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Invisible barriers: Differential sanitary regulations constrain vulture movements across country borders

Eneko Arrondo[a,*], Marcos Moleón[a,b], Ainara Cortés-Avizanda[a,g], José Jiménez[c], Pedro Beja[d,e], José A. Sánchez-Zapata[f], José A. Donázar[a]

[a] Department of Conservation Biology, Doñana Biological Station-CSIC, 26, 41092 Sevilla, Spain
[b] Department of Zoology, University of Granada, 18071 Granada, Spain
[c] Institute for Game and Wildlife Research-CSIC, 13005 Ciudad Real, Spain
[d] CIBIO/InBio-UP, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, 4485-661 Vairão, Portugal
[e] 2CEABN/InBio, Centro de Ecologia Aplicada "Professor Baeta Neves", Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal
[f] Department of Applied Biology, University Miguel Hernández, 03202 Elche, Spain
[g] Animal Ecology and Demography Group, IMEDEA (CSIC-UIB), Miguel Marques 21, 07190 Esporles, Spain

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ABSTRACT

Political boundaries may represent ecological barriers due to differences in wildlife management policies. In the European Union, it might be expected that these differences should be highly diluted, because all countries have to comply with common directives issued by the European Commission. However, the subsidiarity principle may lead to the uneven uptake of European Union regulations, which can impact on biodiversity conservation due to unequal legislation in neighboring countries, particularly in the case of highly mobile organisms. Here we address this issue, by analyzing how EU regulations issued in response to the Bovine Spongiform Encephalopathy (BSE) crisis differentially affected vulture conservation in Portugal and Spain. Taking advantage of the intensive GPS-tracking of 60 griffon (*Gyps fulvus*) and 11 cinereous vultures (*Aegypius monachus*) from Spain, we found that the Spanish-Portuguese border acts as a quasi-impermeable barrier. In fact, there was an abrupt decline in the number of vulture locations across the Spanish-Portuguese border, with modelling showing that this was unlikely to be related to differences in land cover or topography. Instead, the pattern found was likely due to differences in trophic resource availability, namely carcasses from extensive livestock husbandry, resulting from the differential application of European sanitary legislation regarding the mandatory removal of dead livestock from the field. Overall, our results should be seen as a warning signal to policy makers and conservation managers, highlighting the need for a stronger integration of sanitary and environmental policies at the European level.

1. Introduction

Human frontiers are based on political and socio-economic criteria, and seldom have an ecological foundation (López-Hoffman et al., 2010; Dallimer and Strange, 2015). As a consequence, wildlife, especially highly mobile organisms, may encounter different degrees of human impact, disparate conservation regulations, and contrasting environmental policies within otherwise homogeneous ecological regions (Bolger et al., 2008; Perz et al., 2013; Lambertucci et al., 2014; Gervasi et al., 2015). Addressing these differences has been the goal of a range of conservation initiatives, such as international conventions and regulations (e.g., the Bern Convention and the European Habitats and Species Directive). However, undesirable transboundary effects on biodiversity are still common in natural systems and deserve more scientific and management attention.

Transboundary conservation challenges are likely to occur when different countries implement different environmental policies (Gervasi et al., 2015), or when hard borders are planned or implemented, such as the infamous US-Mexico border wall (Cohn, 2007; Lasky et al., 2011). To solve these problems, a number of initiatives have been developed, often based on the creation of transboundary protected areas (Sandwith et al., 2001), or through ambitious projects involving transboundary natural resource management initiatives with wider benefits for conservation and sustainable development (e.g. Wolmer, 2003). It is

* Corresponding author at: Doñana Biological Station-CSIC, Avda. Américo Vespucio, 26, 41092 Sevilla, Spain.
E-mail address: eneko@ebd.csic.es (E. Arrondo).

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possible; however, that even simple coordination of environmental policies in neighboring countries might achieve significant conservation benefits, thereby avoiding abrupt changes in regulations and practices across borders (Gervasi et al., 2015). In Europe, it might be expected that a high degree of policy integration across countries would achieve such biodiversity conservation benefits, as there are general directives emanating from the European Commission that regulate key issues such agriculture, water management, environmental pollution, and biodiversity conservation itself, among other aspects (Hodge et al., 2015). However, the subsidiarity principle adopted by the European Commission implies that countries, and even regions within countries, have a wide flexibility on how the directives are applied in practice, depending on local policy, socioeconomic and ecological contexts (Kukkala et al., 2016). This may have significant implications for conservation, particularly for migratory or otherwise wide-ranging species, though to the best of our knowledge this idea has never been tested explicitly. However, addressing this issue would be important, because it may help guiding efforts for a better integration across Europe of policies that impact on biodiversity conservation (Sánchez-Fernández et al., 2017).

The bovine spongiform encephalopathy (BSE) crisis provides a unique case study to examine the conservation consequences of the differential uptake across countries of regulations emanating from the European Commission regulations. In 2001, after the BSE crisis, the EU prohibited the abandonment of livestock carcasses in the field (EC 1774/2002; Donázar et al., 2009). The subsequent change in carrion availability resulted in disturbances at different ecological levels, including changes in scavenger communities, disruption of intra-guild relationships, and an increment in CO_2 emissions associated with the transport of carcasses to transformation and incineration plants (Morales-Reyes et al., 2015; Cortés-Avizanda et al., 2016). Fortunately, the consensus among scientists and conservation managers led to improved EU legislations (CE 322/2003, CE 830/2005 CE 142/2011; Margalida et al., 2012), which partially reconciled sanitary requirements with biodiversity conservation concerns (Morales-Reyes et al., 2017). Nevertheless, the new legal framework did not establish mandatory guidelines for member states, which are allowed to develop their own regulations concerning livestock carcass disposal. This has resulted in a paradoxical situation where neighboring countries in a continuous ecological region may apply different criteria, as occurs in the Iberian Peninsula. In Spain, home to c. 95% of European vultures (Margalida et al., 2010), the CE 830/2005 made the requirements to dispose carcasses for feeding vultures at authorized feeding points more flexible, and the prohibition on carcass disposal was unofficially lifted. More recently, new European regulations led to the designation of a network of “Protection areas for the feeding of necrophagous species of European interest” (Royal Decree 1632/2011; Morales-Reyes et al., 2017) as an attempt to mitigate food shortage for scavengers and associated environmental costs (Margalida et al., 2010; Morales-Reyes et al., 2015). In contrast, the Portuguese governmental authorities still require livestock breeders to remove dead animals from the field (Decreto-lei 38/2012), with the exception of a few scavenger feeding stations (all located close to the Spanish border) that may be supplied with livestock carcasses under very restrictive licensing conditions (Monteiro et al., 2009).

Here, our main objective was to show that differences in the uptake of EU regulations across countries can impact on biodiversity, using vulture conservation in Portugal and Spain as a case study. Specifically, we wanted to determine how foraging individuals of the two most common Iberian vulture species respond to the asymmetric implementation of EU sanitary regulations, while controlling for potentially confounding factors associated with differences in topography, land cover and livestock density. We took advantage of three GPS-tracking projects, involving two populations of griffon vulture (*Gyps fulvus*) and one of cinereous vulture (*Aegypius monachus*), which provided detailed information on individuals space use in 50-km buffers on each side of the border. Our main prediction is that vultures will avoid the Portuguese territory, where livestock removal from the field has been more rigorous and is still mandatory, thereby resulting in lower food availability.

2. Methods

2.1. Study area

We focused our analyses on vulture foraging around the Spanish-Portuguese border, which is largely defined by river valleys and is not associated with any abrupt or systematic change in terms of climate, topography or land cover (Clark Labs, 2000; AEMET I., 2011; CEC, 2012). We defined our study area in two steps. First, we established the lateral limits by generating a grid of 10 × 10 km cells over a 50 km buffer on both sides of the border. All cells completely or partially included in the 50 km buffer were considered. Second, we selected 90% of locations inside the buffer strips to exclude accidental non informative locations. This established the northern limit at latitudes 40°30′51″ north and the southern limit at 37°43′06″ north. The result is a study area composed by 445 10 × 10 km cells (Fig. A1), being 22,541.55 km^2 (50.7% of the whole study area) in Portugal and 21,958.45 km^2 in Spain. Most of the study area is covered by pastures and crops with scattered native trees (mainly *Quercus ilex* and *Q. suber*), a savanna-like landscape called “dehesa” in Spain and “montado” in Portugal. This habitat has been historically managed for livestock (mainly sheep and pig) and agricultural (mainly cereals) purposes (Acácio et al., 2016; Garrido et al., 2017). This combination of human traditional uses with natural vegetation creates a semi-open habitat, which is very favorable for a range of wildlife species (Moreno et al., 2016), particularly for large scavengers (Carrete and Donázar, 2005). In addition, the study area includes vast expanses of shrubland dominated by *Cistus ladanifer* and *Cytisus scoparius*, and commercial plantations of *Eucalyptus* spp., *Pinus pinaster* and *P. pinea*. Extensive livestock husbandry is widespread on both sides of the border, with animals grazing in dehesa/montado woodlands or in more open pastures (Sales-Baptista et al., 2016). There are also wild ungulates on both sides of the border, mainly red deer *Cervus elaphus* and wild boar *Sus scrofa* (Apollonio et al., 2010), which may provide an additional source of carrion to vultures, but there is no information on spatial variation in their abundance.

2.2. Vulture GPS tracking

Griffon and cinereous vultures, which are considered as Least Concern and Near Threatened respectively (BirdLife International, 2016, 2017), are the main obligate scavenger species of Europe. Iberian Peninsula hold 90% of European population of both species being much abundant griffon vulture (Margalida et al., 2010) which population is estimated in 24,609 breeding pairs (del Moral, 2009) in Spain and 500–1000 breeding pairs in Portugal (ICNB, 2017). Breeding colonies are widely distributed along the Iberian Peninsula (MAPAMA, 2017; Fig. A2). On the other hand, cinereous vulture colonies are mostly distributed in the western-central sector of the peninsula (Fig. A2) and the population estimate is 1845 breeding pairs in Spain (de la Puente et al., 2007) and 11 breeding pairs in Portugal (ICNB, 2017).

We captured and tagged 30 adult griffon vultures in the Guadalquivir Valley, southern Spain (Fig. A2). These birds were monitored between December 2014 and December 2016 (see Table A1). Another 30 adult griffon vultures were tagged in the Ebro Valley, northern Spain (Fig. A2), and monitored between December 2015 and December 2016 (see Table A1). All birds were captured by cannon nets at baits and equipped with 90 g GPS/GPRS-GSM devices from e-obs digital telemetry (http://www.e-obs.de). Cinereous vultures, 9 fledglings captured at the nest and 2 sub adults trapped by folding net (García-Matarranz, 2011), were tagged in Cabañeros National Park, central Spain (Fig. A2). All of them were tracked between July 2006 and March 2009 (see Table A1). Cinereous vulture individuals were equipped with 70 g, Solar Argos/GPS PTT-100 s from Microwave Telemetry Inc. (http://www.microwavetelemetry.com). GPS devices of both species were equipped following the procedures described in Kenward (2000). Details of the birds studied and individual tracking process are provided in supplementary material, Tables A1 and A2.

2.3. Environmental variables

Vulture distributions were modeled in relation to five explanatory variables: i) "country" (i.e., Portugal versus Spain); ii) "livestock", an estimation of the alive domestic species density. This is a common proxy of the potential carrion biomass availability (Margalida et al., 2011; Morales-Reyes et al., 2015) which we calculated as the number of heads of sheep, pigs and goats divided by the surface area of each local municipality. We excluded cattle because they cannot be abandoned in the field either in Portugal or in Spain; iii) dominant "habitat", according to the main CORINE land cover levels in each cell (CEC, 2012); iv) "roughness" or landscape relief, estimated as the mean Topographic Position Index (TPI; Dilts, 2015) of each cell, and v) "distance" to the border. This variable was estimated by rasterizing the study area and calculating for each cell the mean distance (in km) of each pixel to the border.

In the case of the griffon vulture, we did not include a variable coding the "population" because the proportion of flying locations within each country did not differ between individuals belonging to the Guadalquivir and Ebro populations (χ^2: 3.372; df: 1; p: 0.066). We used official sources to obtain the number of livestock heads (MAGRAMA: http://www.magrama.gob.es/; INE: https://www.ign.es/) and the area of each municipality (DGT: http://www.dgterritorio.pt/; IGN: https://www.ign.es/). CORINE categories considered were: agroforestry, sclerophyllous vegetation, broad-leaved forestry, olive grove, grassland, permanently irrigated lands, non-irrigated land, and others, which grouped those habitats that were dominant in < 10 cells. Distance to the border and livestock variables were rescaled by subtracting the mean of the variable to the value of each cell and dividing by the standard deviation.

2.4. Data analysis

We modeled the density of griffon and cinereous vulture locations per squared km using Generalized Linear Models (GLM), with a negative binomial error distribution and logit link function. We fitted separate models for each vulture species, including in each case country, livestock, roughness, habitat and distance, as explanatory variables. We considered as response variable the density of foraging locations (number of foraging locations in each 10 × 10 km cell; Fig. A1). To define foraging locations we adapted the methodology described by Silva et al. (2017). We carried out a visual inspection of the ground speed data distribution and established a conservative threshold of 5 m/s (see Fig. A3). Locations under this ground speed were considered as non-foraging activity and we excluded from the analyses. We established this high threshold to be sure that we were excluding all not foraging activities such as perching, walk or preening.

To discard possible individual effects (e.g. sex, breeding status or period tracked) we performed an alternative set of models. In this case, we modeled the occurrence of griffon and cinereous vultures using Generalized Linear Mixed Models (GLMMs), with binomial error distribution and logit link function. We performed different model for griffon and cinereous vulture, including in both cases the individual identity as random factor and country, livestock, roughness, habitat and distance as explanatory variables. The response variable was, in both cases, presences/pseudo-absences of vulture locations. Vulture locations inside the study area were used as presences and pseudo-absences were randomly distributed within the study area, excluding a buffer of 40 m-radius around each presence location. We generated the same number of pseudo-absences than presence locations (Table A3). Previously, we explored spatial autocorrelation effects performing Spatial Generalized Linear Mixed Models and testing exponential, spherical and power structures (Dormann et al., 2007) in SAS (SAS Institute, 2009). Results of these explorative models did not include any of the structure tested. This allowed us to discard possible spatial autocorrelation effects also in the GLM due to density approaches are more resilient to this kind of bias than presence/absence models (Aarts et al., 2012).

For model selection, in both cases (GLM and GLMM), we first built a saturated model with all the explanatory variables and those interactions that were ecologically sound. We then performed a backward stepwise procedure using the drop1 function, which is based on the Akaike's information criterion (AIC), to remove non-significant variables ($P > 0.05$). Spatial analyses were done using ArcGis 10.2.1 (ESRI, 2016), and models were developed in R (R Core Team, 2016).

3. Results

We obtained a total of 24,302 and 366 locations of griffon and cinereous vultures, respectively inside the study area (see Methods). Thirteen griffon vultures, six from the Guadalquivir Valley (20.0% of the total tagged in this population) and seven from Ebro Valley (23.3% of the total tagged in this population), as well as nine cinereous vultures (81.8% of the total tagged), visited the study area. Only six griffon vultures (four from Guadalquivir and two from Ebro representing 4.4% of the total tagged) and seven cinereous vultures (28.4% of the total tagged) visited the Portuguese side of the study area. A visual inspection of the vulture locations revealed an evident contrasting use of each country (Figs. 1 and A1), with the Spanish-Portuguese border appearing as a quasi-impermeable barrier. The mean distance to the border of griffon vulture locations (including those out of the study area) inside Portugal was 9 km with a maximum distance of 87 km. In the case of the cinereous vulture, the mean distance to the border was 12 km and the farthest location from the border was at 94 km.

GLM and alternative GLMM (Tables 1 and A3) show analogue results, which are in accordance with previous studies which suggest that both modelling approaches (locations density and presence/pseudo-absences) tend to provide very similar outputs (see Aarts et al., 2012). In view of these similarities, we decided to maintain the GLM as main approach because it showed a more accurate influence of the habitat variable (see Tables 1 and A3).

Models selected (Table 1 and A4) for either griffon or cinereous vultures were very similar (Table 1). These models indicated that the density of foraging locations of both species was higher in Spain than in Portugal. There was also a significant interaction between country and distance to the border, indicating that within Portugal the density of foraging locations declined steadily with distance to the border, while within Spain it remained largely constant at higher levels (Fig. A4). Additionally, habitat was important to explain the density of foraging locations of both species, with higher values found in agroforestry, sclerophyllous vegetation, grassland and broad-leaved forestry than in more humanized habitats. The model for griffon vultures also included a positive effect of livestock density, while this variable was not retained in the model selected for cinereous vultures.

4. Discussion

Our results clearly confirm the idea that there is a strong difference in the occurrence patterns of griffon and cinereous vultures between Portugal and Spain. We found that griffon and cinereous vultures from Spain rarely fly beyond the Portuguese border, especially as the distance from Spain increases (see Figs. 1, A1 and A4), even after controlling for the potentially confounding effects of topography, land cover and livestock density. In addition, the low number of non-flying

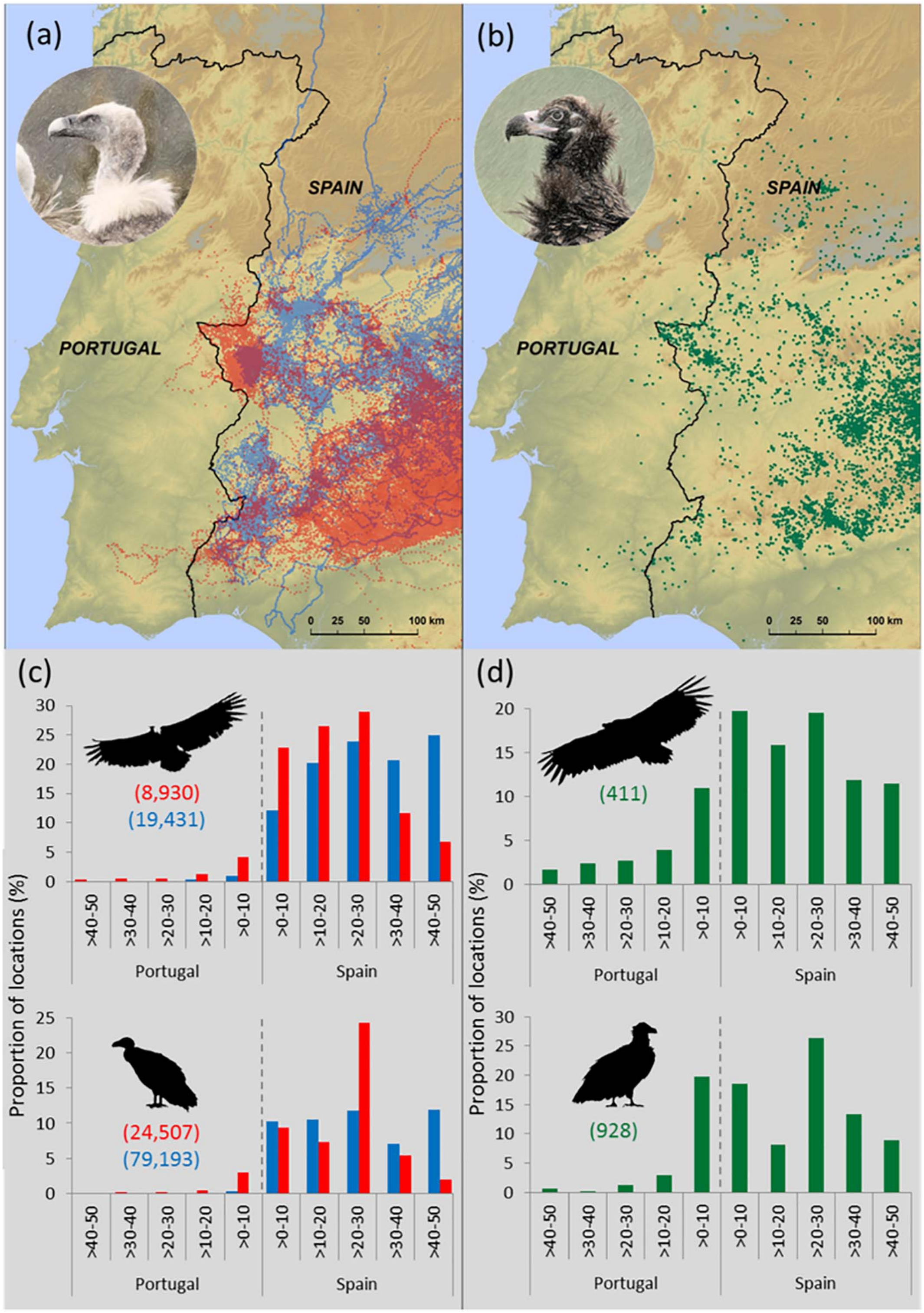

Fig. 1. Locations recorded near the Spanish-Portugal border of GPS-tracked a) griffon and b) cinereous vultures. Griffon vultures were marked in two populations: 30 adult birds in Ebro Valley, northern Spain, and 30 adult birds in Guadalquivir Valley, southern Spain. Cinereous vultures (11 fledglings) were marked in Cabañeros National Park, central Spain. Bottom panels show the proportion (and total number in brackets) of "foraging" locations (ground speed ≥ 5 m/s; flying silhouettes) and "non-foraging" locations (ground speed < 5 m/s; perched silhouettes) locations within a 50 km band on each side of the Spain-Portugal border for c) griffon (red: Guadalquivir valley population; blue: Ebro valley population) and d) cinereous vultures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

locations (i.e., speed ground < 5 m/s; see Fig.1) of both species in Portugal suggests that Spanish vultures rarely feed on that side of the border. This strong border effect seems to be the consequence of the unequal application of European legislation regarding livestock carcass disposal in the Iberian countries. In Portugal, the active removal of carcasses from extensive livestock husbandry systems is probably largely emptying the fields of a key vulture food resource, to the point that the Portuguese side of the Spain-Portugal frontier is avoided by the main European obligate scavengers. Overall, therefore, these results are in line with the idea that the differential uptake of EU regulations across

Table 1
Summary results of the selected generalized linear models. The effects of environmental variables on the density of radiolocations of GPS-tracked griffon and cinereous vultures on 10 × 10 km cells within a 50-km band on each side of the Spain-Portugal border are shown. For each variable, we show the regression coefficients ± standard errors, and the corresponding *Z*-values.

Response variable	Explanatory variable	Level	Estimate ± SE	Z-value
Griffon vulture locations density	Country	Portugal(Intercept)	− 3.04 ± 0.54	− 5.62
		Spain	3.72 ± 0.19	19.18
	Livestock		0.76 ± 0.12	6.43
	Roughness		0.24 ± 0.08	2.86
	Habitat	Non-irrigated arable land (Intercept)	− 3.04 ± 0.54	− 5.62
		Permanently irrigated land	− 0.50 ± 0.42	− 1.18
		Olive groves	− 1.43 ± 0.52	− 2.76
		Agro-forestry areas	0.89 ± 0.26	3.40
		Broad-leaved forest	0.20 ± 0.33	0.59
		Natural grasslands	0.71 ± 0.35	1.98
		Sclerophyllous vegetation	0.36 ± 0.41	0.89
		Transitional woodland-shrub	0.47 ± 0.30	1.58
		Others	− 0.41 ± 0.39	− 1.05
	Distance		− 1.42 ± 0.14	− 10.12
	Country:Distance	Spain:Distance	1.29 ± 0.17	7.64
Cinereous vulture locations density	Country	Portugal (Intercept)	− 1.74 ± 0.32	− 5.47
		Spain	1.41 ± 0.25	5.58
	Habitat	Non-irrigated arable land (Intercept)	− 1.74 ± 0.32	− 5.47
		Permanently irrigated land	− 0.90 ± 0.68	− 1.33
		Olive groves	− 0.18 ± 0.66	− 0.27
		Agro-forestry areas	0.71 ± 0.35	2.04
		Broad-leaved forest	− 0.43 ± 0.49	− 0.88
		Natural grasslands	0.58 ± 0.44	1.33
		Sclerophyllous vegetation	1.41 ± 0.45	3.13
		Transitional woodland-shrub	0.50 ± 0.37	1.30
		Others	− 1.27 ± 0.66	− 1.94
	Roughness		0.39 ± 0.09	4.41
	Distance		− 0.73 ± 0.18	− 4.12
	Country:Distance	Spain:dist	0.73 ± 0.21	3.51

countries can have far-reaching impacts on biodiversity, thereby calling for better sanitary and environmental policies at the European level.

Although our study has some limitations, it is unlikely that they have shaped our main results and conclusions to a significant extent. One potential problem was that we did not track vultures from Portuguese breeding colonies, which are mainly located close to the border (< 50 km; Monteiro et al., 2009; Fig. A2) and thus might use the Portuguese territory more than individuals breeding in Spain. However, some limited GPS tracking of cinereous and griffon vultures tagged in Portugal has shown that the individuals tend to cross the border to feed in Spain (Machado, 2014), which is line with the results of our study. Our results are also supported by the fact that the two vulture species are rarely seen in Portugal, except very close to the border with Spain or during the autumn migration period (Catry et al., 2010; Lourenço, 2011). Other possible source of bias is the lack of fine spatial information about the abundance of wild ungulates, which are important providers of carrion in the Iberian Peninsula (Cortés-Avizanda et al., 2016). Nonetheless, the relative homogeneous distribution of the main wild ungulates species throughout the study area (Apollonio et al., 2010) suggests that the availability of wild ungulate carrion is not abruptly different between the Spanish and the Portuguese sides of the study area.

Also, the marked individuals were biased towards adults in the case of griffon vultures and non-adults in the case of cinereous vultures. This could be a problem because immature vultures usually have expanded home ranges due to dispersal movements (e.g., Margalida et al., 2016). However, the movement pattern in relation to the border was consistent for the two species studied. In addition, our set of marked griffon vultures probably included non-breeder individuals, which are free of reproductive duties and could therefore move in a different way than breeders. However, in view of the similar results obtained by the two modelling approaches used in this study (i.e., GLM and GLMM), is evident that our results are not influenced by individual characteristics. All this suggest that the frontier effect produced by the unequal sanitary policies in Spain and Portugal is strong enough to shape vulture movements beyond age class, sex, breeding status and species. That said griffon and cinereous vultures are known to differ in their trophic resource used. In fact, while griffon vultures are strongly dependent on the carcasses of domestic ungulates (Donázar et al., 2010), the diet of cinereous vultures is more varied, including the remains of small and medium-sized vertebrates such as European rabbits *Oryctolagus cuniculus* (Linnaeus, 1758; European rabbit; Moreno-Opo et al., 2010). This may explain why the density of livestock was included in the model for griffon vultures, but not for cinereous vultures, which was the main difference between the models of both species.

It is also unlikely that the differences between countries observed in our study were due to variation in habitat composition, because the landscapes were rather similar on both sides of the border. We found that both vulture species showed clear preferences for natural and semi-natural vegetation, mainly represented by dehesa/montado landscapes that were widespread in both Portugal and Spain. This is in line with other studies showing the importance of dehesas/montados for vultures (Carrete and Donázar, 2005), and for Mediterranean biodiversity in general (Moreno et al., 2016). However, due to the application of restrictive sanitary regulations, Portuguese montados seem to lack a fundamental component of Mediterranean wood-pasturelands, namely livestock carcasses. Given that many endangered species, such as vultures and large predators, rely largely on ungulate carcasses (Pereira et al., 2014; Mateo-Tomás et al., 2015), carrion-free ecosystems such as montados, as currently managed, seem to lack a high value for scavenger conservation.

Reduced foraging opportunities for vultures in Portugal as a result of the restrictive national regulation on livestock carcass disposal could undermine the effectiveness of local conservation strategies (e.g., two LIFE projects devoted to improving the conservation status of Portuguese vulture populations, with an overall budget of €6.2 million; http://ec.europa.eu/environment/life/project/Projects/). In addition, the large-scale spatial exclusion of keystone species such as vultures might ultimately constrain ecosystem functioning and the provision of key ecosystem services (López-Hoffman et al., 2010; Ogada et al., 2012; Moleón et al., 2014). Thus, our findings highlight the need to evaluate the potential ecological consequences of the implementation of restrictive sanitary policies, especially when they affect highly mobile, endangered species such as vultures (Margalida et al., 2010). We advocate for the traditional system of livestock carcass disposal (Cortés-Avizanda et al., 2010; Arrondo et al., 2015; Cortés-Avizanda et al., 2016), which would benefit European scavenger conservation without compromising animal and human health (Morales-Reyes et al., 2015, 2017). Our results also highlight the role that vultures play as biological indicators of relevant ecological processes at the supra-national scale. Future research including tagging birds of all age classes of these and other vulture species (i.e., Egyptian vulture *Neophron percnopterus*), as well as the fine quantification of both wild and domestic ungulate carrion biomass availability, may help to go more deeply into the effects of the sanitary policies regarding livestock carcass removal on vulture movements.

Biodiversity management is usually implemented at regional and national scales (Kark et al., 2009). However, the spatiotemporal scale of many ecological processes is independent of national socio-economic contexts, which produces a mismatch between wildlife conservation needs and management units (Dallimer and Strange, 2015). Our study demonstrates how uncoordinated environmental management might become an unexpected limiting factor for species of conservation concern. Even inside a relatively homogeneous political entity such as the European Union, where all members comply with the same directives, national variations in policy implementation may still jeopardize large-scale conservation efforts (Gervasi et al., 2015). Thus, trans-boundary biodiversity conservation in Europe would largely benefit from supervision by the EU Commission of local applications of general regulations. In general, more fluid transnational coordination of environment-related policies is encouraged, especially for the sake of conserving highly mobile organisms.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2017.12.039.

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