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*Research Paper*

# Food subsidies shape age structure in a top avian scavenger

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ABSTRACT. Human activities and recent changes in sanitary regulations are currently shaping the availability of carrion resources across ecosystems. How changes in regulations influence demographic parameters in avian scavengers is still poorly known. We combine photographic observations gathered by citizens and observational data from research projects in northern Spain to examine if the age structure of Eurasian Griffon Vulture (*Gyps fulvus*) populations at different trophic resources (natural randomly-distributed carcasses, predictable resources [supplementary feeding sites and farms], and landfills) varied in relation to modifications of sanitary regulations from 2004 onwards. We found that the proportion of immature birds increased significantly after the introduction of new European sanitary regulations allowing farmers to dispose of livestock carcasses in the field, rather than incinerating them. Also, we found that the age structure varied significantly between food resources, such that we detected a higher fraction of immatures at landfills, as well as in sites where carrion was highly clumped. These findings reveal that loss of natural randomness in carrion availability may elicit age-dependent effects on the spatial distribution of the vultures at the mesoscale which may ultimately affect population structure. Our findings shed light on challenges on how to manage food subsidies to preserve avian scavenger populations in an increasingly anthropized world.

## Les apports alimentaires déterminent la structure d'âge chez un charognard aviaire au sommet de la chaîne alimentaire

RÉSUMÉ. Les activités humaines et les récents changements dans la réglementation sanitaire façonnent actuellement la disponibilité des ressources en charognes dans les écosystèmes. La manière dont ces changements de réglementation influent sur les paramètres démographiques des charognards aviaires est encore mal connue. Nous avons combiné des observations photographiques recueillies par des citoyens et des données d'observation provenant de projets de recherche dans le nord de l'Espagne pour examiner si la structure d'âge des populations de Vautours fauves (*Gyps fulvus*) se nourrissant de ressources différentes (carcasses naturelles réparties de façon aléatoire, ressources prévisibles [sites d'alimentation supplémentaires et fermes] et décharges) a varié en fonction des modifications de la réglementation sanitaire à partir de 2004. Nous avons constaté que la proportion d'oiseaux immatures a augmenté de manière significative après l'introduction de nouveaux règlements sanitaires européens permettant aux agriculteurs d'éliminer les carcasses de bétail en les laissant dans les champs plutôt que de les incinérer. Nous avons également constaté que la structure d'âge variait de manière importante selon les ressources alimentaires : une fraction plus élevée d'immatures a été détectée dans les décharges, ainsi que dans les sites où les charognes étaient fortement concentrées. Ces résultats révèlent que la perte du caractère aléatoire naturel de la disponibilité de la charogne peut entraîner des effets dépendants de l'âge sur la répartition spatiale des vautours à l'échelle méso, ce qui peut affecter la structure de la population en fin de compte. Nos résultats mettent en lumière les défis à relever pour gérer les apports alimentaires afin de préserver les populations de charognards aviaires dans un monde de plus en plus anthropisé.

Key Words: *demography; Griffon Vulture; Gyps fulvus; farms, landfills; resource predictability; sanitary regulations; supplementary feeding stations*

## INTRODUCTION

Research in ecology and conservation biology often relies on long-term population monitoring programs, especially when it focuses on the conservation of long-lived vertebrates (White 2019). However, there are constraints in collecting large volumes of information over long periods. For this reason, observations gathered by citizens, over broad spatial scales and temporal periods, are being used in scientific research allowing studies that would otherwise be unfeasible (Chandler et al. 2012). In particular, photographic records of long-lived species may allow for individual identification on the basis of morphological differences (Marshall and Pierce 2012) and in certain cases, this approach may extend to entire populations (Swanson et al. 2016).

Avian scavengers and *Gyps* vultures in particular have suffered a precipitous global decline and consequently many of their populations are considered virtually extinct in wide regions of Eurasia and Africa (Prakash et al. 2007, Ogada et al. 2012). In Western Europe, however, Eurasian Griffon Vulture (*Gyps fulvus*;

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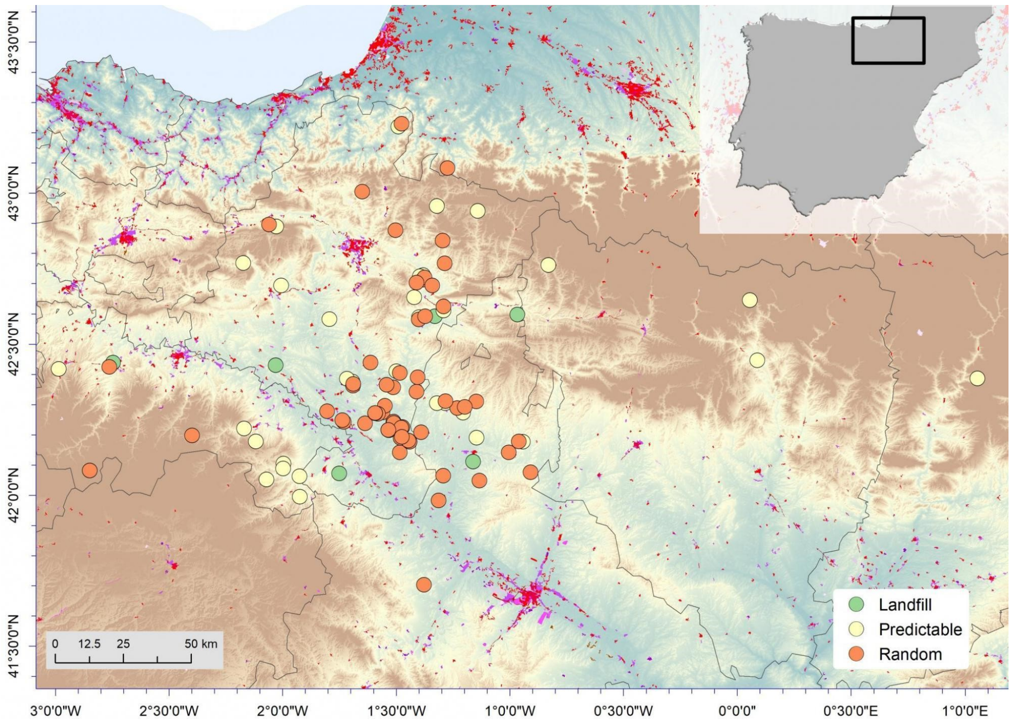
**Fig. 1**. Study areas and locations of studied food sources where all the information was collected. In red and pink, the main cities and human structures in the area.




hereafter Griffon Vulture) populations are still abundant and recovering (see Focal species - Methods). Griffon Vultures are almost entirely dependent on trophic resources provided by human activities such as farming and game hunting (Margalida and Colomer 2012, Monsarrat et al. 2013). As a result, many populations were negatively affected in the late 1990s by the prohibition of livestock carcass abandonment, following the emergence of BSE (Bovine Spongiform Encephalopathy) (Donázar et al. 2010, Cortés-Avizanda et al. 2016). Subsequent European regulations (322/2003/EC, 830/2005/EC, 142/2011/EC) have relaxed this scenario, increasing the availability of carrion from livestock husbandry (Margalida et al. 2012, Arrondo et al. 2018). However, how these changes have affected the demography of avian scavengers remains largely unknown, with the exception of approaches related to breeding parameters and fledgling condition (Margalida and Colomer 2012, Donázar et al. 2020a). This is due to the difficulty in collecting long-term data on a group of birds characterized by conservative life-history traits such as low productivity, delayed sexual maturity, and high longevity.

We used photographs captured by nature photographers and information collected from long-term monitoring of carcass consumption, to examine if the aforementioned changes in sanitary regulations shaped the age structure of Griffon Vultures at different food sources. It has recently been described that immature avian scavengers feed with greater success when resources are more predictable (van Overveld et al. 2018), probably because competition with dominant adults may be higher at randomly distributed sources (Donázar et al. 1999, Moreno-Opo et al. 2020). Additionally, immatures are not spatially attached to breeding areas and frequently perform exploratory displacements (Bamford et al. 2007, Margalida et al. 2013), so they may concentrate at more predictable food sources. Accordingly, we predict that the ratio of immatures to adults at carcasses would be lower in scenarios of reduced food availability, when restrictive sanitary regulations were in force, and would increase as the predictability of the resource is higher.

# METHODS

## Focal species

The Griffon Vulture is present across arid and semi-arid areas of Europe, Asia, and North Africa (Cramp and Simmons 1980). Formerly well distributed and abundant, the species has suffered a severe decline disappearing from large portions of its original distribution. Currently, the Iberian Peninsula holds 95% of the European population with around 34,000 breeding pairs (Margalida et al. 2010, Del Moral and Molina 2018). Griffons have a slow reproductive rate, reaching sexual maturity at 4 calendar years (hereafter c-y, 4 years old) (Blanco et al. 1997). They breed colonially on cliffs and forage over open areas, searching for wild and domestic ungulate carcasses (Martin-Díaz et al. 2020), and usually gather at other food sources, such as landfills and supplementary feeding stations (Cortés-Avizanda et al. 2010, 2012, Monsarrat et al. 2013, Moreno-Opo et al. 2015b).

## Study area, field procedures, and data collection

Our study was performed in the upper Ebro valley, an area covering around 10,000 km$^2$ in northern Spain (Cortés-Avizanda et al. 2012, Fig. 1). This is a lowland region with large extensive cereal cultures and intensive irrigation (Lecina et al. 2005). It is considered one of the most important European regions for avian scavengers (Bijleveld 1974, Cortés-Avizanda et al. 2015, Sanz-Aguilar et al. 2017). During the summer season (April-August) of 2004-2006, we monitored the consumption of 58 experimentally placed carcasses of sheep (*Ovis aries*) and pigs (*Sus scrofa*), the main food sources of avian scavengers in the study area. At each carcass, we surveyed every ten minutes recording the number of griffons of each age class (see details in Cortés-Avizanda et al. 2012). Additionally, we analyzed photographs of feeding Griffon Vultures collected by 15 nature photographers from 2008 to 2019. From each monitored or photographed carcass, we selected the single survey or photograph (hereafter feeding event); which had the largest number of individuals of known age. Accordingly, we selected 110 direct observations and 170 photographs. All data were collected with telescopes (20-60x) and at a distance (>200m) or, alternatively, from hides, to avoid interfering with birds' behavior. We considered two age categories: Immature individuals ranging in age from 1 to 5 c-y and Adults*:* >5cy. These categories correspond respectively to birds with age equal to, or older than, 5 years. Following Forsman 2003 and Zuberogoitia et al. 2013, we considered as immatures all those birds presenting totally brown neck ruff feathers, as well as dark bills. To avoid possible biases, all age categories from both field observations and photographs were determined by the same observers (i.e., ACA, JAD).

## Modeling procedures

We fit a GLM where the response variable was the ratio of immatures in the group of Griffon Vultures of known age for each feeding event (binomial distribution for proportional data; logit link function). We applied a *cbind* procedure to the response variable (see Zuur et al. 2009) to account for the effect of different sample sizes (total number of vultures in the observation and/or photograph). Explanatory variables included:

1. Season: It was defined by two levels: *Winter*: (October - February) and *Summer* (March - September). This division helped distinguish the time periods, in which, the immature portion of the population was present in the study area. It is well known that most immatures abandon breeding colonies and migrate to Africa in October, returning during the spring months (Bildstein et al. 2009).
2. Legislation: with two levels: *Prohibition* (2004-2013): when strict sanitary regulations forbade the abandonment of livestock carcasses, with all the carcasses incinerated, and *Tolerance* (2014-2019): when new regulations allowed the abandonment of carcasses in the field, either disposing of them by piling in designated disposal places or leaving the carcasses in the field for the vultures. We established 2014 as the year when the new regulations came into effect (Donázar et al. 2020b).
3. Resource: following (Cortés-Avizanda et al. 2010) we considered three levels (from higher to lower quantities of food). *Landfill*: landfills and/or composting facilities; *Predictable*: feeding sites associated with intensive and semi-intensive livestock farms and supplementary feeding stations devoted specifically to the recovery of avian scavengers; *Random*: domestic or wild ungulate carcasses found unpredictably in both space and time.

We also considered one interaction with biological significance and a clear predicted effect: *Legislation*Resource* in order to evaluate the resource-specific influence that may result from long-term changes in sanitary regulations. See Table A1.1 for further details on number of observations in relation to explanatory variables.

We used the *dredge* function from the *MuMIn package* (Barton 2019), the *stats package* for the confidence intervals and the *lme4 package* for the GLM analysis (Bates et al. 2015). Model selection was made following the Akaike Information Criterion corrected for small sample sizes (AICc, Sugiura 1978). All analyses were performed in RStudio-3.6.0 (RStudioTeam 2018).

# RESULTS

We identified a total of 7,413 individual records of known age, 2,953 immatures and 4,460 adults. Modeling procedures revealed that a single model accounts for the total weight with the second model being 34 AICc points below (Table A2.1). The top model (Table 1, Fig. 2) showed that the proportion of immature vultures was higher during summer and in all kinds of resources. Additionally, during the tolerance scenario, there were relatively fewer immatures at both random carcasses and predictable feeding sites. However, the proportion of immatures at landfills remained similar or increased slightly between the two periods.

**Table 1**. Estimates and confidence intervals from the best GLM performed for the response variable 'ratio immatures vs. adults' (see also Table A2.1). S.E: standard error, CI: confidence interval.

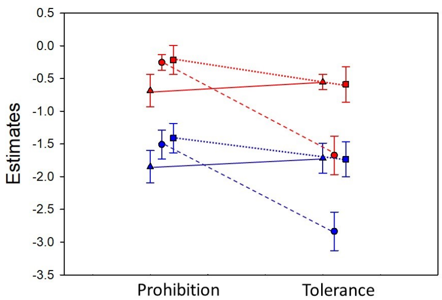
| Variable | Estimate | S. E. | CI - 2.5% | CI - 97.5% |
|---|---|---|---|---|
| Intercept | -1.848† | 0.247 | -2.342 | -1.373 |
| Legislation - Tolerance (after 2014) | 0.130 | 0.231 | -0.315 | 0.595 |
| Season- Summer | 1.164† | 0.117 | 0.939 | 1.397 |
| Resource - Random | 0.430† | 0.222 | 0.004 | 0.878 |
| Resource - Predictable | 0.422 | 0.224 | -0.008 | 0.871 |
| Tolerance (after 2014): Resource Random | -1.549† | 0.294 | -2.138 | -0.982 |
| Tolerance (after 2014): Resource Predictable | -0.455 | 0.268 | -0.988 | 0.063 |

†Informative parameters

# DISCUSSION

Photographers' records are increasing the availability of information in fields where conventional research is progressing slowly, thus enabling robust analyses with large amounts of data. We used information collected through both, scientific research (39% of data) and from photographs captured by naturalists (61%), to demonstrate the existence of long-term changes in the age structure of a vulture population under a scenario of adjusted food resources driven by sanitary regulations. Thus, we recorded that the proportion of immatures at landfills and predictable feeding sites became significantly higher than at random carcasses during the tolerance legislation scenario.

**Fig. 2**. Results of the modeling of the proportion of immature vultures in relation to the total number of individuals observed. We show the estimates (+/- standard error) in relation to the type of resource (triangle: landfill; circle: random; square: predictable), the season (red: summer; blue winter) and the legislation scenario (Prohibition: before 2014, and Tolerance: from 2014 onwards).




We are confident that our results are not biased in methodological procedures. Although visual censuses register more individual records than can be counted in a photograph, there is no reason to believe that this affected the age structure but simply the number of birds recorded in a single event, which, in turn, is controlled in the analyses. Also, we do not believe that photographers biased their photos towards a single age group nor there is reason to believe that different species of livestock carcass (pigs or sheep) are exploited by different age categories (Moreno-Opo et al. 2015a). We know that environmental conditions, not the ungulate species scavenged, determine the interspecific composition of scavenger guilds (Arrondo et al. 2019), and there is no reason to believe that the guild´s composition differs at the intraspecific level.

The first result, showing a higher proportion of immature birds in summer was expected. It is known that immature Griffon Vultures perform short migrations and nomadic displacements mainly during winter (Bernis 1983, Griesinger 1998, Ramírez 2018). More interesting was that, in the years of the Tolerance legislation scenario (from 2014 onwards), with more available food, the proportion of immature vultures decreased at random carcasses and, to a lesser extent in predictable feeding sites. In other words, new food sources in the form of random carcasses (available after farmers were permitted to abandon the remains of livestock) would be exploited preferably by adult birds. Conversely, immature birds still tend to concentrate in landfills. It is well established that immature raptors use different foraging strategies relative to adults, tending to congregate in areas where resources are more abundant, predictable, and clumped (Hiraldo et al. 1995, Carrete et al. 2006, van Overveld et al. 2018). Nevertheless, alternative explanations do exist. The population from our study area, in keeping with the rest of the Iberian Peninsula, had grown by 63% in the previous ten years (Del Moral and Molina 2018). Therefore, the increase in the number of immatures could also be a natural occurrence determined by this population growth. Nevertheless, even within this hypothetical scenario, the survival rate of the immature proportion of the population would be required to have increased, but there is no demographical evidence supporting this. Of note, from 1990 to 2005, multiple poisoning events occurred in Spain, resulting in the deaths of up to 16,820 Griffon Vultures (WWF/Adena 2008). No information is currently available to discern whether this unnatural mortality event might have differentially affected particular age demographics, a phenomenon that has been demonstrated among other bird species (e.g., Greater flamingo, *Phoenicopterus roseus*, Egyptian vulture, *Neophron percnopterus*) (Tavecchia et al. 2001, Sanz-Aguilar et al. 2017).

The maintenance or slight increase of the proportion of immatures at landfills during the whole study period is remarkable. Landfills, although considered to be lower-quality food sources, are frequently visited by obligate and facultative scavengers (Oro et al. 2008, Tauler et al. 2015, McGrady et al. 2018). We propose different explanations for this finding. Firstly, landfills may act as extremely predictable food sources where non-breeding individuals can feed successfully, with less direct competition with adults. This is a phenomenon that has been reported in many avian species including gulls, other diurnal raptors, and other scavengers (Donázar 1992, Skórka and Wójcik 2008, Turrin et al. 2015). Secondly, it is possible that the availability of livestock carcasses has not increased dramatically despite the introduction of less severe sanitary regulations. This may be a result of relatively few livestock farmers availing of the opportunities provided by the legislation or, more importantly, the large-scale decline of extensive farming practices (Pereira and Navarro 2015). Furthermore, the larger aggregations of immatures found at landfills could be in response to a possible specialization on a certain type of resource (in our case random carcasses) with age (Araújo et al. 2011, Sanz-Aguilar et al. 2015), and/or to an increase in the intra-specific competition at random resources, linked to the abandonment of traditional farming practices and land uses (Cortés-Avizanda et al. 2015). Such scenarios may lead to the displacement of immatures to less profitable and lower-quality food sources, which ultimately may lead to death caused by malnutrition, higher chances of contracting diseases, or the ingestion of toxins or pathogens (Plaza and Lambertucci 2018, Blanco et al. 2019). Additionally, landfills, which are generally placed in highly anthropogenic areas may also induce higher risk of non-natural mortality (Arrondo et al. 2020). This may act as an ‘ecological trap’ (Begon et al. 2006), potentially reducing the survival rates of non-breeding birds which can ultimately affect population viability of the remaining European population of Griffon Vultures (Oro et al. 2013).

## Perspectives

Our results revealed that the age structure of a focal top-scavenger population responded to changes in the availability and predictability of trophic resources mediated by sanitary regulations. In particular, we show age-specific resource exploitation patterns, with adult birds profiting more from more randomly distributed resources and immatures depending on low-quality feeding sites such as landfills. To disentangle the contribution of these factors is not banal since it is well-known that populations of endangered species are sensitive to modifications of food subsidies (Gouar et al. 2008, Oro et al. 2008, Margalida and Colomer 2012). The management of predictable resources has been considered a tool in the recovery of endangered vulture populations (Cortés-Avizanda et al. 2016, Tauler-Ametller et al. 2017), but here we show that this can have hidden consequences. Further research is required to achieve a better understanding of how food subsidization and anthropization affect the scavenging guild, the associated ecosystem, and the services it provides for society.

*Responses to this article can be read online at:*
https://www.ace-eco.org/issues/responses.php/2104

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**Author Contributions:**

*Conceived and designed the study: ACA and JAD. Fieldwork: ACA and JAD. Designed the methodology: LFG ACA and JAD. Compiled the data, prepared data and performed analyses: LFG, ACA and FB. LFG, ACA, PT and JAD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.*

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**APPENDIX 1:**

Table A1.1. Number of observations in relation to Resource, Season and Legislation scenario. N samples includes both censuses and photos. Only a census or photo was considered per feeding event.

| Legislation scenario | Season | Resource | N samples |
|---|---|---|---|
| Prohibition (2004-2013) | | Random | 2 |
| | Winter | Predictable | 18 |
| | | Landfill | 1 |
| | | Random | 52 |
| | Summer | Predictable | 65 |
| | | Landfill | 23 |
| Tolerance (2014-2019) | | Random | 37 |
| | Winter | Predictable | 9 |
| | | Landfill | 48 |
| | | Random | 3 |
| | Summer | Predictable | 9 |
| | | Landfill | 13 |

**APPENDIX 2:**

Table A2.1. Comparison of the models resulting from the GLM performed to identify factors affecting the response variable reflecting the ratio between immature and adult griffon vultures observed at feeding places. Only models with informative parameters are shown.

| Model | Variables | K | LogLike | AICc | ΔAICc | Weight |
|---|---|---|---|---|---|---|
| 16 | Legislation + Resource + Season + Legislation:Resource | 7 | -788.927 | 1592.3 | 0 | 1 |
| 8 | Legislation + Resource + Season | 5 | -808.188 | 1626.6 | 34.33 | 0 |
| 6 | Legislation + Season | 3 | -811.409 | 1628.9 | 36.64 | 0 |
| 7 | Resource + Season | 4 | -831.429 | 1671.0 | 78.74 | 0 |
| 5 | Season | 2 | -837.664 | 1679.4 | 87.11 | 0 |
| 12 | Legislation + Resource + Legislation:Resource | 6 | -847.206 | 1706.7 | 114.45 | 0 |
| 4 | Legislation + Resource | 4 | -863.956 | 1736.1 | 143.79 | 0 |
| 2 | Legislation | 2 | -874.638 | 1753.3 | 161.05 | 0 |
| 3 | Resource | 3 | -910.459 | 1827.0 | 234.74 | 0 |
| 1 | Null model | 1 | -919.434 | 1840.9 | 248.62 | 0 |