Landscape anthropization shapes the survival of a top avian scavenger

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Abstract

Events of non-natural mortality in human-dominated landscapes are especially challenging for populations of large vertebrates with K strategies. Among birds, vultures are one of the most threatened groups experiencing sharp population declines due to non-natural mortality. Factors causing non-natural mortality are usually studied separately. However, the potential use of an integrated index able to predict large-scale mortality risks of avian scavengers could be especially useful for planning conservation strategies. Here, we used the Human Footprint index to examine the impact of landscape anthropization on the survival rates of 66 GPS-tagged adult Eurasian griffon vultures (*Gyps fulvus*) in two Spanish regions. Foraging in more anthropized areas resulted in a significantly higher individual mortality risk mainly due to collisions with vehicles, poisonings, electrocutions and fatalities with wind turbines. Mean yearly survival rates were estimated at 0.817 ± 0.043 SE and 0.968 ± 0.018 SE for individuals from the more and less anthropized regions, respectively. Additional research should investigate whether some vulture populations could be acting as sinks unnoticed due to metapopulation dynamics. From a broader point of view, our study shows that a straightforward Human Footprint was a useful index to predict the survival of top scavengers and can be highly applicable to planning large-scale conservation measures.

Keywords Griffon · Vulture · Human footprint · Non-natural mortality · Anthropization

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Introduction

The continuous growth of human populations entails the sequestration of land, and the subsequent deep alterations of the biosphere (Vitousek 1997; Ibisch et al. 2016; Popp et al. 2017). Large vertebrates are particularly sensitive to these shifts because of their life history strategies include low fecundity, delayed maturity and high adult survival (Owens and Bennett 2000; Carrete et al. 2009). The main proximate factor driving the plummeting of large vertebrate populations is non-natural mortality caused by a panoply of factors including direct persecution, roadkills, electrocutions, impacts with human structures (e.g. collisions and entanglements) and zoonoses (D'Amico et al. 2015; Loss et al. 2015; Millán et al. 2016; Sánchez-Zapata et al. 2016; Bernardino et al. 2018; Badía-Boher et al. 2019). Nevertheless, anthropized areas can also provide refuge, food and/or protection from predators (Oro et al. 2013; Rebolo-Ifrán et al. 2017; Payo-Payo et al. 2017; Luna et al. 2018).

Old World vultures are closely intertwined with humans. Traditionally, they have been associated with agro-grazing societies in Eurasia and Africa in a “win-win” relationship (Olea and Mateo-Tomás 2009) in which the birds benefited from carcass provisioning while farmers profited from the provision of ecosystem services (Dupont et al. 2012; Moleón et al. 2014; Cortés-Avizanda et al. 2015; Morales-Reyes et al. 2015; DeVault et al. 2016). However, since the mid-twentieth century, traditional agro-grazing systems in mountainous areas have been progressively abandoned and subjected to passive rewilding processes, whilst in lowlands traditional farming practices are being replaced by more intensive exploitations (Foley et al. 2011; Cortés-Avizanda et al. 2015; Navarro and Pereira 2015). The result is a polarized situation with some regions that are highly anthropized and dominated by intensive land uses and others subjected to human abandonment and rewilding (Perino et al. 2019). The great movement capacity of vultures (Monsarrat et al. 2013; Fluhr et al. 2017; Arrondo et al. 2018) allows them to respond to land transformation by nesting in abandoned and relatively well-conserved areas (García-Barón et al. 2018) while feeding in anthropized landscapes (Henriques et al. 2018) that offer them important trophic subsidies (Oro et al. 2013). This strategy, however, may entail an increased risk of non-natural mortality a concerning issue behind the decline of avian scavenger populations worldwide (Ogada et al. 2012). Landscape anthropization increments the density of human structures such as roads and power lines that can be extremely dangerous for large scavengers (Vidal-Vallés et al. 2018; Boshoff et al. 2011; Angelov et al. 2013; Sanz-Aguilar et al. 2015b). In addition, vultures feeding in highly anthropic environments such as landfills or intensive farms can be exposed to higher risks of poisonings (Tauler-Amettler et al. 2017; Blanco et al. 2019). Thus, foraging in human-dominated landscapes could lead to higher mortality risks. Consequently, individuals from different areas or showing different behaviors in terms of the use of space and foraging strategies may experience different threats and survival probabilities (Sanz-Aguilar et al. 2015a).

From a conservation point of view, it would be extremely useful to evaluate the synergistic effect of large-scale landscape anthropization on the survival of large body-sized vultures. Here, we evaluated the survival rates of 66 adult Eurasian griffon vultures (*Gyps fulvus*), captured and GPS-tracked in two Spanish populations, in relation to the anthropization of the individuals' home ranges. To achieve this, we used the Human Footprint index (Venter et al. 2016) as a proxy of landscape anthropization. Our main purpose was to assess if the Human Footprint index successfully predicts the survival rates of this top scavenger. We hypothesized that individuals with higher values of the Human Footprint index within their home ranges should have a lower survival probability.

Methods

Target species and study areas

The griffon vulture is a large avian scavenger (weighing up to 12 kg) that was historically distributed across large arid and semi-arid regions of Southern Europe, North Africa, the Middle East and Central Asia (Cramp and Simmons 1980). The species has largely disappeared and/or declined from most of its former Western Palearctic range, and today is only abundant in the Iberian Peninsula (Margalida et al. 2010). Given its relative abundance, foraging capacity, and social habits, it is the main species providing regulatory ecosystem services to Spanish farmers (Morales-Reyes et al. 2018). The griffon vulture is a gregarious species breeding colonially in mountain cliffs and foraging over large portions of land, where it looks for carcasses of wild and domestic animals, mainly ungulates (Margalida et al. 2011). Griffons are highly mobile species with home ranges covering thousands of square kilometers (Monsarrat et al. 2013; Fluhr et al. 2017 and see results). This facility for long-distance displacements means that griffons are able to travel throughout the Iberian Peninsula (Arrondo et al. 2018).

We captured 30 adult griffon vultures in southern Spain between December 2014 and January 2015, and 36 adult individuals in northern Spain between December 2015 and March 2016 (Fig. 1, S.T.1). The 83.3% of the individuals tagged in Northern Spain and 86.7% of the birds tagged in Southern Spain were detected breeding at least one time and always within a radius of 65, and 28 km from their trapping point. All of the remaining birds were never detected breeding during the study but all of them had activity centers within the same radiuses. In consequence, we are confident that our study focused on two distinct and well-separated Iberian populations.

The northern population occupies the Middle Ebro Valley, a flat, semi-arid area surrounded by mid-sized mountains (up to 1500 m a.s.l.). The vultures breed in cliffs along rivers and plateaus. Most of the land in the region has been largely transformed for intensive agricultural purposes (Lecina et al. 2005). Additionally, traditional sheep livestock has been partially replaced by intensive farming (Martín-Queller et al. 2010). The southern population was located in the “Sierras de Cazorla Segura y las Villas” Natural Park where the birds breed in the cliffs of mountains, which range from 500 to 2107 m a.s.l.. The area is mostly covered by Mediterranean woodlands, pasturelands and pine reforestation where the main human uses are traditional sheep farming, big game hunting, forestry and tourism (Campos et al. 2019).

In both areas, vultures were captured by cannon nets with livestock carcasses as baits and were equipped with 90 g GPS/GPRS-GSM devices from e-obs digital telemetry (<https://www.e-obs.de>), which additionally incorporates accelerometer sensors. We adapted GPS settings to weather conditions (S.T.2) while accelerometers recorded information with constant frequency. All birds were monitored from capture until December 2018, except in cases of early device failure or death of the vulture (see S.T.1 for individual information and tracking setting details). All birds were sexed using molecular procedures (Wink et al. 1998). The age of the individuals was determined by plumage moult and other external features (e.g. color of culmen and eye). Birds more than 6 years of age were assigned as adults (Zuberogoitia et al. 2013).

We combined accelerometer and GPS information to localize dead vultures (Sherub et al. 2017). When we perceived multiple GPS fixes at the same place for several days and confirmed the inexistence of vital activities by accelerometer signal, we visited the last

Fig. 1 Sum of individual 95% kernel contour for griffons from Northern population (Upper panel, yellow) and Southern population (Lower panel, blue). In both cases, black stars indicate the trapping location for each population. Human Footprint index for Iberian Peninsula is represented from white to red (from 0 to 50)

GPS location and searched actively for the bird. We recovered all the dead animals except one. Necropsies were carried out in regional wildlife rescue centers.

Anthropization of vulture home ranges

We estimated home range areas of individuals by kernel density models in the *adehabitatHR* package (Calenge and Fortmann-Roe 2013) run in R version 3.0.3 (R Core Team 2014). The spatial use of each individual was estimated using as a smoothing parameter the *ad hoc* method and with a resolution of one ha (Margalida et al. 2016). We calculated the 95% (KDE95) and 50% kernel (KDE50) density contours representing the home range and the core area of activity, respectively.

We used the Human Footprint index as an anthropization proxy (<https://weshumanfootprint.org/>). It expresses, on a scale from 0 to 50, a measure of human influence in a particular area (1km² resolution) integrating the human population density and the main human land uses: crop surface, pasturelands surface, nightlights, built environments, railway coverage, major roadway coverage, and navigable waterways (Venter et al. 2016). In our study area (Iberian Peninsula), Human Footprint is especially high surrounding large cities, along the coast and inside the natural corridors formed by the most important rivers such as the Ebro and Guadalquivir Basins (Fig. 1).

For each individual, we quantified the median Human Footprint at the home range and core areas. For this purpose, we intersected each individual's KDE95 and KDE50 with the European Human Footprint map. We compared both by t-test to detect possible co-variation ($R=0.88$ p value <0.001). Based on these results, we decided to use only the median Human Footprint at the KDE95 as a proxy of anthropization experienced by individuals for subsequent statistical analyses.

Survival analyses

The effects of sex (male/female), population (Northern/Southern) and anthropization (see above) on individual survival probabilities were tested using known-fate capture-recapture models. We used known-fate data on monthly live and dead encounters of individuals to estimate survival probabilities using the program MARK (White and Burnham, 1999). Because anthropization (Human Footprint) and population were not independent ($t=11.17$, $df=56.07$, $p<0.001$, see results), we did not include both effects simultaneously within the same model. Model selection was conducted using the Akaike's Information Criterion adjusted for the effective sample size, AICc (Burnham and Anderson 2002). Models within a $\Delta AICc < 2$ were considered equivalent and the Akaike weight was used to calculate model averaged survival estimates (Burnham and Anderson 2002). Annual survival estimates were derived by transforming monthly estimates (Powell, 2007). Effects whose confidence intervals of the beta slope overlapped with zero were considered as non-significant.

Results

The average individual home ranges (KDE95) were $8\,386.4 \pm 8\,358.2$ km² (mean and SD) in the Northern population ($n=36$) and $11\,249.8 \pm 5\,956$ km² (mean and SD) in the Southern population ($n=30$; S. T1). Vultures of the Northern population exploited a total area of $113\,248.6$ km² compared to $58\,417.2$ km² in the Southern population

(Fig. 1). Individuals from each population preferentially exploited those areas near breeding sites but both shared a secondary and distant foraging area in the southwestern Iberian Peninsula characterized by a “dehesas” landscape (Fig. 1; see also Arrondo et al. 2018). Home ranges of individuals from the Northern population showed higher values of Human Footprint than those of Southern individuals (Wilcoxon-test: $w = 1068$, $p < 0.001$; Fig. 2).

During the study period, we found fifteen dead vultures (eleven males and four females) from the Northern population (41.7%). On the contrary, we only recorded three dead vultures (one male and two females) from the Southern population (10.0%). The main mortality causes were all non-natural: run over by vehicles (33.3%), poisoning (27.8%), electrocution (22.2%), and collision with wind turbines (11.1%) (S.T.1).

Capture-recapture analyses showed that the best model in terms of AICc included a negative effect of anthropization on survival probabilities (Model 1, Tables 1 and 2, Fig. 3). An additional model including the additive effect of sex and anthropization was almost equivalent in terms of AICc (Model 2, Table 1). The next model (Model 3, Table 1, $\Delta AIC = 3.24$) accounted for the effect of anthropization in interaction with sex, but the effect was only significant for males (Table 2). On the other hand, model selection including the effects of population indicated that the best model in terms of AIC included the effect of population in interaction with sex (Table 2). However, this model was equivalent in terms of AICc to a model without a sex effect and to a model with an additive effect of population and sex (Table 1). Model averaged estimates indicated that survival probabilities were especially low for the Northern males but very similar for both males and females from the Southern population (Table 3). Globally, model averaged estimates indicated that griffon vultures monitored in the Northern population showed a lower survival (monthly = 0.98 ± 0.00 SE; yearly = 0.82 ± 0.04 SE) than those of the Southern population (monthly = 0.10 ± 0.00 SE; yearly = 0.968 ± 0.02 SE) (Model 7, Table 1).

Fig. 2 Distribution of Human Footprint index (rounded median values) of vultures' home ranges from the Northern and Southern populations. Human Footprint index scale is from 0 to 50

Table 1 Model selection testing the effects of the anthropization (i.e. Human Footprint index), population, and sex on the monthly survival probabilities of griffon vultures. Anthropization (Models 1–5) and population effects were tested separately (Models 4–8) because of a lack of independence

Model	Effect on survival	Np	Dev	AICc	$\Delta AICc$	AICw
1	Human footprint	2	192.32	196.33	0.00	0.64
2	Human footprint + sex	3	192.30	198.31	1.98	0.24
3	Human footprint* sex	4	191.55	199.57	3.24	0.13
4	Constant	1	205.63	207.63	11.31	0.01
5	Sex	2	205.09	209.10	12.77	0.00
6	Population* sex	4	189.66	197.68	0.00	0.40
7	Population	2	194.01	198.01	0.33	0.34
8	Population + sex	3	192.63	198.64	0.96	0.25
4	Constant	1	205.63	207.63	9.95	0.00
5	Sex	2	205.09	209.10	11.41	0.00

Model notation: + additive effect; * interaction effect, *Np* number of parameters, *Dev* deviance, *AICc* second-order corrected Akaike's information criterion, $\Delta AICc$ AICc difference from the model with the lowest AICc (in bold), *AICw* Akaike weights

Table 2 Beta estimates of intercepts and linear slopes for the models testing the effects of anthropization (Human Footprint) on griffon vulture monthly survival (Table 1)

Model	Effects considered	$\beta \pm SE$	Low 95% CI	Upp 95% CI
1	Intercept	7.13 $\pm$ 0.76	5.65	8.61
	Slope Human Footprint	-0.27 $\pm$ 0.07	-0.41	-0.13
2	Intercept females	7.15 $\pm$ 0.77	5.65	8.65
	Intercept males	7.07 $\pm$ 0.85	5.41	8.74
3	Slope Human Footprint	-0.27 $\pm$ 0.07	-0.41	-0.13
	Intercept females	7.36 $\pm$ 0.93	5.53	9.19
	Intercept males	5.87 $\pm$ 1.55	2.83	8.91
	Slope Human Footprint females	-0.12 $\pm$ 0.18	-0.42	0.24
	Slope Human Footprint males	-0.30 $\pm$ 0.08	-0.45	-0.14

Discussion

Our results show that exploiting highly anthropized home ranges (areas with larger human densities and more extensive infrastructure networks) entails large non-natural mortality risks for griffon vultures.

Non-natural mortality has demonstrated to be a major concern for vulture conservation, responsible for vulture populations collapses worldwide (Ogada et al. 2012). However, anthropogenic mortality causes are highly context dependent. For example, in Asia uncontrolled use of veterinary drugs caused a drastic decline of vulture populations (Green et al. 2004), while in Africa intentional poisoning (due to conflicts with livestock and/or poachers) is the main threat (Ogada et al. 2016). Nevertheless, there are some common worldwide threats affecting vulture survival such as collisions with human infrastructures or electrocutions (Bevanger 1994; Boshoff et al. 2011; de Lucas et al. 2012; Angelov et al. 2013; Dixon et al. 2013). In this study, 66.6% of the vultures recovered dead died because

Fig. 3 Estimates of monthly and yearly survival probabilities (black and red solid lines, respectively) and 95% CI (black and red dashed lines, respectively) in relation to the Human Footprint index (Model 1, Table 1)

Table 3 Model averaged estimates and SE of monthly and yearly survival probabilities of male and female vultures marked at the Northern and Southern populations (Models 6–10, Table 1)

Group	Monthly survival $\pm$ SE	Yearly survival $\pm$ SE
Northern males	0.98 ± 0.01	0.78 ± 0.07
Northern females	0.99 ± 0.01	0.86 ± 0.06
Southern males	1.00 ± 0.00	0.97 ± 0.02
Southern females	1.00 ± 0.00	0.96 ± 0.03

of electrocution in power lines and collisions with vehicles or wind turbines (see Table S.T.1). Given that landscape anthropization is expected to continue increasing in the future (Venter et al. 2016) the mortality risks associated with infrastructures such as power lines, wind farms or roads could also increase (Ibisch et al. 2016; Bernardino et al. 2018).

Human Footprint index is an excellent tool for the conservation of scavengers in general and vultures in particular (Santangeli et al. 2019; Sebastián-González et al. 2019). In this sense, our study highlights that it can be also an effective predictor of mortality rates for top scavengers. Our results indicate that the Human Footprint index of the home ranges of adult vultures marked in the Northern and the Southern Spanish populations greatly differed, being higher for northern birds. In the north, the most exploited foraging areas within the Ebro Valley have many semi-extensive sheep farms whose owners have been authorized to abandon dead animals for vultures since the approval of the new European sanitary regulations (Morales-Reyes et al. 2017). In addition, there are many intensive farms whose remains are often abandoned for scavengers, although these practices are prohibited by law (authors' unpublished data). The lack of sanitary control of these illegal inputs of carrion may lead to a greater exposure to veterinary drugs including toxins and

antibiotics (Pitarch et al. 2017; Blanco et al. 2019). In addition, the highly transformed areas of the Ebro Valley include large rubbish dumps, which provide vultures with predictable food sources (Donázar et al. 2010; Tauler-Ametller et al. 2017) but present further risks such as toxin ingestion and pathogen transmission (Boxall et al. 2003; Plaza and Lambertucci 2017). Moreover, the abundance of intensive farms may also increase the risk of electrocution because the power lines installed are generally of dangerous design (Pérez-García et al. 2017). Thus, vultures from the Northern population are likely attracted to human-dominated areas where food is abundant and predictable but risky. On the contrary, in the south, individuals forage on large extensive farming systems ("dehesas") that still hold large numbers of free-ranging livestock (Morales-Reyes et al. 2015) but also wild ungulates (Apollonio et al. 2010). Thus, home ranges of southern vultures present minor levels of Human footprint and lower density of dangerous human structures, (e.g. roads or power lines) than in the northern area. These results emphasize the importance of these "dehesas" landscape and traditional livestock practices (e.g. unstable and transhumance) in the conservation of vultures (Carrete and Donázar 2005; Olea and Mateo-Tomás 2009; Arrondo et al. 2019).

The annual survival probabilities estimated for Northern individuals (0.81 ± 0.05 ; mean and SD), were lower than those described for growing griffon populations, which typically are higher than 0.9 (Sarrazin et al. 1994; Le Gouar et al. 2008; Schaub et al. 2009). We cannot make further demographic inferences at the population level because of the limitations of our study (relatively short period and small sample size), nonetheless, the scenario is concerning. Griffon vultures lay a single egg, and can start breeding at four years old (Sarrazin et al. 1996) and probably later in dense populations as studied here (Ferrer et al. 2004). The viability on this kind of long-lived species is based on adults survival (Sæther and Bakke 2000; Schaub et al. 2009; Sanz-Aguilar et al. 2015b; Chantepie et al. 2016). Thus, if the survival detected in Northern individuals is representative of the whole population, a local decline could be expected (see Table S.T.3). Nevertheless, last national census (del Moral et al. 2018) does not evidence an abrupt decline in any population. However, both the existence of high adult mortality and population stability can be possible (Sanz-Aguilar et al. 2016). Adult mortality could be compensated by local recruitment of immature individuals, (Oro et al. 2008), but this scenario seems highly unrealistic, given the relatively low productivity in the Northern area (See Table S.T.3). In a more realistic scenario (i.e. a metapopulation scenario) the emigration from source to sink populations may compensate the losses of breeding adults (Schaub et al. 2010; Sanz-Aguilar et al. 2016), as shown for some of the French populations of griffon (Le Gouar et al. 2008) and other raptor species. (Carrete et al. 2009; Hernández-Matías et al. 2013). Current monitoring programs focus their efforts on estimating the breeding size and the reproductive success of different populations (del Moral et al. 2018). However, there is an important lack of knowledge on the non-breeding fraction of the population (i.e. their size and role in metapopulation dynamics). Thus, and because of the global importance of the Iberian griffon population (Margarida et al. 2010), managers should develop new more exhaustive monitoring programs to evaluate demographic dynamics (Le Gouar et al. 2008).

Recent studies have reported sexual segregation as a relevant issue in land birds conservation (Bennett et al. 2019). Our models suggest a potential existence of sex-biased mortality rates associated with anthropization. While our model results are weak, a recent model interpretation paradigm recommends not overlooking non-significant results (McShane et al. 2019). It is plausible that males could be more susceptible to death in highly anthropized areas as found in other large body-sized scavenger species also showing little sexual dimorphism, namely the Egyptian vultures *Neophron percnopterus* (Sanz-Aguilar

et al. 2017). Griffons present very little sexual dimorphism (Xirouchakis and Poulakakis 2008) and do not show apparent foraging behavioral differences between sexes (Bosè and Sarrazin 2007; Bosè et al. 2012; Monsarrat et al. 2013). However, sex-partitioning of the trophic niche at the micro-scale cannot be discarded, as occurs in the Egyptian Vulture (van Overveld et al. 2018). Accordingly, although differences in mortality between sexes have not been found in healthy populations (Le Gouar et al. 2008, birds marked in the Southern population in this study), we recommend further research to examine if behavioral differences between sexes could lead to sex-biased mortality risks in highly anthropized areas.

In summary, our study highlights that future local and regional processes of land abandonment and land use intensification are bound to have consequences for the demography of large scavengers (Cortés-Avizanda et al. 2015; Henriques et al. 2018). While anthropization will decrease in the future in many rural European areas through rewilding processes (Perino et al. 2019), it will increase sharply in others leading to a dangerous mosaic landscape for large scavengers. Moreover, even if foraging in abandoned areas is safer for avian scavengers, the loss of traditional grazing practices will reduce the availability of food resources that may not be sufficient to maintain their current populations (Margalida et al. 2011; García-Barón et al. 2018). Furthermore, the concentration of foraging activities in intensive farming areas and rubbish dumps could lead to an ecological trap jeopardizing the future of their populations in the long-term (Schlaepfer et al. 2002). Thus, appropriate management of land uses as a consequence of abandonment/intensification processes, conservation of traditional livestock farming practices and associated landscapes (relatively unaltered by humans and with low levels of Human Footprint) are advisable for vulture conservation. Also, the mitigation of the impact of present dangerous human infrastructures and the careful planning for the development of new infrastructures (i.e. wind farms, roads, power lines) appear to be key to maintaining and recovering vulture populations. Finally, we suggest the use of the Human Footprint index as a proxy for evaluating vulture survival at large spatial scales and improving the planning of current and future conservation measures.

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References

- Angelov I, Hashim I, Oppel S (2013) Persistent electrocution mortality of Egyptian vultures *Neophron percnopterus* over 28 years in East Africa. *Bird Conserv Int* 23(1):1–6. <https://doi.org/10.1017/S0959270912000123>
- Apollonio M, Andersen R, Putman R (2010) European ungulates and their management in the 21st century. Cambridge University Press, Cambridge
- 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

- Arrondo E, Morales-Reyes Z, Moleón M, Cortés-Avizanda A, Donázar JA, Sánchez-Zapata JA (2019) Rewilding traditional grazing areas affects scavenger assemblages and carcass consumption patterns. *Basic Appl Ecol* 41:56–66
- Badia-Boher JA, Sanz-Aguilar A, de la Riva M, Gangoso L, van Overveld T, García-Alfonso M, Luzardo OP, Suarez-Pérez A, Donázar JA (2019) Evaluating European LIFE conservation projects: improvements in survival of an endangered vulture. *J Appl Ecol*. <https://doi.org/10.1111/1365-2664.13350>
- Bennett RE, Rodewald AD, Rosenberg KV (2019) Overlooked sexual segregation of habitats exposes female migratory landbirds to threats. *Biol Conserv* 240:108266
- Bernardino J, Bevanger K, Barrientos R, Dwyer JF, Marques AT, Martins RC, Shaw JM, Silva JP, Moreira F (2018) Bird collisions with power lines: state of the art and priority areas for research. *Biol Conserv* 222:1–13
- Bevanger K (1994) Bird interactions with utility structures: collision and electrocution, causes and mitigating measures. *Ibis* 136(4):412–425
- Blanco G, Cortés-Avizanda A, Frías Ó, Arrondo E, Donázar JA (2019) Livestock farming practices modulate vulture diet-disease interactions. *Glob Ecol Conserv* 17:e00518
- Bosè M, Sarrazin F (2007) Competitive behaviour and feeding rate in a reintroduced population of griffon vultures *Gyps fulvus*. *Ibis* 149(3):490–501
- Bosè M, Duriez O, Sarrazin F (2012) Intra-specific competition in foraging griffon vultures *Gyps fulvus*: 1 Dynamics of group feeding. *Bird Study* 59(2):182–192
- 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(3):311–327
- Boxall AB, Kolpin DW, Halling-Sørensen B, Tolls J (2003) Peer reviewed: are veterinary medicines causing environmental risks? *Environ. Sci. Technol* 37(15):286A–294A. <https://doi.org/10.1021/es032519b>
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach (2nd edn). In: *Ecological modelling*. Springer Science & Business Media, New York
- Calenge C, and Fortmann-Roe S (2013) AdehabitatHR: home range estimation. R package version 0.4, 7
- Campos P, Caparrós A, Oviedo JL, Ovando P, Álvarez-Farizo B, Díaz-Balteiro L, Carranza J, Beguería S, Díaz M, Herruzo AC, Martínez-Peña F, de Fruto P, Aldea J, Almazána E, Concepción ED, Mesa B, Romero C, Serrano-Notivol R, Fernández C, Torres-Porras J, Montero G (2019) Bridging the gap between national and ecosystem accounting application in andalusian forests, Spain. *Ecol Econ* 157:218–236
- Carrete M, Donázar JA (2005) Application of central-place foraging theory shows the importance of Mediterranean dehesas for the conservation of the cinereous vulture *Aegypius monachus*. *Biol Conserv* 126(4):582–590
- 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(12):2954–2961
- Chantepe S, Teplitsky C, Pavard S, Sarrazin F, Descaves B, Lecuyer P, Robert A (2016) Age-related variation and temporal patterns in the survival of a long-lived scavenger. *Oikos* 125(2):167–178
- Cortés-Avizanda A, Donázar JA, Pereira HM (2015) Top scavengers in a wilder Europe. In: *Rewilding European landscapes*, Springer, Cham pp. 85–106
- Cramp S, Simmons KEL (1980) *The birds of the western palearctic*, 2nd edn. Oxford University Press, Oxford
- D'Amico, M., Román, J., De los Reyes, L., & Revilla, E. (2015) Vertebrate road-kill patterns in Mediterranean habitats: who, when and where. *Biol Conserv* 191:234–242
- De Lucas M, Ferrer M, Bechard MJ, Muñoz AR (2012) Griffon vulture mortality at wind farms in southern Spain: distribution of fatalities and active mitigation measures. *Biol Conserv* 147(1):184–189
- De Vault TL, Beasley JC, Olson ZH, Moleón M, Carrete M, Margalida A, Sánchez-Zapata JA (2016) Ecosystem services provided by avian scavengers. Why birds matter: avian ecological function and ecosystem services. University of Chicago Press, Chicago, pp 235–270
- Del Moral JC, y Molina B (eds) (2018) *El buitre leonado en España, población reproductora en 2018 y método de censo*. SEO/BirdLife, Madrid
- Dixon A, Maming R, Gunga A, Purev-Ochir G, Batbayar N (2013) The problem of raptor electrocution in Asia: case studies from Mongolia and China. *Bird* 23(4):520–529
- Donázar JA, Cortés-Avizanda A, Carrete M (2010) Dietary shifts in two vultures after the demise of supplementary feeding stations: consequences of the EU sanitary legislation. *Eur. J Wildl Res* 56(4):613–621
- Dupont H, Mihoub JB, Bobbé S, Sarrazin F (2012) Modelling carcass disposal practices: implications for the management of an ecological service provided by vultures. *J Appl Ecol* 49(2):404–411

- Ferrer et al (2004) Density-dependent age of first reproduction as a buffer affecting persistence of small populations. *Ecol Appl* 14:616–624
- Fluhr J, Benhamou S, Riotte-Lambert L, Duriez O (2017) Assessing the risk for an obligate scavenger to be dependent on predictable feeding sources. *Biol Conserv* 215:92–98
- Foley JA, Ramankutty N, Brauman KA, Cassidy ES, Gerber JS, Johnston M, Mueller ND, O'Connell C, Ray DK, West PK, Balzer C, Bennett EM, Carpenter SR, Hill J, Monfreda C, Polasky S, Rockström J, Seehan J, Siebert S, Tilman D, Zaks DPM (2011) Solutions for a cultivated planet. *Nature* 478(7369):337
- García-Barón I, Cortés-Avizanda A, Verburg PH, Marques TA, Moreno-Opo R, Pereira HM, Donazar JA (2018) How to fit the distribution of apex scavengers into land abandonment scenarios? The Cinereous vulture in the Mediterranean biome. *Divers Distrib* 24(7):1018–1031
- Green RE, Newton IAN, Shultz S, Cunningham AA, Gilbert M, Pain DJ, Prakash V (2004) Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. *J Appl Ecol* 41(5):793–800
- Henriques M, Granadeiro JP, Monteiro H, Nuno A, Lecoq M, Cardoso P, Regalla A, Catry P (2018) Not in wilderness: African vulture strongholds remain in areas with high human density. *PLoS ONE* 13(1):e0190594
- Hernández-Matías A, Real J, Moleón M, Palma L, Sánchez-Zapata JA, Pradel R, Arroyo B, Fernández C, Vincent-Martin N, Ravayrol A, Benítez JR, Ferreiro E, García J (2013) From local monitoring to a broad-scale viability assessment: a case study for the Bonelli's Eagle in western Europe. *Ecol Monogr* 83(2):239–261
- Ibisch PL, Hoffmann MT, Kreft S, Pe'er G, Kati V, Biber-Freudenberger L, DellaSala DA, Vale MM, Hobson P, Selva N (2016) A global map of roadless areas and their conservation status. *Science* 354(6318):1423–1427
- Le Gouar P, Robert A, Choisy JP, Henriquet S, Lecuyer P, Tessier C, Sarrazin F (2008) Roles of survival and dispersal in reintroduction success of griffon vulture (*Gyps fulvus*). *Ecol Appl* 18(4):859–872
- Lecina S, Playán E, Isidoro D, Dechmi F, Causapé J, Faci JM (2005) Irrigation evaluation and simulation at the irrigation district V of Bardenas (Spain). *Agric Water Manag* 73(3):223–245
- Loss SR, Will T, Marra PP (2015) Direct mortality of birds from anthropogenic causes. *Ann Rev Ecol Evol Syst* 46:99–120
- Luna Á, Romero-Vidal P, Hiraldo F, Tella JL (2018) Cities favour the recent establishment and current spread of the Eurasian collared dove *Streptopelia decaocto* (Frivaldszky, 1838) in Dominican Republic. *Bioinvasions Rec* 7(1):95–99
- Margalida A, Donazar 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(4):931–935
- Margalida A, Colomer MÀ, Sanuy D (2011) Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. *PLoS ONE* 6:e20248
- Margalida A, Pérez-García JM, Afonso I, Moreno-Opo R (2016) Spatial and temporal movements in Pyrenean bearded vultures (*Gypaetus barbatus*): Integrating movement ecology into conservation practice. *Sci Rep* 6:35746
- Martín-Queller E, Moreno-Mateos D, Pedrocchi C, Cervantes J, Martínez G (2010) Impacts of intensive agricultural irrigation and livestock farming on a semi-arid Mediterranean catchment. *Environ Monit Assess* 167(1–4):423–435
- McShane BB, Gal D, Gelman A, Robert C, Tackett JL (2019) Abandon statistical significance. *Am Stat* 73(1):235–245
- Millán J, López-Bao JV, García EJ, Oleaga Á, Llaneza L, Palacios V, de la Torre A, Rodríguez A, Dubovi EJ, Esperón F (2016) Patterns of exposure of Iberian wolves (*Canis lupus*) to canine viruses in human-dominated landscapes. *EcoHealth* 13(1):123–134
- Moleón M, Sanchez-Zapata JA, Margalida A, Carrete M, Owen-Smith N, Donazar JA (2014) Humans and scavengers: the evolution of interactions and ecosystem services. *Biosci J* 64(5):394–403
- Monsarrat S, Benhamou S, Sarrazin F, Bessa-Gomes C, Bouten W, Duriez O (2013) How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? *PLoS ONE* 8(1):e53077
- Morales-Reyes Z, Pérez-García JM, Moleón M, Botella F, Carrete M, Lazcano C, Sánchez-Zapata JA (2015) Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. *Sci Rep* 5:7811
- Morales-Reyes Z, Pérez-García JM, Moleón M, Botella F, Carrete M, Donazar JA, Cortés-Avizanda A, Arrondo E, Moreno-Opo R, Jiménez J, Margalida M (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* 54(4):1120–1129
- Morales-Reyes M, Martín-López B, Moleón M, Mateo-Tomás P, Botella F, Margalida A, Donazar JA, Blanco G, Pérez I, Sánchez-Zapata JA (2018) Farmer perceptions of the ecosystem services provided by scavengers: what, who and to whom. *Conserv Lett* 11:e12392
- Navarro LM, Pereira HM (2015) Rewilding abandoned landscapes in Europe. *Rewilding European landscapes*. Springer, Cham, pp 3–23
- Ogada DL, Keesing F, Virani MZ (2012) Dropping dead: causes and consequences of vulture population declines worldwide. *Ann N Y Acad Sci* 1249(1):57–71
- Ogada D, Shaw P, Beyers RL, Buij R, Murn C, Thiollay JM, Krüger SC, Botha A, Virani MZ, Monadjem A, Sinclair ARE (2016) Another continental vulture crisis: Africa's vultures collapsing toward extinction. *Cons Lett* 9(2):89–97
- Olea PP, Mateo-Tomás P (2009) The role of traditional farming practices in ecosystem conservation: the case of transhumance and vultures. *Biol Conserv* 142(8):1844–1853
- Oro D, Margalida A, Carrete M, Heredia R, Donazar JA (2008) Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. *PLoS ONE* 3(12):e4084
- Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A (2013) Ecological and evolutionary implications of food subsidies from humans. *Ecol Lett* 16(12):1501–1514
- Owens IP, Bennett PM (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc Natl Acad Sci* 97(22):12144–12148
- Payo-Payo A, Genovart M, Sanz-Aguilar A, Greño JL, García-Tarrasón M, Bertolero A, Picardo J, Oro D (2017) Colonisation in social species: the importance of breeding experience for dispersal in overcoming information barriers. *Sci Rep* 7:42866
- Pérez-García JM, DeVault T, Botella F, Sánchez-Zapata JA (2017) Using risk prediction models and species sensitivity maps for large-scale identification of infrastructure-related wildlife protection areas: the case of bird electrocution. *Biol Conserv* 210:334–342
- Perino A, Pereira HM, Navarro LM, Fernández N, Bullock JM, Ceaşu S, Cortés-Avizanda A, van Klink R, Kuemmerle T, Lomba A, Peer G, Plieninger T, Rey Benyas JM, Sandom CJ, Svenning JC, Wheeler HC (2019) Rewilding complex ecosystems. *Science* 364(6438):eaav5570
- Pitarch A, Gil C, Blanco G (2017) Oral mycoses in avian scavengers exposed to antibiotics from livestock farming. *Sci Total Environ* 605:139–146
- Plaza PI, Lambertucci SA (2017) How are garbage dumps impacting vertebrate demography, health, and conservation? *Glob Ecol Conserv* 12:9–20
- Popp A, Calvin K, Fujimori S, Havlik P, Humpenöder F, SteHuman Footprintest E, LeonBodirsky B, PhilippDietrich J, Doelmann JC, MykolaGusti M, Tomoko-Hasegawa T, Kyle P, Obersteiner M, Tabeau A, Takahashi K, Valin H, Waldhoff S, Weindl I, van Vuuren DP (2017) Land-use futures in the shared socio-economic pathways. *Global Environ Chang* 42:331–345
- Powell LA (2007) Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *Condor* 109:949–954
- R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org>.
- Rebolo-Ifrán N, Tella JL, Carrete M (2017) Urban conservation hotspots: predation release allows the grassland-specialist burrowing owl to perform better in the city. *Sci Rep* 7(1):3527
- Sæther BE, Bakke Ø (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81(3):642–653
- Sánchez-Zapata JA, Clavero M, Carrete M, DeVault TL, Hermoso V, Losada MA, Polo MJ, Sánchez-Navarro S, Pérez-García JM, Botella F, Ibáñez C, Donazar JAC (2016) Effects of renewable energy production and infrastructure on wildlife. *Current trends in Wildlife Research*. Springer, Cham, pp 97–123
- Santangeli A, Girardello M, Buechley E, Botha A, Minin ED, Moilanen A (2019) Priority areas for conservation of Old World vultures. *Conserv Lett*. <https://doi.org/10.1111/cobi.13282>
- Sanz-Aguilar A., De Pablo, F., & Donazar, J. A. (2015a). Age-dependent survival of island vs. mainland populations of two avian scavengers: delving into migration costs. *Oecologia*, 179(2), 405–414.
- Sanz-Aguilar A, Sánchez-Zapata JA, Carrete M, Benítez JR, Ávila E, Arenas R, Donazar JA (2015b) Action on multiple fronts, illegal poisoning and wind farm planning, is required to reverse the decline of the Egyptian Vulture in southern Spain. *Biol Conserv* 187:10–18
- Sanz-Aguilar A, Igual JM, Tavecchia G, Genovart M, Oro D (2016) When immigration mask threats: the rescue effect of a Scopoli's shearwater colony in the Western Mediterranean as a case study. *Biol Conserv* 198:33–36

- Sanz-Aguilar A, Cortés-Avizanda A, Serrano D, Blanco G, Ceballos O, Grande JM, Tella JL, Donazar JA (2017) Sex- and age-dependent patterns of survival and breeding success in a long-lived endangered avian scavenger. *Sci Rep* 7:40204
- Sarrazin FO, Bagnolini C, Pinna JL, Danchin E, Clobert J (1994) High survival estimates of griffon vultures (*Gyps fulvus fulvus*) in a reintroduced population. *Auk* 111(4):853–862
- Sarrazin F, Bagnolini C, Pinna JL, Danchin E (1996) Breeding biology during establishment of a reintroduced Griffon Vulture *Gyps fulvus* population. *Ibis* 138(2):315–325
- Schaub M, Aebischer A, Gimenez O, Berger S, Arlettaz R (2010) Massive immigration balances high anthropogenic mortality in a stable eagle owl population: lessons for conservation. *Biol Conserv* 143(8):1911–1918
- Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. *Trends Ecol Evol* 17(10):474–480
- Sebastián-González E, Barbosa JM, Pérez-García JM, Morales-Reyes Z, Botella P, Olea PP, Mateo-Tomás P, Moleón M, Hiraldo F, Arrondo E, Donazar JA, Cortés-Avizanda A, Selva N, Lambertucci SA, Bhat-tacharjee A, Brewer A, Anadón JD, Abernethy E, Rhodes OE, Turner K, Beasley JC, DeVault TL, Ordiz A, Wikenros C, Zimmermann B, Wabakken P, Wilmers CC, Smith JA, Kendall CJ, Ogada D, Buechley ER, Frehner E, Allen ML, Wittmer HU, Butler JRA, Toit JT, Read J, Wilson D, Jerina K, Krofel M, Kostecke R, Inger R, Samson A, Naves-Alegre L, Sánchez-Zapata JA (2019) Scavenging in the Anthropocene: Human impact drives vertebrate scavenger species richness at a global scale. *Global Change Biology* 25(9):3005–3017
- Sherub S, Fiedler W, Duriez O, Wikelski M (2017) Bio-logging, new technologies to study conservation physiology on the move: a case study on annual survival of *Himalayan vultures*. *J Comp Physiol A* 203(6–7):531–542
- Tauler-Ametller H, Hernández-Matías A, Pretus JL, Real J (2017) Landfills determine the distribution of an expanding breeding population of the endangered Egyptian Vulture *Neophron percnopterus*. *Ibis* 159(4):757–768
- van Overveld T, García-Alfonso M, Dingemanse NJ, Bouten W, Gangoso L, de la Riva M, Serrano D, Donazar JA (2018) Food predictability and social status drive individual resource specializations in a territorial vulture. *Sci Rep* 8(1):15155
- Venter O, Sanderson EW, Magrath A, Allan JR, Beher J, Jones KR, Possingham HP, Laurance WF, Wood P, Fekete BM, Levy MA, Watson JEM (2016) Global terrestrial Human Footprint maps for 1993 and 2009. *Sci Data* 3:160067
- Vidal-Vallés D, Rodríguez A, Pérez-Collazos E (2018) Bird roadkill occurrences in Aragon Spain. *Anim Biodiv Conserv* 41(2):379–388
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth's ecosystems. *Science* 277(5325):494–499
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(1):S120–S139
- Wink M, Sauer-Gürth H, Martínez F, Doval G, Blanco G, Hatzofe O (1998) The use of (GACA) 4 PCR to sex Old World vultures (Aves: Accipitridae). *Mol Ecol* 7(6):779–782
- Xirouchakis SM, Poulakakis N (2008) Biometrics, sexual dimorphism and gender determination of griffon vultures *Gyps fulvus* from Crete. *Ardea* 96(1):91–98
- Zuberogoitia I, De La Puente J, Elorriaga J, Alonso R, Palomares LE, Martínez JE (2013) The flight feather molt of griffon vultures (*Gyps fulvus*) and associated biological consequences. *J Raptor Res* 47(3):292–304

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