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Evaluation of the network of protection areas for the feeding of scavengers in Spain: from biodiversity conservation to greenhouse gas emission savings

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Summary

1. Protected areas are one of the most common strategies for wildlife conservation world-wide. However, their effectiveness is rarely evaluated. In Europe, after the outbreak of bovine spongiform encephalopathy, a restrictive sanitary regulation (EC 1774/2002) prohibited the abandonment of dead livestock in extensive farming (extensive livestock) in the field, which led to negative consequences for scavengers. As an attempt to mitigate this negative impact, a new regulation was approved (EC 142/2011) to allow farmers to leave extensive livestock carcasses in the so-called 'Protection areas for the feeding of necrophagous species of European interest' (PAFs).

2. Our general aims were to quantify (i) the proportion of breeding distribution of targeted scavenger species overlapping PAFs; (ii) the extensive livestock carrion biomass available inside PAFs; (iii) the proportion of breeding distribution of non-targeted scavenger species falling within PAFs; (iv) the overlap between the home range of vultures and PAFs, as well as the extent to which vultures move through different administrative units; and (v) the savings in greenhouse gas (GHG) emissions in relation to the pre-PAF scenario.

3. After assessing the status of PAF implementation in every region of peninsular Spain, we analysed the large-scale spatial information of extensive livestock carrion availability and scavenger breeding distribution, movement data of GPS-tracked vultures, and the annual GHG emissions associated with the transport of livestock carcasses.

4. Most regions established PAFs in their territories, although design criteria were variable. The breeding distribution of targeted species was better represented within PAFs than that of non-targeted species. The extensive livestock carrion biomass potentially available for scavengers within PAFs represented 34·9% of the annual extensive livestock biomass generated in peninsular Spain. The overlap between the home range of GPS-marked vulture populations and PAFs ranged between 63·4% and 100%. The minimum convex polygon of these and other GPS-tracked vulture populations in peninsular Spain encompassed 3–14 Spanish

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regions and 1–4 countries. Post-PAF there was a potential reduction of c. 55·7% of GHG emissions compared to pre-PAF.

5. *Synthesis and applications*. The implementation of the new sanitary regulation by means of areas for the feeding of scavengers could mean an important improvement in scavenger conservation and a noteworthy reduction in greenhouse gas emissions: in Spain, extensive livestock carrion availability might increase to 33 474 t yr^{-1}, and 43 344 t of CO_2 eq. might be saved annually. However, we identified some gaps related to the distribution of endangered facultative scavengers. Moreover, given that vultures are highly mobile organisms, the design and management of these feeding areas should be coordinated at both the supra-regional and supra-national scales.

Key-words: carrion availability, conservation effectiveness, ecosystem services, EU sanitary policies, facultative scavengers, home range, movement ecology, PAFs, protected areas, vultures

Introduction

The establishment of protected areas (PAs) is one of the most common strategies for wildlife conservation worldwide (e.g. Ervin 2003; Gaston *et al.* 2008a). According to the World Database on Protected Areas (WDPA), 20·6 million square kilometres (15·4%) of terrestrial areas are covered by PAs (UNEP-WCMC 2014). However, despite the numerous international agreements to protect the natural world, global biodiversity continues to decline (e.g. Butchart *et al.* 2010; Craigie *et al.* 2010; Regan *et al.* 2015). This may be partly due to a deficient design and implementation of management guidelines within PAs, as well as to a spatial mismatch between PAs and conservation priorities (Rodrigues *et al.* 2004). For instance, many PAs have focused on a few emblematic threatened species (Bonn, Rodrigues & Gaston 2002), while other species of conservation concern have been ignored. Moreover, PA limits have often been demarcated around breeding areas of target species. However, movements outside the breeding distribution during key ecological and behavioural activities (e.g. foraging and social interactions; Bennett *et al.* 2009) have often been neglected. In addition, trans-jurisdictional conservation strategies that reconcile PA limits beyond jurisdictional (regions and countries) borders are largely missing. This may have important consequences for highly mobile organisms such as large predators and soaring birds (e.g. Block *et al.* 2011; Lambertucci *et al.* 2014). Therefore, the continuous scientific evaluation of conservation effectiveness to provide corrective feedback to policy makers should be a key ingredient of PAs' management strategies (e.g. Ervin 2003; Chape *et al.* 2005; Gaston *et al.* 2008b; Leverington *et al.* 2010). However, this critical step has rarely been taken (McLain & Lee 1996).

The PA network should recognize the changing socio-economic context (Walters 1986). The outbreak of the bovine spongiform encephalopathy that occurred in Europe in 2001 led to the approval of a sanitary regulation (EC 1774/2002) that forced farmers to remove livestock carcasses from the field and transport them to authorized plants for their transformation (for industrial purposes, e.g. to produce organic fertilizers) or incineration. In Spain, which is home to >90% of European vulture population (Tella 2001; Margalida *et al.* 2010), this regulation caused a food shortage for these and other scavengers of conservation concern (e.g. Donázar *et al.* 2009; Margalida *et al.* 2010), which largely rely on domestic ungulates in Mediterranean landscapes (Donázar 1993). This, in turn, affected their behaviour (Donázar, Cortés-Avizanda & Carrete 2010; Margalida, Campión & Donázar 2011; Cortés-Avizanda *et al.* 2012), demographic parameters (Margalida, Colomer & Oro 2014) and the ecosystem services they provide (Margalida & Colomer 2012; Moleón *et al.* 2014). This conflicting sanitary regulation originated a new source of greenhouse gas (GHG) emissions, associated with the carcass transport of livestock in extensive farming (hereafter, extensive livestock; Morales-Reyes *et al.* 2015).

To ensure sufficient food supply to sustain the breeding populations of vultures and other avian scavengers (bearded vulture *Gypaetus barbatus*, cinereous vulture *Aegypius monachus*, Egyptian vulture *Neophron percnopterus*, Eurasian griffon vulture *Gyps fulvus*, golden eagle *Aquila chrysaetos*, Spanish imperial eagle *Aquila adalberti*, black kite *Milvus migrans* and red kite *Milvus milvus*), a new regulation was recently approved (EC 142/2011) to allow farmers to abandon extensive livestock carcasses in certain areas ('Protection areas for the feeding of necrophagous species of European interest'; hereafter, PAFs) at the place of death or at nearby fenced feeding stations (Margalida *et al.* 2012). This legislation was applied in Spain through the Royal Decree 1632/2011, which urged every autonomous community (hereafter, region) to design their own PAF network, with implementation in 2013. PAFs must be included in Natura 2000 spaces with the presence of necrophagous species of European interest, areas devoted to conservation plans of such species and/or important areas for the feeding of these species. Once PAFs are approved, every farm within their limits must apply for permission to abandon carcasses in the field; also, farms have to meet several technical (e.g. only livestock in extensive farming) and sanitary requirements (see Royal Decree 1632/2011 for more details). This new regulation was well received among conservationists and wildlife managers (Margalida *et al.* 2012). However, no evaluation has been conducted to assess the adequacy of the PAF network to improve target scavenger conservation, or minimizing other negative impacts associated with the original, highly restrictive sanitary regulation.

Our main goal was to assess the conservation and environmental consequences of the Spanish PAF network. First, we evaluated the main criteria used to define PAFs. For this purpose, we quantified (i) the proportion of breeding distribution of targeted scavenger species falling within PAFs and (ii) the extensive livestock carrion biomass available inside PAFs. Second, we identified major gaps that need to be taken into account to improve the current PAF network. For this purpose, we calculated (iii) the proportion of breeding distribution of other major, non-targeted scavenger species falling within PAFs and (iv) the overlap between the home range of GPS-tracked vultures and PAFs, with special emphasis on determining the use of different administrative units by particular individuals and populations. Third, we assessed indirect, unintended benefits of PAF implementation by (v) estimating the potential savings in GHG emissions associated with livestock carcass transport in relation to the pre-PAF scenario (Morales-Reyes *et al.* 2015).

Materials and methods

PAFS

We contacted every region of peninsular Spain ($n = 15$ regions; Fig. S1, Supporting Information) to gather information about their PAFs. As of October 2015, 11 of these regions had approved specific PAF legislation, whereas three regions had drafted the spatial limits of their PAFs and one region showed no progress in PAF establishment (Table S1). For each region, we extracted the area occupied by PAFs, the criteria used for their design, and the livestock species permitted to be abandoned in these areas (Table S1).

OVERLAP BETWEEN PAFS AND THE BREEDING DISTRIBUTION OF TARGETED SCAVENGER SPECIES

To assess the spatial overlap between PAFs and the breeding distribution of the scavenger species included in the new European regulation (EC 142/2011), we used maps from the Spanish National Biodiversity Inventory (MAGRAMA 2012), which represent species occurrence according to a Universal Transverse Mercator system (UTM) 10 × 10 km grid square. For each species, we used ArcGIS 9.3 (ESRI 2009) to calculate the overlap as the percentage of the breeding distribution included inside the PAFs.

LIVESTOCK CARRION BIOMASS AVAILABILITY IN RELATION TO PAFS

We obtained the abundance of the most important extensive livestock species (i.e. cattle, sheep, goat and pig) per municipality of peninsular Spain in 2012 and the average weight per age class from the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA 2012). We used this information, together with the annual mortality rate of each species of livestock per age class (Government of Castilla y León 2013; Table S2), to calculate the carrion biomass available for scavengers per year across peninsular Spain and within PAFs. For this purpose, we took into account the legislation specified in each region (Table S1). For the three regions that had only drafted the limits of the PAFs, we assumed that sheep and goats were the livestock species permitted to be disposed in the field within PAFs, i.e. the most commonly authorized species in the other regions (Table S1). Our calculations represent the maximum carrion biomass available because not all the farmers are actually permitted to abandon their livestock carcasses, i.e. each farm within the PAFs must request the corresponding permit from the regional administration. We represented the spatial distribution of maximum carrion biomass availability (t yr^{-1}) according to the UTM 10 × 10 km grid square. When a grid belonged to more than one region, the biomass availability was distributed according to their areas.

OVERLAP BETWEEN PAFS AND THE BREEDING DISTRIBUTION OF NON-TARGETED SCAVENGER SPECIES

We evaluated several major avian (raven *Corvus corax* and carrion crow *Corvus corone*) and mammalian (grey wolf *Canis lupus*, brown bear *Ursus arctos*, red fox *Vulpes vulpes* and stone marten *Martes foina*; Mateo-Tomás *et al.* 2015) facultative scavengers not included in the abovementioned European regulation (EC 142/2011). We assessed the spatial overlap between PAFs and the breeding distribution of these scavengers in peninsular Spain using the same approach as for targeted species (see above; MAGRAMA 2012). We then compared the scavenger breeding distribution-PAF overlap between targeted and non-targeted species, as well as between vultures and facultative scavengers. We compared the scavenger breeding distribution-PAF overlap between endangered (i.e. listed as 'Critically Endangered', 'Endangered' or 'Vulnerable') and non-endangered species (i.e. listed as 'Near Threatened' or 'Least Concern') according to Spanish (Madroño, González & Atienza 2004; Palomo, Gisbert & Blanco 2007) and global lists (IUCN 2016). Comparisons were made by means of Mann–Whitney tests.

VULTURE MOVEMENTS IN RELATION TO PAFS AND ADMINISTRATIVE BOUNDARIES

To analyse vulture movements, we tracked 71 birds equipped with GPS transmitters from different Spanish PAFs: 30 *G. fulvus* from Sierras de Cazorla, Segura y Las Villas Natural Park (south-eastern Spain), 11 *A. monachus* from Cabañeros National Park (central Spain), 19 *G. barbatus* from the Pyrenees (northern Spain) and 11 *N. percnopterus* from Cádiz (southern Spain). We selected these cases because they offer the most complete information, i.e. a higher number of GPS-marked individuals in a single population, for each species in Spain. Sex, age and the number of fixes of each tracked vulture, as well as tracking period, are detailed in Table S3. Migratory movements of *N. percnopterus* (from Europe to Africa) were excluded.

We used movement data for two purposes. First, we calculated the home range sizes of each tracked bird using kernel h reference models as the activity utilization distributions (UD; Worton 1989) at the 50% and 90% level (hereafter k50% and k90%, respectively). We selected these kernel levels because they provide information on conservative home ranges (Börger *et al.* 2006). UD surface maps were created using the adehabitatHR package (Calenge 2006) of R (R Core Team 2014) in combination with ArcGIS 9.3 (ESRI 2009). We then evaluated the overlap between PAFs and home ranges (k50% and k90%; excluding marine areas), both at the population (i.e. considering all tracked individuals of a given species together) and individual levels.

Second, we estimated the 100% minimum convex polygon (MCP) to calculate the number of administrative units, i.e. countries and regions within peninsular Spain, used by each tracked population and individual. Additionally, we reviewed the published studies on the home range of vultures (MCP) equipped with GPS tracking systems in Spain that provided enough spatial information to assess the number of regions and countries included in their home ranges (Table S3).

GREENHOUSE GAS EMISSIONS SAVINGS

We quantified the annual GHG emissions associated with the transport of extensive livestock carcasses from farms to authorized plants in peninsular Spain according to IPCC (2006) and following the methodology described in Morales-Reyes *et al.* (2015). Calculations included the transport of carcasses from outside the PAFs, as well as from inside the PAFs in the case of those livestock species not permitted to be left in the field (i.e. those which must collected and transported to plants) according to each regional legislation (see Table S1). We assumed that all extensive farms inside PAFs are authorized to abandon their livestock carcasses in the field, so the resulting figure is a maximum estimate. We then compared the national GHG emissions per year associated with the previous regulation (EC 1774/2002; Morales-Reyes *et al.* 2015) with the estimated annual GHG emissions after the implementation of the PAF regulation (EC 142/2011).

Results

PAFS

PAFs occupy an area of 300 997 km², representing 61·2% of peninsular Spain. The regional surface occupied by PAFs ranged between 13% and 100% (mean = 48·0%, SD = 31·4%). Guidelines for the design of PAFs were highly heterogeneous among the 11 regions that had approved specific legislation (Table S1). All regions (n = 11) allowed the abandonment of sheep carcasses in their PAFs; this figure was lower for goats (90·9%), cattle (81·8%), horses (81·8%) and pigs (45·5%) (Table S1).

OVERLAP BETWEEN PAFS AND THE DISTRIBUTION OF SCAVENGER SPECIES

The breeding distribution of targeted species (mean = 89·6%, SD = 9·3%) was better represented in PAFs than that of non-targeted species (mean = 77·0%, SD = 4·0%; W = 6, P = 0·02). The PAF network included >95% of the breeding distribution of all vulture species (mean = 95·5%, SD = 4·8%) and ≥70% of the facultative scavengers (mean = 79·7%, SD = 7·0%), showing a significantly better coverage for the first group than for the second (W = 1, P = 0·004). We found that endangered species were better represented within PAFs than the rest of the species considered in this study, according to both Spanish (90·9% vs. 79·2%; W = 6, P = 0·02) and global lists (IUCN 2016) of endangered species (89·8% vs. 83·2%; W = 6, P = 0·35; differences were non-significant in this case; Table 1).

LIVESTOCK CARRION BIOMASS AVAILABILITY INSIDE AND OUTSIDE OF PAFS

The maximum extensive livestock carrion biomass potentially available to scavengers within PAFs was 33 474 t in 2012. This represented c. 35% of the annual extensive livestock biomass generated in peninsular Spain. The percentage of carrion biomass available in PAFs relative to the total in each region varied between 0·8% and 95·5% (mean = 36·9%, SD = 30·7%; Table S4). The highest amount of carrion biomass within PAFs was located in the central-west part of peninsular Spain (Fig. 1), mainly due to the presence of an important number of cattle.

Table 1. Proportion (%) of the breeding distribution of scavenger species included in PAFs and their conservation status (according to IUCN Red List categories)

Species	Breeding distribution	IUCN (Spain)	IUCN (Global)
*Gypaetus barbatus**	100	EN	NT
*Aegypius monachus**	98·7	VU	NT
*Gyps fulvus**	93·6	–	LC
*Neophron percnopterus**	89·6	EN	EN
Total vultures	95·5		
*Aquila adalberti**	90·0	EN	VU
*Aquila chrysaetos**	86·9	NT	LC
*Milvus milvus**	87·7	EN	NT
*Milvus migrans**	70·0	NT	LC
Total other raptors	83·7		
Corvus corax	77·0	–	LC
Corvus corone	75·1	–	LC
Total corvids	76·1		
Ursus arctos	79·2	CR	LC
Canis lupus	83·7	NT	LC
Vulpes vulpes	72·8	LC	LC
Martes foina	74·2	LC	LC
Total mammals	77·5		

*Targeted species according to EC 142/2011.

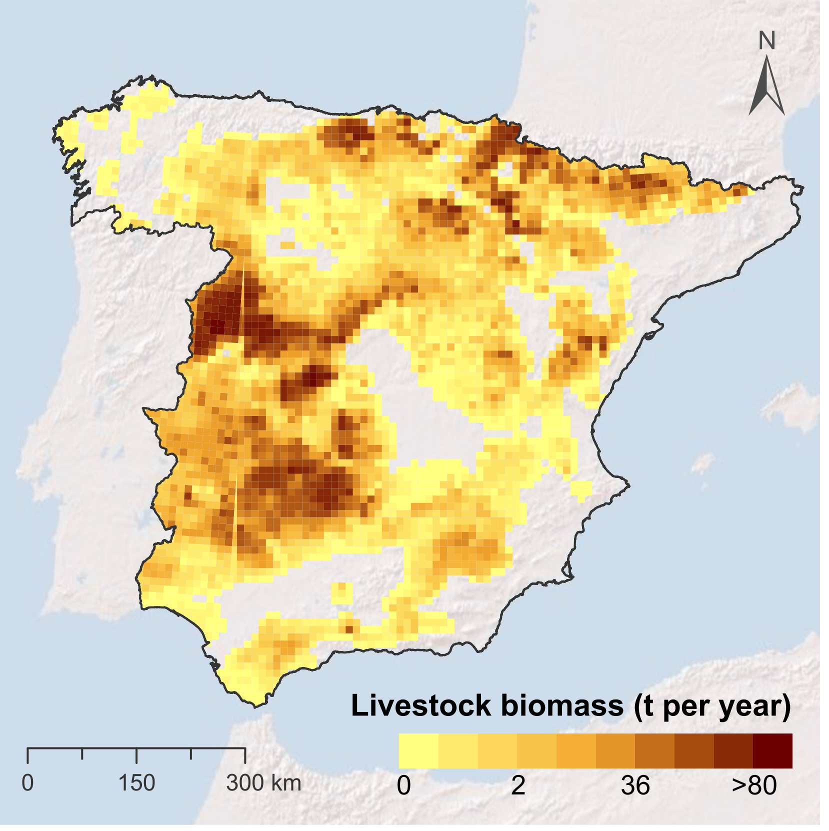

Fig. 1. Spatial distribution of carrion biomass availability (*t*) per 10 × 10 km grid per year and protection areas for the feeding of necrophagous species (PAFs) in peninsular Spain.

Table 2. Home range size (km^2) of the GPS-tracked populations of the four obligate scavenger species estimated by kernel utilization density (k50% and k90%) and percentage of home range included inside Spanish protection areas for the feeding of necrophagous species (PAF coverage) at both the population and individual (mean ± SD) levels

	k50%			k90%		
		PAF Coverage (%)			PAF Coverage (%)	
Vulture species	Total km^2	Population	Individual	Total km^2	Population	Individual
Gypaetus barbatus	3240	63·4	80·3 ± 24·4	18 497	64·9	79·3 ± 15·4
Aegypius monachus	2101	100	100 ± 0	41 688	97·2	97·1 ± 2·8
Gyps fulvus	4146	99·8	99·1 ± 2·6	46 038	91·4	95·2 ± 4·4
Neophron percnopterus	37 785	78·4	90·8 ± 15·2	179 685	67·1	83·9 ± 15·3

VULTURE MOVEMENTS IN RELATION TO PAFS AND ADMINISTRATIVE BOUNDARIES

The home range of the four vulture species together, calculated using information from 428 086 locations, was 47 272 km^2 (k50%) and 285 908 km^2 (k90%). The overlap between the home range of each vulture population and PAFs was similar for k50% (mean = 85·4%, range = 63·4–100%) and k90% (mean = 80·2, range = 64·9–97·2%; Table 2; Fig. 2). At the individual level, mean overlap of all species together was 92·9% (range = 20·7–100%) for k50% and 89·5% (range = 45·2–100%) for k90% (see Table 2 for data separated by species).

Vulture populations (GPS-tracked either in this study or in the reviewed studies) moved across different Spanish peninsular regions (range = 3–14) and countries (range = 1–4; Spain, Portugal, Andorra and France; see Table 3). Vulture individuals used an average of 3·4 regions (range = 1–12) and 1·5 countries (range = 1–3; see Table 3 for data separated by species and studies).

GHG EMISSIONS SAVINGS

The transport of dead livestock from farms to authorized plants after the new regulation (considering both the livestock outside of PAFs and the livestock species that must be collected inside PAFs according to each regional rule) meant a minimum emission of 34 300 metric tons of CO_2 equivalents to the atmosphere per year. The south-western and north-eastern extremes of peninsular Spain showed

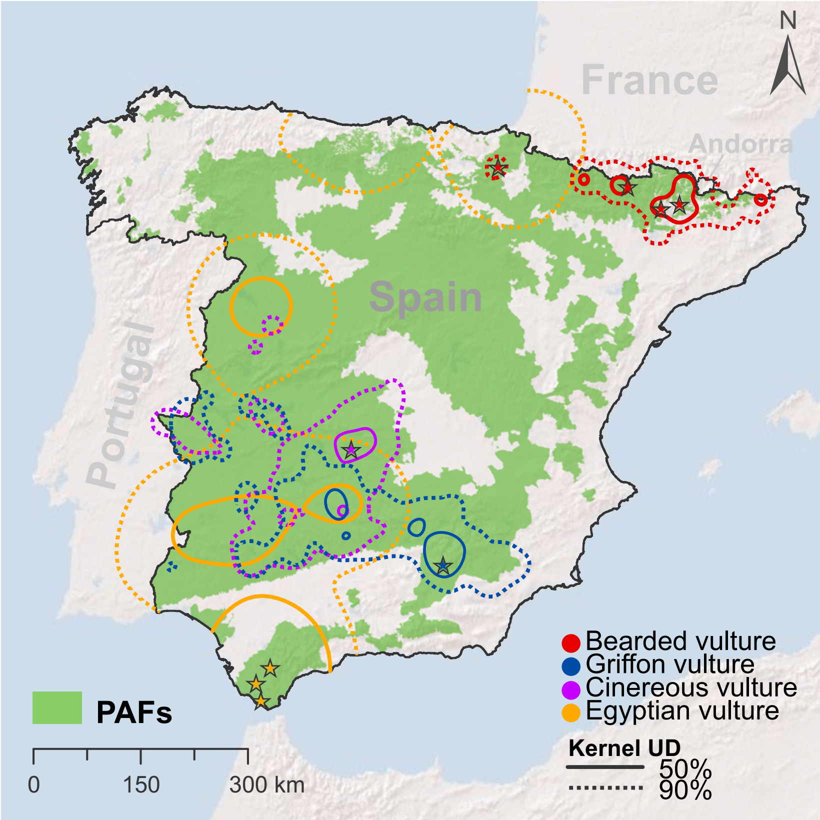

Fig. 2. Spatial distribution of home ranges (k50% and k90% UD) of vultures and protection areas for the feeding (PAFs) of necrophagous species in peninsular Spain. Stars show places of capture.

Table 3. Regions and countries included in the minimum convex polygon (MCP) obtained for different vulture populations (total number of regions/countries) and individuals (mean number of regions/countries; range is shown in parenthesis). Information was compiled from studies performed using birds equipped with GPS tracking systems in peninsular Spain

	Spanish regions		Countries		
Vulture species	Population	Individual	Population	Individual	Reference
Gypaetus barbatus	4	2·2 (1–4)	3	2·2 (1–3)	This study
	14	–	4	–	Margalida *et al.* (2013)
Aegypius monachus	10	5·8 (4–10)	3	1·7 (1–2)	This study
	9	4·1 (1–9)	2	1·5 (1–2)	Castaño *et al.* (2015)
Gyps fulvus	4	3·4 (2–4)	2	1·1 (1–2)	This study
	7	3·0 (2–6)	1	1·0 (1)	García-Ripollés, López-López & Urios (2011)
Neophron percnopterus	12	2·9 (1–12)	3	1·5 (1–3)	This study

the highest levels of GHG emissions (Fig. 3). Considering that the GHG emissions in the pre-PAF scenario was 77 344 metric tons of CO_2 equivalents to the atmosphere per year (Morales-Reyes *et al.* 2015), the post-PAF scenario meant a potential reduction of c. 55·7% in GHG emissions. The percentage of reduction in GHG emissions ranged between 2·3% and 95·7% (mean = 44·7%, SD = 30·7%) depending on the region considered (Table S4).

Discussion

Our findings show that PAFs created specifically to ensure areas for the feeding of necrophagous species after the new European sanitary regulation (EC 142/2011) have resulted in significant improvements in relation to the previous regulation based on the percentage of the breeding distribution of the targeted species covered by these areas and the amount of feeding resources available within them. We also show that the implementation of the new regulation potentially leads to a considerable reduction in the GHG emissions associated with artificial carcass disposal. However, given the large movements performed by individual birds throughout the year as well as the by the targeted species considered, there are still several aspects that should be improved to properly ensure the long-term conservation of scavenger species.

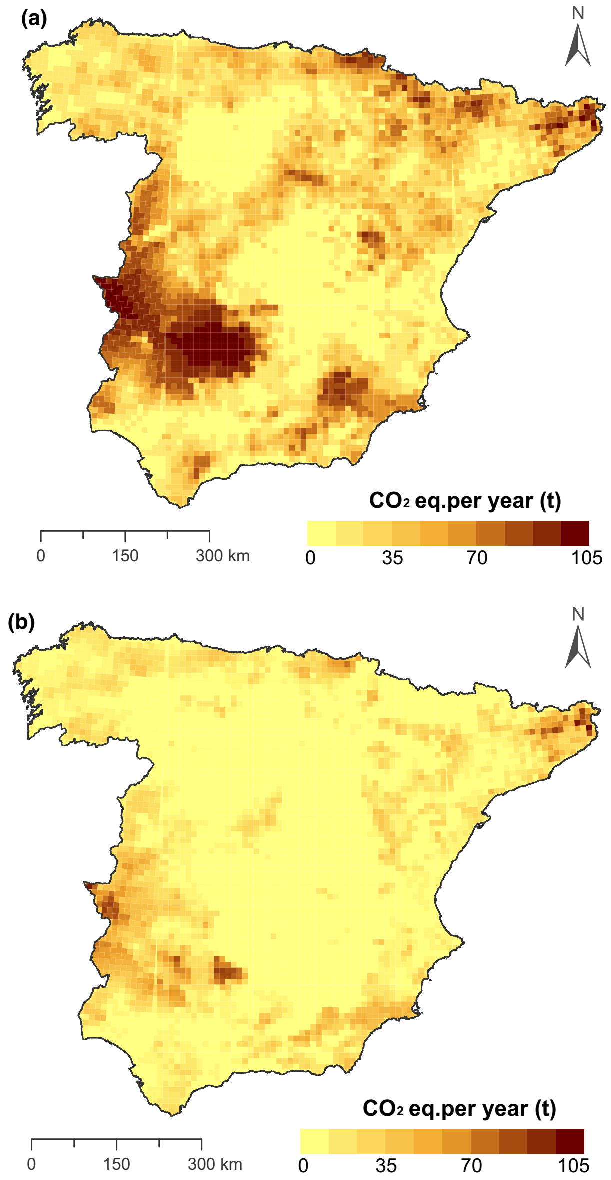

Fig. 3. GHG emissions (in metric tons of CO_2 eq. per 10×10 km grid per year) before (a) and after (b) the implementation of the protection areas for the feeding (PAFs) of necrophagous species in peninsular Spain.

PAF PERFORMANCE IN RELATION TO TARGETED SPECIES AND CARRION AVAILABILITY

Importantly, the breeding distribution of priority species, particularly vultures, was better represented in PAFs than the distribution of other facultative scavengers not included as targeted species. In this sense, Spanish PAFs may meet their purpose reasonably well. However, there are still populations of targeted species outside PAFs. Efforts to protect these populations should be especially encouraged in the case of the most endangered species at the national and global scales, i.e. *N. percnopterus*, *A. adalberti* and *M. milvus*.

As expected as a consequence of the application of the new European regulation permitting the disposal of carrion in the field, we found a significant increment in the availability of food resources for scavengers (measured as tons of carrion) within these areas. This may alone imply a significant step in the conservation of the Spanish and, by extension, European vulture populations. In particular, the Spanish PAF network could potentially provide c. 4–6 times the carrion needed annually by the whole Spanish vulture population (Margalida & Colomer 2012). However, calculations are not available for the rest of the species included in this study and we must recognize the spatial heterogeneity in both scavenger and carrion abundance. It is worth noting that our results are not exact figures of food availability as some regions do not fully apply the recently approved regulations while others, mainly those located in remote areas (i.e. high mountains, far from roads and trails), have never removed carcasses due to the logistic constraints in locating them. Moreover, to predict the carrying capacity of these areas to maintain healthy populations of vultures and other facultative scavengers in Spain, it is important to simultaneously assess the role played by wild ungulate carcasses as another source of food for these species (Mateo-Tomás *et al*. 2015).

HOW CAN BE THE PAF NETWORK BE IMPROVED?

Non-targeted facultative scavengers can also benefit from the resources available within PAFs. For example, the application of the previous EU sanitary regulation led to changes in the diet of wolves (e.g. increased large domestic ungulate consumption; Lagos & Bárcena 2015; Llaneza & López-Bao 2015), possibly affecting their role in the ecosystem (Lagos & Bárcena 2015) and exacerbating human–wolf conflicts (Llaneza & López-Bao 2015). Regarding *U. arctos*, carrion is an important resource for this species (Clevenger & Purroy 1991; Naves *et al*. 2003; Mateo-Tomás *et al*. 2015), which is critically endangered (CR) in Spain. Its inclusion as a priority species in PAFs might significantly contribute to improving its conservation status. Thus, we encourage the inclusion of additional facultative scavengers of special conservation concern and those associated with outstanding human-wildlife conflicts when designing PAFs.

The most important failure of current PAF design is probably their focus on the breeding distribution of scavengers. Vultures are soaring birds that can travel several hundreds of km daily from breeding to foraging areas (see Table 2) across physical and political boundaries (see Table 3). Long-distance daily movements are common in seabirds that often cross different jurisdictions (Yorio 2009) or large carnivores that have large spatial requirements (e.g. Falcucci *et al*. 2013; Trouwborst, Krofel & Linnell 2015). In these cases, conservation strategies that consider movements outside of breeding areas are highly desirable (Lambertucci *et al*. 2014). Previous studies have described vulture foraging movements related to the use of carrion resources (i.e. vulture restaurants) at the local scale through GPS tracking (e.g. Monsarrat *et al.* 2013; López-López, García-Ripollés & Urios 2014), but not at a large scale as in this study. We observed that the breeding distribution of the four vulture species were well represented in PAFs, while the fit between their home ranges and PAFs was less adequate, especially for young birds. This clearly highlights another important avenue for the improvement of the new sanitary regulation, which should recognize the combination of breeding and foraging areas. However, although our case studies rely on a large number of individuals, expanding the number of GPS-tracked vultures (e.g. taking into account other areas and seasons, as well as individuals of different age classes and breeding status) would provide an improved, more comprehensive assessment of the new regulation. For instance, pre-adult *G. barbatus* from the Pyrenean population moved much less than individuals reintroduced in Andalusia, which may be related to the abundance and predictability of food resources (Margalida *et al.* 2013). In any case, our results offer an unprecedented starting point and reveal interesting hypotheses that can be further tested. Our findings indicate that PAFs may be more efficient for breeders than for floaters, whose home ranges can be considerably larger. In the case of *G. barbatus* in the Pyrenees, the overlap of core areas (k50%) of breeders with PAFs reached 90·6%, while the overlap was only 64·2% for floaters.

COLLATERAL BENEFITS OF PAFS

The previous European sanitary regulation resulted in a new source of GHG emissions associated with carcass collection and transport to authorized plants (Morales-Reyes *et al.* 2015). The new regulation meant a substantial GHG emission reduction (see Fig. 3), although there is still c. 44% of the original emissions that could be saved. The areas that currently accumulate most of the GHG emissions are associated with a high number of livestock of species not included in the regional regulations and located far from authorized plants. For example, in south-western Spain, where there are many cattle and other extensive livestock species, the regional PAF regulation only allows farmers to abandon sheep carcasses in the field (see Table S1) and in north-eastern Spain, only lands above 1400 m are included within PAFs (Table S1). In parallel, the new regulation meant important economic savings to farmers and to regional and national administrations when compared to the previous situation in terms of payments to insurance companies for carcass transport (Morales-Reyes *et al.* 2015). Including all livestock species in the PAFs of all regions would further reduce these environmental and economic costs.

MANAGEMENT IMPLICATIONS AND CONCLUSIONS

Our results show that the implementation of the new regulation regarding the management of extensive livestock debris may greatly improve the previous rules and have obvious positive effects on scavenger conservation. Also, the PAFs' scenario means an important tool to reduce the environmental (and economic) costs associated with the artificial removal and processing of livestock carcases. However, the Spanish network of PAFs should be improved to cover the full distribution range of priority species and additional facultative scavengers of special conservation concern. Moreover, to maximize the effectiveness of PAFs in Spain, managers should recognize that vultures are highly mobile organisms that must move daily from breeding to foraging areas across physical and political boundaries. Thus, management should be performed, or at least coordinated, at a supra-regional scale. As a first step, regional administrations should avoid establishing how much carrion can be left in the field based only on the scavengers present in their region. Additionally, the design criteria of PAFs and the livestock species subject to regulation should be unified among Spanish regions at the national level. Supra-national coordination with neighbouring European countries that support vulture populations is also desirable. PAFs should recognize that movements of scavengers are age-dependent and take into account the foraging strategies of floaters.

Protected areas have been the cornerstone of biodiversity conservation world-wide (e.g. Ervin 2003; Gaston *et al.* 2008a). Thus, the evaluation of their conservation effectiveness (e.g. Chape *et al.* 2005; Gaston *et al.* 2008b; Leverington *et al.* 2010) is an essential component of conservation strategies. The findings from our work support the utility of combining large scale information on biodiversity, movement ecology of target species and the evaluation of ecosystem services to inform political and technical decisions regarding environmental conservation policies.

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Data accessibility

Raw data on scavenger and livestock distribution have not been archived because they belong to the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA) and they are accessible on request (at_sgb4@magrama.es). GPS locations have not been archived as they contain sensitive information on endangered species. They belong to different regional governments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Map of regions of peninsular Spain, indicating if they have approved or drafted specific regulations regarding PAFs.

Table S1. Livestock species permitted to be abandoned inside PAFs, total area of the region, percentage of the area occupied by PAFs and PAFs design criteria for each region of peninsular Spain.

Table S2. Age class, number of individuals, average weight and annual mortality rate of the major extensive livestock species in peninsular Spain.

Table S3. Number of individuals tracked, sex, age class, tracking period, total number of GPS fixes used, place of capture and tracking devices used for the monitoring of four vulture populations from different PAFs within peninsular Spain.

Table S4. Total livestock carrion biomass available in each region, livestock carrion biomass available in PAFs relative to the total of each region, total GHG emissions after the implementation of PAFs in each region and GHG emissions savings in relation to a pre-PAF scenario.