging movements toward the interior of protected areas where energy expended in foraging is more likely to be rewarded. It is well-known that the spatial heterogeneity in carrion resource arrangement, rather than ungulate abundance, influences the spatial distribution of vultures in other areas (e.g., Murn and Anderson 2008; Cortés-Avizanda et al. 2011; Kendall et al. 2014; Arrondo et al. 2018). Moreover, both intra- and interspecific social information is a key mechanism in finding food for vulture species such as *G. fulvus* and *G. africanus* (Spiegel et al. 2013; Cortés-Avizanda et al. 2014). Therefore, vulture aggregations inside of the studied African protected reserves could act as an attractor that prevents vulture foraging outside of their limits, thus exacerbating the effects of food shortage in the unprotected matrix. The presence of secure roosting sites inside protected areas could also shape vulture distribution. In our case, however, roosts alone are unlikely to fully explain why we very rarely observed vultures outside the studied African protected areas since count points outside were within 20 km from the boundaries of protected areas, a distance that can be covered in minutes by vultures roosting inside them. Opportunistic facultative scavengers, with their ability to exploit other food resources, such as live prey and refuse, would be less sensitive to the lack of large carcasses. In Spain, richness and abundance of avian facultative scavengers were higher outside of protected areas, which could be related to increased landscape heterogeneity in non-protected areas (Sánchez-Zapata and Calvo 1999).

A shortage of carrion in areas outside of African protected areas could result from two factors: the absence of large ungulates and/or the inaccessibility of ungulate carcasses to vultures. Although wild ungulates are rare outside of protected reserves in our African study area, livestock is abundant and the total number of heads probably exceeds the number of wild ungulates present inside of protected reserves. Thus, carrion shortage outside of protected areas must be likely due to carcasses being unavailable to vultures. In the nearby Limpopo Province of South Africa, most carrion from dead livestock in subsistence farms is consumed by the household (Stroebel et al. 2011). Similarly, a questionnaire-based survey conducted in 2012 on 147 households in 11 communities living within our study area (Claire Geoghegan, unpublished data) indicated that people frequently use dead livestock "from head to toe", meaning that livestock carcasses were never made available to vultures. Local cultural practices, together with the perceived value of meat and animal products, ensures that meat is preferentially consumed by householders regardless of whether the animal died from senescence, disease-related or human-induced causes, and small scraps are given directly to the feral dogs that roam each property and are used as protection. The intestines, skin, sinew and horns are all used for decoration, traditional medicine, to make tools or to sell. Products from deceased livestock are also gifted to people both within and outside of the immediate family, or to pay debts. Furthermore, local farmers are very careful to prevent decaying matter from attracting predators to their homestead and livestock kraals. Around HiP, the mean number (± SD) of domestic ungulates (mainly cattle and goats) per household and person were, respectively, 25.9 ± 20.1 and 3.3 ± 3.0. In these subsistence farms, where livestock numbers are limited and essential for household survival, the death of a head of livestock rarely goes unnoticed or unused, thus leading to low opportunities of carrion provisioning to wildlife.

We recognize that our findings cannot be extrapolated to all areas of Africa, as even within South Africa there is considerable ecological, cultural and social diversity. For instance, in contrast to our study area, surveyed subsistence farmers in the Eastern Cape Province of South Africa declared that dead cows, horses and donkeys are usually available to vultures (Pfeiffer et al. 2015). Furthermore, tracking studies of immature white-backed vultures in the North West Province revealed that these vultures moved mainly through unprotected land (Phipps et al. 2013). This is probably favored by the young age of the marked birds, the frequent use of 'vulture restaurants' outside of protected areas, and the predominance of commercial livestock and game farmland within the unprotected matrix of their study area (Phipps et al. 2013). However, there are some reasons to think that the carrion shortage problem identified here may be widespread across the African continent. First, subsistence farming is the most common livestock production system in Africa (ILRI 1995). Second, wild ungulate populations are undergoing severe declines throughout the continent, mostly outside of protected areas (Ogutu et al. 2011; Durant et al. 2014). Third, unlike vultures (Thiollay 2006a, b, 2007; Pomeroy et al. 2015; Ogada et al. 2016a), avian facultative scavengers such as kites and corvids are still frequent outside of protected reserves (Thiollay 2007; Herremans and Herremans-Tonnoeyr 2000).

Conservation implications

Our study supports the general idea that protected areas may have differential effects on different ecological guilds depending on the socio-ecological context surrounding a site. Thus, protected area management cannot be considered in isolation, and must take into account the evolving human activities that take place outside of their boundaries (Wells and

Brandon 1992). This is especially important when dealing with the conservation of highly mobile, endangered species such as vultures. Our findings are in agreement with the ongoing defaunation that is being observed outside of African protected areas (Newmark 2008). Also, we show how by studying basic biological questions, such as occurrence patterns, we may help to identify new and complex threats to wildlife.

Constraining vultures to protected areas could exert important effects on vulture population dynamics. For instance, constrained vulture foraging movements could restrict or lessen the movement of individuals between protected areas (Arrondo et al. 2018), thus disconnecting different local populations and potentially affecting the future dynamics of the whole population (Carrete et al. 2009). In contrast, confinement to protected areas could decrease anthropogenic risks to vultures, such as electrocution from power lines and collision with wind turbines, which cause many vulture losses every year in unprotected areas of Africa and elsewhere (Carrete et al. 2009; Boshoff et al. 2011; Angelov et al. 2013). In the case of poisoning, however, vultures inside of protected reserves are not invulnerable because of poison baits left by elephant and rhino poachers (Ogada 2014; Ogada et al. 2016b).

The ongoing depletion of wild ungulates makes the role of domestic livestock as a food resource for vultures increasingly important. A future scenario of livestock husbandry in Africa tending towards a widespread establishment of commercial farming of livestock (and/or game) could produce higher carrion availability to vultures (Murn and Anderson 2008), as occurs in Europe (Morales-Reyes et al. 2017), compared to subsistence farming systems in which most dead livestock are used by householders. However, the development of livestock farming systems should not be at the expense of wild ungulate populations (Ogutu et al. 2011). Also, the risk of poisoning related to livestock-carnivore conflicts (e.g., Newmark et al. 1994) should be anticipated, given that poisoned carcasses seem to be more frequently associated with commercial farming than subsistence farming (Pfeiffer et al. 2015; Santangeli et al. 2016). In the short-term, one management tool to deal with carrion shortage already exists in the form of supplementary feeding sites (SFS), also known as vulture restaurants. Our study suggests that their deployment might allow vultures to expand their usage of areas located outside of protected areas. However, SFS had also limitations, and should be species- and goal-oriented designed (Cortés-Avizanda et al. 2016). Assessing the distribution of SFS in relation to vulture distribution, and their impact on vulture populations in Africa should be a high priority for future research (Brink et al. 2020).

Considerable research has highlighted that poisoning is the single biggest threat to vultures in Africa (e.g., Ogada 2014; Ogada et al. 2016b). However, whilst recognizing the impact of poison, we argue that the research community should not ignore other critical threats (Ogada et al. 2016a). While poisoning undisputedly kills many vultures every year (including our study areas; see above), failure to identify other constraining factors could limit our ability to prevent declines of African vultures. Here, we provide evidence that food shortage may be an important concern for vulture conservation in some areas of Africa, deserving broad scientific, political and social awareness.

Acknowledgements

We are indebted to Geoff Clinning, Dave Druce, M. Sophie García-Heras, Dennis Kelly, Tarik Bodasing, Skhumbuzo Mdletshe and Manuel de la Riva. MM was supported by postdoctoral grants from the Spanish Ministry of Education (Plan Nacional de I+D+i 2008–2011), the Severo Ochoa Program for Centres of Excellence in R+D+I (SEV-2012-0262) and the Ramón y Cajal Program (RYC-2015-19231). ACA was supported by a contract Juan de la Cierva Incorporación (IJCI-2014-20744) from the Spanish Ministry of Economy and Competitiveness and a postdoctoral contract Programa Viçent Mut of Govern Balear, Spain (PD/039/2017). The study was partly supported by the Spanish Ministry of Science and Innovation through projects CGL2012-40013-C02-02, CGL2015-66966-C2-1-R and CGL2017-89905-R, and ERDF funds.

Data availability

The datasets generated during the current study are available in the (name to be provided upon publication) repository (link to be provided upon publication).

References

Acevedo P, Quirós-Fernández F, Casal J, Vicente J (2014) Spatial distribution of wild boar population abundance: baisc information for spatial epidemiology and wildlife management. Ecol Ind 36:594–600

Amar A, Cloete D (2018) Quantifying the decline of the Martial Eagle *Polemaetus bellicosus* in South Africa. Bird Conserv Int 28:363–374

Anderson MD (2007) Vulture crises in South Asia and West Africa and monitoring, or the lack thereof, in Africa. Ostrich 78:415–416

Angelov I, Hasim I, Oppel S (2013) Persistent electrocution mortality of Egyptian vultures *Neophron percnopterus* over 28 years in East Africa. Bird Conserv Int 23:1–6

Arrondo E, Moleón M, Cortés-Avizanda A, Jiménez J, Beja P, Sánchez-Zapata JA, Donázar JA (2018) Invisible barriers: differential sanitary regulations constrain vulture movements across country borders. Biol Conserv 219:46–52

Balme GA, Slotow R, Hunter LT (2010) Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa. Anim Conserv 13:315–323

Bernués A, Ruiz R, Olaizola A, Villalba D, Casasús I (2011) Sustainability of pasture-based livestock farming systems in the European Mediterranean context: synergies and trade-offs. Livest Sci 139:44–57

Boshoff AF, Minnie JC, Tambling CJ, Michael MD (2011) The impact of power line-related mortality on the Cape Vulture *Gyps coprotheres* in a part of its range, with an emphasis on electrocution. Bird Conserv Int 21:311–327

Brashares JS, Arcese P, Sam MK (2001) Human demography and reserve size predicts wildlife extinction in West Africa. Proc R Soc B 268:2473–2478

Brink CW, Santangeli A, Amar A, Wolter K, Tate G, Krüger S, Tucker AS, Thomson RL (2020) Quantifying the spatial distribution, resource contribution and trends of vulture supplementary feeding sites in South Africa. Anim Conserv. https://doi.org/10.1111/acv.12561

Buechley ER, Sekercioglu CH (2016) The avian scavenger crisis: looming extinctions, trophic cascades, and loss of critical ecosystem functions. Biol Conserv 198:220–228

Cano C, de la Bodega D, Ayerza P, Mínguez E (2016) El veneno en España. WWF-SEO/BirdLife, Madrid

Carrete M, Sánchez-Zapata JA, Benítez JR, Lobón M, Donázar JA (2009) Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. Biol Conserv 142:2954–2961

Cocca G, Sturaro E, Gallo L, Ramanzin M (2012) Is the abandonment of traditional livestock farming systems the main driver of mountain landscape change in Alpine areas? Land Use Policy 29:878–886

Corlett RT (2016) The role of rewilding in landscape design for conservation. Curr Landsc Ecol Rep 1:127–133

Cortés-Avizanda A, Almaraz P, Carrete M, Sánchez-Zapata JA, Delgado A, Hiraldo F, Donázar JA (2011) Spatial heterogeneity in resource distribution promotes facultative sociality in two trans-Saharan migratory birds. PLoS ONE 6:e21016

Cortés-Avizanda A, Jovani R, Carrete M, Donázar JA (2012) Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. Ecology 93:2570–2579

Cortés-Avizanda A, Jovani R, Donázar JA, Grimm V (2014) Birds sky networks: how do avian scavengers search for carrion resource. Ecology 95:1799–1808

Cortés-Avizanda A, Donázar JA, Pereira HM (2015a) Top scavengers in a wilder Europe. In: Pereira HM, Navarro L (eds) Rewilding European landscapes. Springer, New York, pp 85–106

Cortés-Avizanda A, Colomer MA, Margalida A, Ceballos O, Donázar JA (2015b) Modeling the consequences of the demise and potential recovery of a keystone-species: wild rabbits and avian scavengers in Mediterranean landscapes. Sci Rep 5:17033

Cortés-Avizanda A, Blanco G, DeVault TL, Markandya A, Virani MZ, Brandt J, Donázar JA (2016) Supplementary feeding and endangered avian scavengers: benefits, caveats, and controversies. Front Ecol Environ 14:191–199

Cushman SA, McGarigal K (2002) Hierarchical, multi-scale decomposition of species-environment relationships. Landsc Ecol 17:637–646

DeFries R, Hansen A, Turner BL, Reid R, Liu J (2007) Land use change around protected areas: management to balance human needs and ecological function. Ecol Appl 17:1031–1038

DeVault TL, Rhodes OE Jr, Shivik JA (2003) Scavenging by vertebrates: behavioural, ecological and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102:225–234

DeVault TL, Beasley JC, Olson ZH, Moleón M, Carrete M, Margalida A, Sánchez-Zapata JA (2016) Ecosystem services provided by avian scavengers. In: Sekercioglu ÇH, Wenny DG, Whelan CJ (eds) Why birds matter. Avian ecological function and ecosystem services. The University of Chicago Press, Chicago, pp 235–270

del Hoyo J, Elliot A, Sargatal J (eds) (1994) Handbook of the birds of the world, vol 2. New World Vultures to Guineafowl. Lynx Edicions, Barcelona

del Moral JC, Molina B (eds) (2018) El buitre leonado en España. Población reproductora en 2018 y método de censo. SEO/BirdLife, Madrid

Durant SM, Wacher T, Bashir S, Woodroffe R, De Ornellas P, Ransom C, Newby J, Abáigar T, Abdelgadir M, El Alqamy H, Baillie J, Beddiaf M, Belbachir F, Belbachir-Bazi A, Berbash AA, Bemadjim NE, Beudels-Jamar R, Boitani L, Breitenmoser C, Cano M, Chardonnet P, Collen B, Cornforth WA, Cuzin F, Gerngross P, Haddane B, Hadjeloum M, Jacobson A, Jebali A, Lamarque F, Mallon D, Monkowski K, Monfort S, Ndoassal B, Niagate B, Purchase G, Samaïla S, Samna AK, Sillero-Zubiri C, Soultan AE, Stanley Price MR, Pettorelli N (2014) Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. Divers Distrib 20:114–122

Fynn RW, Bonyongo MC (2011) Functional conservation areas and the future of Africa's wildlife. Afr J Ecol 49:175–188

Garbett R, Maude G, Hancock P, Kenny D, Reading R, Amar A (2018) Association between hunting and elevated blood lead levels in the critically endangered African white-backed vulture *Gyps africanus*. Sci Total Environ 630:1654–1665

Gaston KJ, Jackson SF, Cantú-Salazar L, Cruz-Piñón G (2008) The ecological performance of protected areas. Annu Rev Ecol Evol Syst 39:93–113

Grande JM, Serrano D, Tavecchia G, Carrete M, Ceballos O, Díaz-Delgado R, Tella JL, Donázar JA (2009) Survival in a long-lived territorial migrant: Effects of life-history traits and ecological conditions in wintering and breeding areas. Oikos 118:580–590

Grange S, Owen-Smith N, Gaillard JM, Druce DJ, Moleón M, Mgobozi M (2012) Changes of population trends and mortality patterns in response to the reintroduction of large predators: the case study of African ungulates. Acta Oecol 42:16–29

Herremans M, Herremans-Tonnoeyr D (2000) Land use and the conservation status of raptors in Botswana. Biol Conserv 94:31–41

Houston DC (1979) The adaptations of scavengers. In: Sinclair ARE, Griffiths MN (eds) Serengeti, dynamics of an ecosystem. University of Chicago Press, Chicago, pp 263–286

Howells B, Craigie J, Nanni G (2011) Aerial survey of Zululand tree nesting vultures, 2011. Internal EKZNW Report, Kwazulu-Natal

ILRI (International Livestock Research Institute) (1995) Livestock Policy Analysis. ILRI Training Manual 2. ILRI, Nairobi

Kendall CJ, Virani MZ, Hopcraft JGC, Bildstein KL, Rubenstein DI (2014) African vultures don’t follow migratory herds: scavenger habitat use is not mediated by prey abundance. PLoS ONE 9:e83470

Kinnaird MF, O’Brien TG (2012) Effects of private-land use, livestock management, and human tolerance on diversity, distribution, and abundance of large African mammals. Conserv Biol 26:1026–1039

Krüger SC, Simmons RE, Amar A (2015) Anthropogenic activities influence the abandonment of Bearded Vulture (*Gypaetus barbatus*) territories in southern Africa. Condor 117:94–107

Legendre P, Legendre L (1998) Numerical ecology, 2nd edn. Elsevier, Amsterdam

Loveridge AJ, Searle AW, Murindagomo F, Macdonald DW (2007) The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biol Conserv 134:548–558

Margalida A (2012) Baits, budget cuts: a deadly mix. Science 338:192

Margalida A, Moleón M (2016) Toward carrion-free ecosystems? Front Ecol Environ 14:183–184

Margalida A, Donázar JA, Carrete M, Sánchez-Zapata JA (2010) Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. J Appl Ecol 47:931–935

Margalida A, Colomer MA, Oro D (2014) Man-induced activities modify demographic parameters in a long-lived species: effects of poisoning and health policies. Ecol Appl 24:436–444

Márquez C, Vargas JM, Villafuerte R, Fa JE (2013) Understanding the propensity of wild predators to illegal poison baiting. Anim Conserv 16:118–129

Mateo-Tomás P, Olea PP (2010) Diagnosing the causes of territory abandonment by the Endangered Egyptian vulture *Neophron percnopterus*: the importance of traditional pastoralism and regional conservation. Oryx 44:424–433

Mateo-Tomás P, Olea PP, Moleón M, Vicente J, Botella F, Selva N, Viñuela J, Sánchez-Zapata JM (2015) From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Divers Distrib 21:913–924

Mateo-Tomás P, Olea PP, Moleón M, Selva N, Sánchez-Zapata JM (2017) Both rare and common species suppor ecosystem services in scavenger communities. Global Ecol Biogeogr 26:1459–1470

McClure CJW, Westrip JRS, Johnson JA, Schulwitz SE, Virani MZ, Davies R, Symes A, Wheatley H, Thorstrom S, Amar A, Buij R, Jones VR, Williams NP, Buechley ER, Butchart SHM (2018) State of the world’s raptors: distributions, threats, and conservation recommendations. Biol Conserv 227:390–402

McCullagh P, Searle SR (2000) Generalized, linear and mixed models. Wiley-Interscience, New York

Moleón M, Sánchez-Zapata JA, Margalida A, Carrete M, Donázar JA, Owen-Smith N (2014) Humans and scavengers: the evolution of interactions and ecosystem services. Bioscience 64:394–403

Moleón M, Sánchez-Zapata JA, Sebastián-González E, Owen-Smith N (2015) Carcass size shapes the structure and functioning of an African scavenging assemblage. Oikos 124:1391–1403

Monadjem A, Garcelon DK (2005) Nesting distribution of vultures in relation to land use in Swaziland. Biodivers Conserv 14:2079–2093

Morales-Reyes Z, Pérez-García JM, Moleón M, Botella F, Carrete M, Donázar JA, Cortés-Avizanda A, Arrondo E, Moreno-Opo R, Jiménez J, Margalida A, Sánchez-Zapata JA (2017) Evaluation of the network of protection areas for the feeding of scavengers in Spain: from biodiversity conservation to greenhouse gas emission savings. J Appl Ecol. https://doi.org/10.1111/1365-2664.12833

Murn C, Anderson MD (2008) Activity patterns of African White-backed Vultures *Gyps africanus* in relation to different land-use practices and food availability. Ostrich 79:191–198

Navarro LM, Pereira HM (2015) Rewilding abandoned landscapes in Europe. Rewilding European landscapes. Springer, Cham, pp 3–23

Newmark WD (2008) Isolation of African protected areas. Front Ecol Environ 6:321–328

Newmark WD, Manyanza DN, Gamassa D-GM, Sariko HI (1994) The conflict between wildlife and local people living adjacent to protected areas in Tanzania: human density as a predictor. Conserv Biol 8:249–255

Nikolaus G (2001) Bird exploitation for traditional medicine in Nigeria. Malimbus 23:45–55

Ogada DL (2014) The power of poison: pesticide poisoning of Africa's wildlife. Ann NY Acad Sci 1322:1–20

Ogada DL, Buij R (2011) Decline of the hooded vulture (*Necrosyrtes monachus*) across its African range. Ostrich 82:101–113

Ogada DL, Keesing F, Virani MZ (2012) Dropping dead: causes and consequences of vulture population declines worldwide. Ann NY Acad Sci 1249:57–71

Ogada D, Shaw P, Beyers RL, Buij R, Murn C, Thiollay JM, Beale CM, Holdo RM, Pomeroy D, Baker N, Krüger SC, Botha A, Virani MZ, Monadjem A, Sinclair ARE (2016a) Another continental vulture crisis: Africa’s vultures collapsing toward extinction. Conserv Lett 9:89–97

Ogada D, Botha A, Shaw P (2016b) Ivory poachers and poison: drivers of Africa’s declining vulture populations. Oryx 50:593–596

Ogutu JO, Owen-Smith N, Piepho H-P, Said MY (2011) Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. J Zool 285:99–109

Olea PP, Mateo-Tomás P (2009) The role of traditional farming practices in ecosystem conservation: the case of transhumance and vultures. Biol Conserv 142:1844–1853

Palomo J, Gisbert J, Blanco JC (eds) (2007) Atlas y Libro Rojo de los Mamíferos Terrestres de España. DGB-SECEM-SECEMU, Madrid

Parrish JD, Braun DP, Unnasch RS (2003) Are we conserving what we say we are? Measuring ecological integrity within protected areas. Bioscience 53:851–860

Pfeiffer MB, Venter JA, Downs CT (2015) Identifying anthropogenic threats to Cape Vultures *Gyps coproteres* using community perceptions in communal farmland, Eastern Cape Province. South Africa Bird Conserv Int 25:353–365

Phipps WL, Willis SG, Wolter K, Naidoo V (2013) Foraging ranges of immature African white-backed vultures (*Gyps africanus*) and their use of protected areas in southern Africa. PLoS ONE 8:e52813

Plieninger T, Hui C, Gaertner M, Huntsinger L (2014) The impact of land abandonment on species richness and abundance in the Mediterranean Basin: a meta-analysis. PLoS ONE 9:e98355

Pomeroy D, Shaw P, Opige M, Kaphu G, Ogada DL, Virani MZ (2015) Vulture populations in Uganda: using road survey data to measure both densities and encounter rates within protected and unprotected areas. Bird Conserv Int 25:399–414

R Core Team, 2013. R: A language and environment for statistical computing. - R Foundation for Statistical Computing <https://www.R-project.org/>

Rivas-Martínez S (1986) Mapas de las Series de Vegetación de España. ICONA, Madrid

Ruxton GD, Houston DC (2004) Obligate vertebrate scavengers must be large soaring fliers. J Theor Biol 228:431–436

Sánchez-Zapata JA, Calvo JF (1999) Raptor distribution in relation to landscape composition in semiarid Mediterranean habitats. J Appl Ecol 36:254–262

Sánchez-Zapata JA, Donázar JA, Delgado A, Forero MG, Ceballos O, Hiraldo F (2007) Desert locusts outbreaks in the Sahel: resource competition, predation and ecological effects of pest control. J Appl Ecol 44:263–269

Santangeli A, Arkumarev V, Rusk N, Girardello M (2016) Understanding, quantifying and mapping the use of poison by commercial farmers in Namibia—implications for scavengers' conservation and ecosystem health. Biol Conserv 204:205–211

Schabo DG, Heuner S, Neethling MV, Roesner S, Uys R, Farwig N (2017) Long-term data indicates that supplementary food enhances the number of breeding pairs in a Cape Vulture *Gyps coprotheres* colony. Bird Conserv Int 27:140–152

Sergio F, Blas J, Forero M, Fernández N, Donázar JA, Hiraldo F (2005) Preservation of wide-ranging top predators by site-protection: black and red kites in Doñana National Park. Biol Conserv 125:11–21

Sirami C, Brotons L, Burfield I, Fonderflick J, Martin JL (2008) Is land abandonment having an impact on biodiversity? A meta-analytical approach to bird distribution changes in the north-western Mediterranean. Biol Conserv 141:450–459

Soulé ME, Noss R (1998) Rewilding and biodiversity: complementary goals for continental conservation. Wild Earth 8:18–28

Spiegel O, Getz WM, Nathan R (2013) Factors influencing foraging search efficiency: why do scarce lappet-faced vultures outperform ubiquitous white-backed vultures? Am Nat 181:E102–E115

Spiegel O, Harel R, Centeno-Cuadros A, Hatzofe O, Getz WM, Nathan R (2015) Moving beyond curve fitting: using complementary data to assess alternative explanations for long movements of three vulture species. Am Nat 185:E44–E54

Stroebel A, Swanepoel FJC, Pell AN (2011) Sustainable smallholder livestock systems: a case study of Limpopo Province, South Africa. Livest Sci 139:186–190

Thiollay JM (2006a) The decline of raptors in West Africa: long-term assessment and the role of protected areas. Ibis 148:240–254

Thiollay JM (2006b) Severe decline of large birds in the Northern Sahel of West Africa: a long-term assessment. Bird Conserv Int 16:353–365

Thiollay JM (2007) Raptor declines in West Africa: comparisons between protected, buffer and cultivated areas. Oryx 41:322–329

Tusting LS, Bisanzio D, Alabaster G, Cameron E, Cibulskis R, Davies M, Flaxman S, Gibson HS, Knudsen J, Mbogo C, Okumu FO, von Seidlein L, Weiss DJ, Lindsay SW, Gething PW, Bhatt S (2019) Mapping changes in housing in sub-Saharan Africa from 2000 to 2015. Nature 568:391–394

United Nations (2015) World Population Prospects, 2015 Revision. United Nations Department of Economic and Social Affairs, New York

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York

Villafuerte R, Viñuela J, Blanco JC (1998) Extensive predator persecution caused by population crash in a game species: the case of red kites and rabbits in Spain. Biol Conserv 84:181–188

Virani MZ, Kendall C, Njoroge P, Thomsett S (2011) Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem. Kenya Biol Conserv 144:746–752

Watson JEM, Dudley N, Segan DB, Hockings M (2014) The performance and potential of protected areas. Nature 515:67–73

Weladji RB, Laflamme-Mayer K (2011) Influence of environmental conditions on sex allocation in the black rhinoceros population of Mkhuze Game Reserve, South Africa. Afr J Ecol 49:471–480

Wells M, Brandon K (1992) People and parks: linking protected area management and local communities. World Bank, Washington

Wittemyer G, Elsen P, Bean WT, Burton ACO, Brashares JS (2008) Accelerated human population growth at protected area edges. Science 321:123–126

Woodroffe R, Ginsberg JR (1998) Edge effects and the extinction of populations inside protected areas. Science 280:2126–2128

Xu W, Xiao Y, Zhang J, Hull V, Wang Z, Zheng H, Liu J, Polasky S, Jiang L, Xiao Y, Shi X, Rao E, Lu F, Wang X, Daily GC, Ouyang Z (2017) Strengthening protected areas for biodiversity and ecosystem services in China. Proc Natl Acad Sci USA 114:1601–1606