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RESEARCH ARTICLE

Wildlife as sentinels of compliance with law: An example with GPS-tagged scavengers and sanitary regulations

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Abstract

1. Monitoring compliance with environmental laws is essential to overcoming possible implementation shortfalls jeopardizing their effectiveness. Besides improving our ecological understanding of wildlife, remote tracking technologies also allow us to take advantage of such ecological knowledge to use wildlife as sentinels of compliance with law.
2. We illustrate this sentinel potential of wildlife using GPS tracking of large scavengers with complementary functional traits (i.e. 21 griffon vultures and 13 wolves) to assess compliance with EU sanitary regulations allowing livestock carcass disposal in the field.
3. Wildlife sentinels allowed the systematic evaluation of 489 livestock carcasses left in the field, which revealed an important mismatch between on-paper and in-reality implementation of these regulations. While <45% of the carcasses were placed in authorized areas, compliance with all the criteria required by the regulations on livestock carcass disposal (e.g. from carcass characteristics such as species, age or production system to its location far away from water, buildings or roads) ranged from 0% to 4.2%, with no major differences between regions with uneven implementation.
4. Major gaps in compliance pointed towards insufficient and over-bureaucratized designation of scavenger feeding zones, where livestock carcass disposal is authorized. The indiscriminate nature of distance criteria from carcasses to watercourses, buildings and infrastructure further affected compliance.

5. *Synthesis and applications*. GPS-tagged scavengers allow the on-ground monitoring of carcasses, the addressing of potential risks for wildlife, livestock and human health, the quantitative assessment of compliance with the law and would improve estimates of carcass availability, substantially contributing to more effective legislation enforcement. Our results show the huge potential of GPS-tagged wildlife as sentinels for monitoring compliance to enhance the environmental rule of law.

KEYWORDS
biomonitoring, environmental rule of law, GPS-tracking, law enforcement, livestock carcasses, vulture, wolf

1 | INTRODUCTION

Environmental laws are acknowledged as conservation tools whose benefits extend far beyond nature preservation (e.g. Greenwald et al., 2019; Sanderson et al., 2016), from sustainable socioeconomic development to public health and security (UNEP, 2019). The integration of environmental concerns into other sectorial policies (i.e. Environmental Policy Integration; Jordan & Lenschow, 2010) contributes to achieving conservation goals by, for example, reducing pollution or slowing down habitat degradation (Biermann & Kim, 2020). Despite the global rise of environmentally concerned legal instruments and institutions (UNEP, 2019), several shortfalls jeopardize the effectiveness of environmental laws (Trouwborst et al., 2017). Slow transposition, poor coordination, under-resourcing or deprioritizing against economic gain weakens enforcement and compliance (López-Bao & Margalida, 2018; Mateo-Tomás, Olea, López-Bao, González-Quirós, et al., 2019; Treib, 2014; UNEP, 2019).

Monitoring outstands as an integral part of the law implementation process, to evaluate the degree of enforcement and compliance, identify implementation gaps and adapt accordingly (IMPEL, 2022; UNEP, 2019). Approaches often used to monitor compliance include official inspections, self-monitoring by affected stakeholders, third-party contributions (e.g. from citizens and NGOs), or tracking environmental parameters susceptible to be affected by the regulations. Biomonitoring (i.e. using living organisms) is also a powerful monitoring tool, due to its capacity of synthesizing information from complex systems over whole areas (Markert et al., 2003). From microbes and plants to invertebrates and vertebrates, living organisms can bridge the gap between policy, science and the public in terms of awareness of the enforced regulations (Markert et al., 2003). For example, while lichens are recommended as a biomonitoring tool for assessing compliance in industrial activities emitting air pollutants (Vitarana, 2013), fishes are used to monitoring water quality (Kuklina et al., 2013). Examples also exist with birds, for example, analysing the gizzard content of waterfowl to assess compliance with bans on lead ammunition in wetlands (Vallverdú-Coll, 2012), and marine mammals, whose bycatch are used as bioindicators to improve compliance with fishing gear regulations (Palka, Orphanides, et al., 2008; Palka, Rossman, et al., 2008).

The rise of remote monitoring techniques has added a new dimension to the concept of biomonitoring (traditionally linked to disciplines such as chemistry or ecotoxicology; Burger, 2006): the use of space-based systems such as satellite imagery or global positioning system (GPS) devices for detailed monitoring of wildlife (Jezt et al., 2022). From tracking pollution in ecosystems (e.g. Biermann et al., 2020) to detecting illegal persecution of wildlife (e.g. Stoynov et al., 2018; Weimerskirch et al., 2020), these applications have a strong potential to inform conservation and management policies. Besides informing on direct threats causing species mortality or habitat degradation (Biermann et al., 2020; Jezt et al., 2022; Stoynov et al., 2018), GPS-tracked animals can provide additional insights on how to effectively assess the level of compliance with law, including regulations on biodiversity conservation, sustainable development or human well-being. Thus, for example, GPS-tagged albatrosses have allowed the detection of unreported fishing vessels, whose illegal activity jeopardizes species conservation and the sustainable use of resources of major importance to humans such as those provided by fisheries (Weimerskirch et al., 2020). Similarly, GPS tracking of jaguars in Brazil has been reported as a useful tool to detect illegal wildlife poisoning (Csermak et al., 2023) while GPS tagging of hen harriers in the British countryside has helped to identify areas where the species is illegally shot (Murgatroyd et al., 2019).

Here, we offer an illustrative example of the potential of GPS-tagged wildlife for monitoring the level of compliance with law. By using scavengers as wildlife sentinels, we assess compliance with sanitary regulations concerned with, but not strictly focused on, wildlife conservation. We show how GPS-tracked vultures and large carnivores shed light on compliance with European sanitary regulations implemented for aligning biodiversity conservation and public health by allowing the disposal of livestock carcasses in the field for feeding scavengers (i.e. Regulations EU 1069/2009 and 142/2011). According to their uneven implementation in Europe (Mateo-Tomás et al., 2018) and based on previous results pointing towards a lack of compliance with the enforced regulations (Gigante et al., 2021; Mateo-Tomás et al., 2022), here we take advantage of GPS-tracked vertebrate scavengers to quantify the level of compliance with these sanitary regulations across national and subnational borders in the Iberian Peninsula. We later discuss how the major gaps identified could be addressed to effectively achieve the objectives of these regulations.

2 | MATERIALS AND METHODS

2.1 | The uneven management of livestock carcasses in the Iberian Peninsula

Our work focused on two countries, that is, Portugal and Spain, and three Spanish autonomous regions, that is, Asturias, Castilla y León and Galicia; while the Portuguese central government and its regulatory authorities are the competent bodies for implementing regulations on nature conservation and public health, in Spain this competence is held by the autonomous regions. Two major geographical areas were considered: (i) the Cantabrian Mountains in north-western Spain and (ii) the Douro River at the Portuguese–Spanish border (Appendix S1). Livestock rearing is a major activity in both areas, with an important presence of extensive and semi-extensive farming (Appendix S1).

Livestock carcasses are managed differently across administrative borders according to the uneven implementation of EU Regulations 1069/2009 and 142/2011 (Mateo-Tomás et al., 2018; Mateo-Tomás, Olea, López-Bao, González-Quirós, et al., 2019; Appendix S2). In Spain, Castilla y León and Asturias implemented these regulations to allow the disposal of livestock carcasses in the countryside in 2013 and 2017 respectively. Galicia allows the abandonment of carcasses of only free-ranging horses since 2016. Farmers in Castilla y León must apply for an official permit, which limits the number of carcasses to dispose at scavenger feeding zones (SFZs; i.e. officially designated areas where fallen livestock can be left in situ for feeding wildlife according to EU Regulations 1069/2009 and 142/2011). Contrastingly, all farmers complying with some sanitary requirements can leave livestock carcasses in situ within SFZs in Asturias. Farmers in Galicia, on the contrary, must inform the veterinarian authorities of the exact location where carcasses were abandoned. Although recent changes in Portuguese legislation provide new opportunities for leaving livestock carcasses in the field outside artificial feeding stations (Appendix S2), SFZs are not yet implemented. At the time of this study, livestock carcasses in Portugal should be either collected or buried if located within remote areas declared by the competent authorities.

2.2 | GPS tracking of large vertebrates for carcass monitoring

Available livestock carcasses for wildlife to feed on were located in the field by GPS-tracking two scavenging vertebrates: griffon vultures (*Gyps fulvus*) and Iberian wolves (*Canis lupus signatus*). Between 2017 and 2020, 21 adult griffon vultures were captured and equipped with solar-powered GPS-GSM trackers by Ornitela® in Spain and Portugal, and GPS-Iridium Followit® collars were deployed on 13 Iberian wolves (11 from 9 different packs and 2 floaters) captured in NW Spain (see Appendix S3 for capture details). From the vertebrate scavenger community inhabiting the Iberian Peninsula (Mateo-Tomás et al., 2015, 2017), these two species are perfectly fitted for purpose since they are tightly related to consumption of large ungulate carcasses in the study area and elsewhere (e.g. Llaneza & López-Bao, 2015; Mateo-Tomás et al., 2015; Mohammadi et al., 2019; Tella, 2001). Griffon vultures are obligate scavengers adapted to feed mostly on carcasses of large ungulates, because they are highly specialized for the efficient location of dead animals over vast areas from the air (Ruxton & Houston, 2004). Contrastingly, large terrestrial carnivores such as wolves retain the flexibility of feeding by either predation or scavenging, being frequently recorded as facultative scavengers (Llaneza & López-Bao, 2015; Mateo-Tomás et al., 2015). 92% of the griffon vultures in Europe inhabit Spain and Portugal, with >3000 breeding pairs estimated in the study area (Del Moral & Molina, 2018; Monteiro et al., 2018). The Iberian wolf population has its main stronghold in NW Spain (Chapron et al., 2014), with 43 wolf packs detected in Asturias in 2021 (Hernández-Palacios & Quirós, 2021), where the GPS-tracked wolves were monitored for carcass location. All procedures that included the capture, handling and GPS tagging of vultures and wolves were specifically approved by the competent authorities (i.e. Principado de Asturias, Junta de Castilla y León and Instituto da Conservação da Natureza e das Florestas, permits Res. 17-02-2017, Res. 19-07-2017, Res. 01-03-2018, 2019/007875, 886-891/2019/CAPT, 623-628/2020/CAPT, AUES/LE/92/2020, 2020277030). All field procedures and animal handling were carried out in accordance with animal welfare regulations (Directive 2010/63/EU, Orden ECC/566/2015).

GPS locations were collected at fixed intervals of 10 min for vultures and 20 min for wolves, in order to detect livestock carcasses (i.e. scavenging events). Both schemes have been previously proven useful to track the activity of both species in north-western Iberia, and to detect feeding events (Planella et al., 2016; Rodríguez-Pérez, 2020). For vultures, potential feeding events were first identified by randomly selecting clusters of at least two consecutive locations with a speed ≤15 km/h recorded by the GPS (i.e. indicating possible stops; Spiegel et al., 2013) within a radius of 200 m. These features are part of an approach that has previously allowed us to differentiate vulture feeding sites from resting locations with an accuracy >70% (Rodríguez-Pérez, 2020). For wolves, we took advantage of an intensive GPS schedule providing a location every 20 min during 1 week per month (we opted for one intensive week per month only, in order to maintain an acceptable balance between battery life and monitoring period; the rest of time we obtained 2–6 GPS locations per day). The criteria to identify potential feeding events were two or more locations during the intensive period with a maximum distance between them <60 m (this distance was selected as the double of GPS error). We did not visit clusters related to long periods of inactivity during daylight hours, considering those as resting sites; as well as recurrent clusters in the same location where we previously found prey remains. After identifying GPS clusters for vultures and wolves, we visited them in the field within 1–5 days whenever possible (>90% of clusters were visited within this period). All GPS locations identified in a cluster were visited, and in every location, we explored a 30-m radius (based on GPS error) searching for carcass remains (Planella et al., 2016; Rodríguez-Pérez, 2020). In the case of wolves, prey remains were additionally evaluated to discriminate between predation and scavenging (e.g. presence of wounds or subcutaneous haematoma compatible with depredation; López-Bao et al., 2017), and only scavenging events on livestock were considered for subsequent analyses.

For each located carcass, we evaluated whether it fulfilled the different criteria required by the regulations (Appendix S4). To allow transboundary comparisons, we considered three hierarchical levels for compliance (Figure 1): (i) If the carcass was located within an authorized SFZ, (ii) whether carcass characteristics, such as species, age and husbandry practices, complied with the requirements set by the regulations and (iii) if the carcass location met the distance criteria set in the regulations to minimize potential risks for wildlife and public health, that is, distances to water, buildings, roads, power lines and windfarms. Regarding carcass location within authorized SFZs, in the case of Castilla y León, we had access only to the livestock species authorized per municipality, not to the specific farms authorized to leave dead livestock in the field. Therefore, we assumed compliance if the livestock species of the carcass was authorized within the municipality where found, regardless of its farm of origin. In Galicia, we considered that a horse carcass was within an authorized SFZ if the carcass location had been communicated to the competent authorities, a compulsory requirement for authorization. For the second level of compliance, whenever possible, we recorded the species, breed and age of each carcass (mostly based on dentition; Dyce et al., 2009; König & Liebich, 2001). By visual inspection of the surroundings, we also determined if the animal had died in situ or if the carcass had been thrown away at the place where located. Based on this information and the breed and livestock farming activity observed in the surroundings (e.g. grazing areas, intensive farms), we determined if the animal was free-grazing or came from intensive farming. Finally, to check if the carcass location met the distance criteria set in the sanitary regulations, besides on-ground verifications, we also used official cartography on the location of these points of interest to calculate distances (CIGeoE, 2022; IGN, 2022).

3 | RESULTS

3.1 | Livestock carcasses revealed by sentinel GPS-tagged scavengers

GPS-tagged scavengers revealed 489 livestock carcasses in a total of 300 different feeding events in 2017–2021 (Appendix S4). A mean of two livestock carcasses (median: 1; range 1–45) were found per feeding event. From a total of 1161 clusters visited in the field (750 of vultures and 411 of wolves), we retrieved 381 feeding events of vultures and 104 of wolves. These feeding events included 379 livestock carcasses located in Spain by vultures and wolves (320 and 59, respectively), and 110 livestock carcasses found by GPS-tracking vultures in Portugal (Figure 2). Thus, the 63.2% of the vulture and the 55.8% of the wolf feeding events were on livestock carcasses of interest in this study. For vultures, where clusters were previously classified as feeding or non-feeding before on-ground visits, our approach correctly identified the 70.2% of feeding events, with a total accuracy of 77.2% to differentiate vulture feeding and resting sites.

Overall, carcasses from equine dominated in Asturias (45.5%, followed by cattle, 35.6%) and, especially, in Galicia (90.0%) (Appendix S5). In contrast, most of the carcasses recorded in Castilla y León (62.9%) were of ovine and caprine, which also dominated the sample recorded in Portugal (70.0%). In Asturias, where vultures and wolves were tracked, bovine and equine species dominated the carcasses found by both scavenging species, agreeing with major livestock practices in the area (see Appendixes S4 and S5). Most carcasses found by vultures in Asturias were in open land (i.e. 89.9% in shrubland and pastures), and only the 10.1% were in forested areas. Conversely, the 31.6% of the carcasses located by wolves in the same region were in forested areas, resulting in significant differences in the habitats where both species retrieved livestock carcasses (Chi-squared test: 11.656, $p < 0.001$).

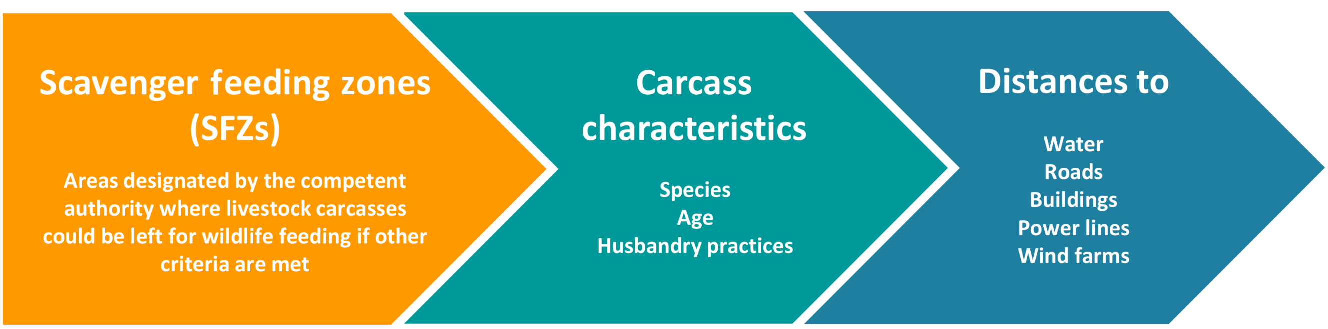

FIGURE 1 Despite the uneven implementation of the sanitary regulations allowing the disposal of livestock carcasses across Europe (Mateo-Tomás et al., 2018), major requirements include the official designation of scavenger feeding zones where fallen livestock can be left for feeding wildlife. Other criteria, related to the characteristics of the abandoned animal (e.g. species, age or origin) and the proximity to water sources, buildings and infrastructures could be required to safeguard public health and wildlife.

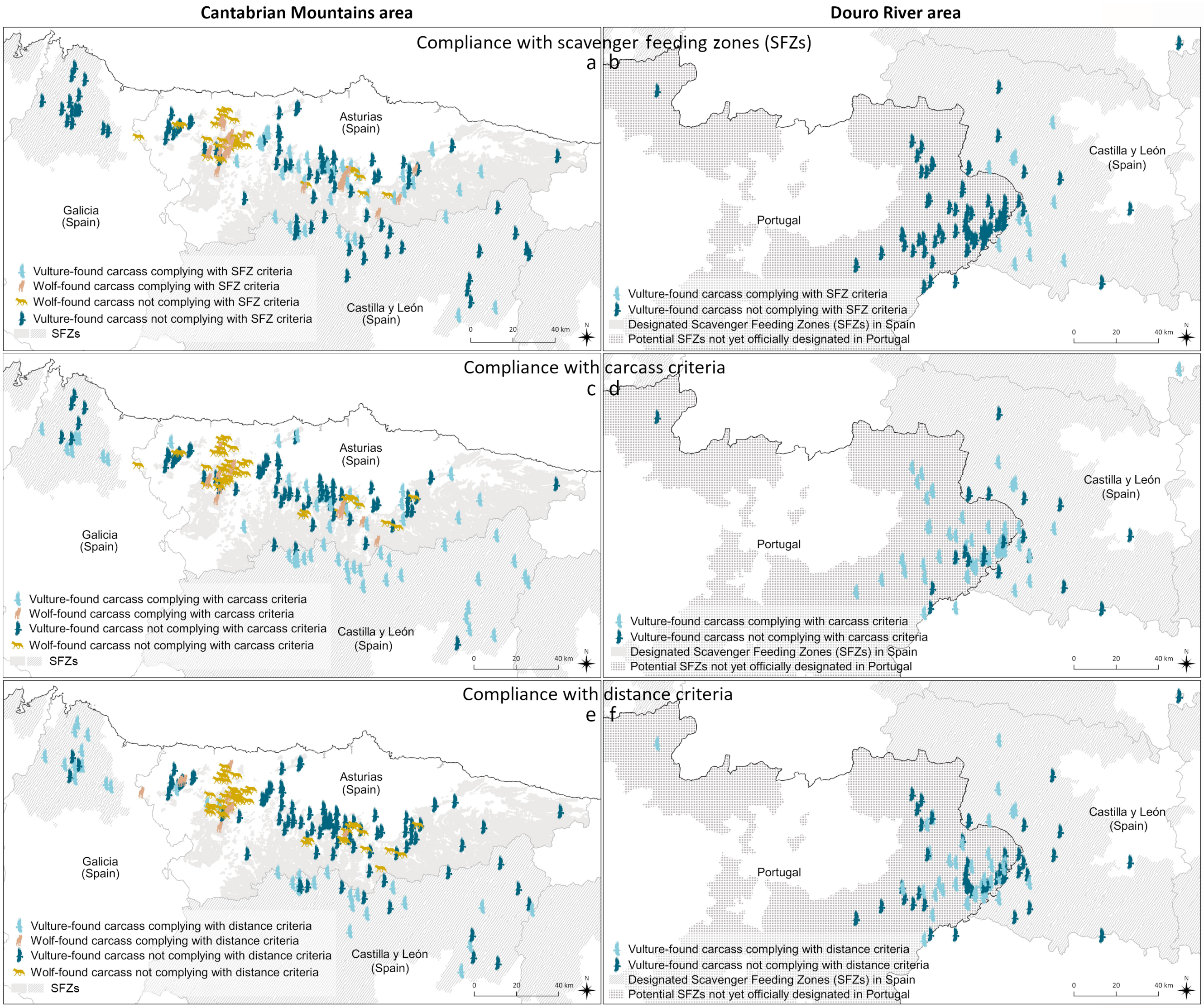

FIGURE 2 Spatial variation in compliance with the three groups of criteria required by the legislation for carcass disposal enforced across the study areas, that is, three Spanish autonomous regions in the Cantabrian Mountains (left column) and Portugal and Spain in the Douro River area (right column). Panels (a) and (b) show compliance with criteria for disposal within scavenger feeding zones; panels (c) and (d) display compliance with all the carcass characteristics criteria and panels (e) and (f) exhibit compliance with all the distances established to reduce potential risks for human and animal health.

3.2 | Compliance with EU sanitary regulations

The proportion of carcasses that simultaneously complied with all the legally required criteria was negligible in both countries (2.1 vs. 0% in Spain and Portugal respectively). The total level of compliance across autonomous regions in Spain ranged from 0% to 4.2% (Figure 3). The highest compliance level was observed in Asturias, but barely four of 100 livestock carcasses found fulfilled all the criteria required by the law. None of the carcasses found in Castilla y León and Galicia met all the criteria simultaneously (Figure 3; Appendix S4).

Overall, the main reason for non-compliance was livestock carcasses found outside authorized SFZs (Figure 3). Focusing on this criterion only, we observed similar levels of compliance in Asturias and Castilla y León, with ~45% of the carcasses found within SFZs (Figures 2a,b and 3; Appendix S4). Contrastingly, all carcasses found in Galicia and Portugal were outside authorized SFZs. Although 95.2% of the carcasses in Galicia were located within areas of free-grazing horses where carcasses abandonment could be authorized (Figure 2a), none of the carcasses were communicated to the competent authorities, and therefore, they were not considered within authorized SFZs (Xunta de Galicia, pers. comm.; Figures 2a and 3). Contrasting with the SFZ criterion, most livestock carcasses (>75.0%) corresponded to species, ages and husbandry practices authorized by the enforced regulations in Spain (Figure 3; Appendix S4). This resulted in a high level of compliance with all the carcass characteristic criteria simultaneously in all regions but Asturias (Figure 2c,d), where almost half of the carcasses did not comply the criteria of

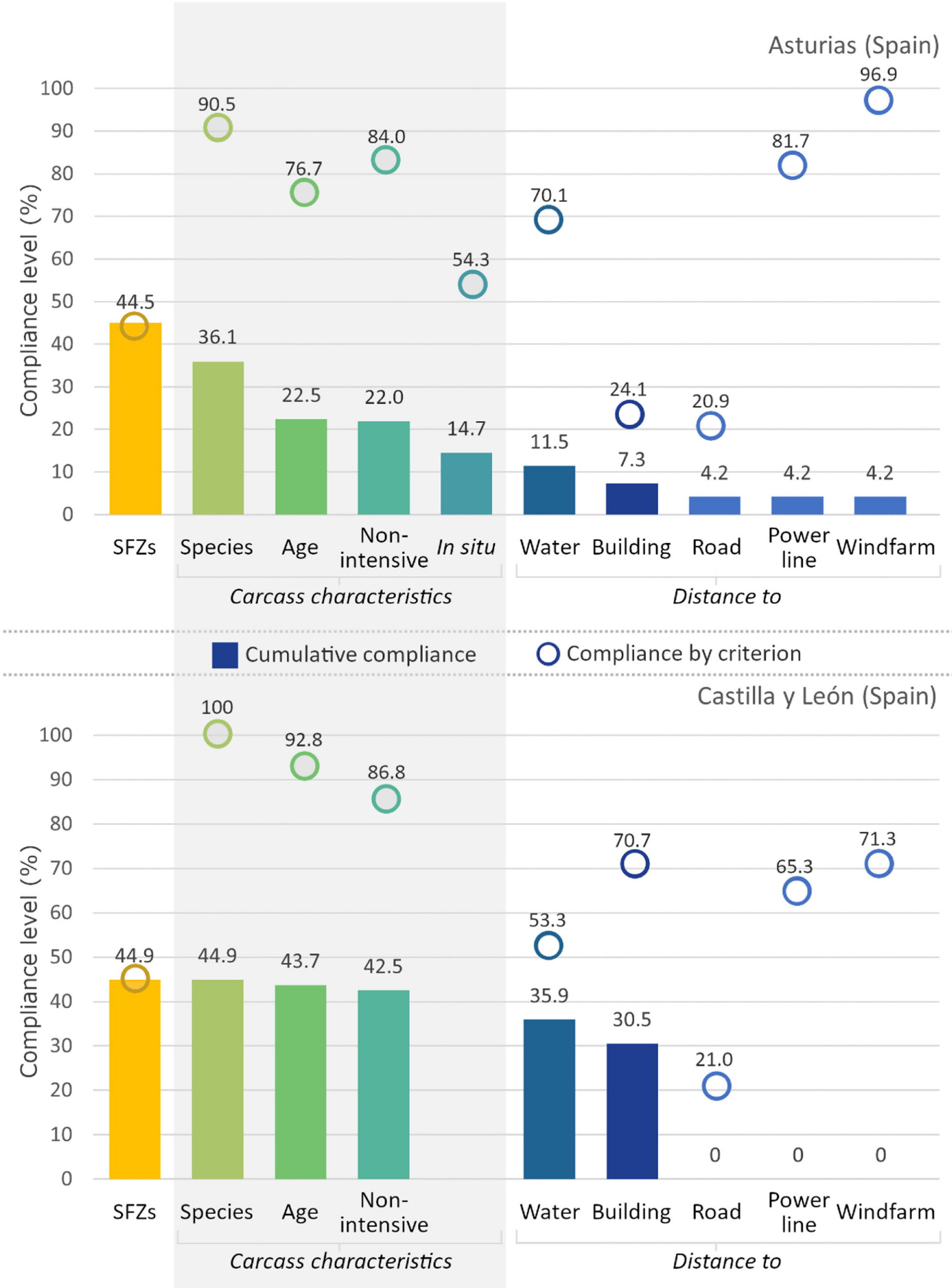

FIGURE 3 The level of compliance with the legislation for carcass disposal enforced at each study area at the time of this study progressively reduced as overlapping the different criteria (solid bars), until reaching a total compliance varying from four of 100 livestock carcasses simultaneously fulfilling all the legal requirements in Asturias (Spain) to none in the other three regions analysed, including Galicia and Portugal. Graphs for these two last regions are not shown here (but see Appendix S6) because initial compliance was zero, since no carcasses were located within officially declared scavenger feeding zones (SFZs). Circles show compliance with each criterion separately (see Table S4.2).

being abandoned in situ (Figure 3; Appendix S4). When overlapping authorized SFZs with carcass characteristics, compliance decreased below 45% in Asturias and Castilla y León, with a sharper decrease in Asturias (up to 14.6%; Figure 3). Finally, adding the distance criteria further reduced the overall compliance levels well below 5%, reaching zero in Castilla y León. Although the 28.6% of the carcasses found in Galicia simultaneously fulfilled most of the required criteria regarding carcass characteristics and distances to water and buildings (Appendixes S4 and S6), no communication to the competent authorities reduced total compliance to zero (Figure 3). Similarly, the level of total compliance in Portugal could slightly increase up to 16.4% if SFZs would be officially designated according to recommendations in Despacho 7148/2019, that is, in remote areas where the burial of fallen livestock is already allowed and in areas prioritized for the conservation and supplementary feeding of necrophagous birds (Figure 2b; Appendix S6).

4 | DISCUSSION

Our study shows the utility of GPS-tagged wildlife as sentinels to monitor compliance with the law. Our approach was useful to locate livestock carcasses (Planella et al., 2016; Rodríguez-Pérez, 2020), and thus GPS tracking of large scavengers, such as griffon vultures and wolves, enabled us to illustrate a remarkably low level of compliance with the enforced EU sanitary regulations, regardless of the region and the contrasting implementation (Mateo-Tomás et al., 2018; Mateo-Tomás, Olea, López-Bao, González-Quirós, et al., 2019). Poor compliance with laws intended for environmental conservation has been detected also in other contexts through, for example, biomonitoring porpoise bycatch on the Atlantic coast of North America (Orphanides & Palka, 2013), or by GPS-tracking albatrosses in the south Indian Ocean between Africa and New Zealand (Weimerskirch et al., 2020). All these results support previous concerns about the lack of correspondence between on-paper and in-reality implementations and reinforce the need of improving data collection to identify major gaps in enforcement and compliance with environmental law (UNEP, 2019). GPS-tagged sentinel wildlife emerges therefore as a good ally to monitor compliance with laws, and to identify major gaps that can otherwise remain unnoticed or give rise to misleading interpretations. For example, in line with their uneven implementation across Europe (Mateo-Tomás et al., 2018), EU Regulations 1069/2009 and 142/2011 have been considered a major conservation success for scavengers in countries like Spain, with officially designated SFZs (Morales-Reyes et al., 2017). On the contrary, the lack of SFZs has been depicted as a cause of food shortages in countries like Portugal (Arrondo et al., 2018). However, previous evidence from both countries already pointed towards a lack of correspondence between the methods authorized for livestock carcass management and those actually used by farmers (e.g. Gigante et al., 2021; Mateo-Tomás et al., 2022). Our results confirm these mismatches and provide additional insights into their magnitude and characteristics to better inform law enforcement.

A key factor limiting compliance in our case concerned the designation of SFZs. Designating as much surface as possible and reducing the bureaucracy burden for inclusion in SFZs have been recommended to increase the effectiveness of EU sanitary regulations regarding livestock carcass availability across scavengers' foraging areas (Mateo-Tomás et al., 2022; Mateo-Tomás, Olea, López-Bao, González-Quirós, et al., 2019). GPS-tagged scavengers revealed how these two drawbacks truly reduce the level of compliance. In Asturias, with a low bureaucracy burden (i.e. farmers do not need to apply for inclusion in designated SFZs; Appendix S2), insufficient land designated as SFZs substantially reduced compliance (44.5%) as many livestock carcasses were found outside SFZs. Designating new SFZs in the north-western part of this autonomous region would increase the level of compliance, as vultures, wolves and other species often scavenge on livestock carcasses there (Figure 2a). In contrast, in Castilla y León, bureaucracy would limit compliance. Indeed, farmers interviewed in this region complained about the complex process of application for SFZs (Mateo-Tomás et al., 2022). This level of compliance could be even lower than the one here provided, as we assumed compliance if the livestock species found was authorized for disposal at municipality level (see Methods). Other bureaucratic requirements, that is, farmers' communication to the authorities of carcass location, sharply decreased compliance in Galicia (from 28.6% to 0%; Figure 3). Worth mentioning, all the carcasses found in Portugal were within areas that may be potentially designated as SFZs in the future (Figure 2b; Appendix S4). Our results from Spanish autonomous regions provide useful guidance for enhancing the effectiveness of this designation through, for example, cutting red tape.

Compliance and traceability may benefit from closer collaboration between environmental and animal health authorities (Mateo-Tomás, Olea, & López-Bao, 2019). Similarly, fluent communication with insurance carriers could increase the information retrieved by the authorities in charge of monitoring carcass disposal. Collaboration among stakeholders has, for example, allowed the Cameroon government to improve compliance and enforcement of wildlife laws, achieving up to 87% success rates in prosecuting violators (Clynes, 2010; UNEP, 2006). As most farmers are not aware of the sanitary regulations implemented for handling livestock carcasses (Gigante et al., 2021; M. Fernández-García, P. Mateo-Tomás, J. V. López-Bao, P. P. Olea), improving communication with stakeholders to increase their knowledge of the enforced regulations would impact compliance. Indeed, outreach on existing regulations was considered to increase by >20% compliance of fishermen with using gear modifications required by law to reduce porpoise bycatch (Palka, Rossman, et al., 2008).

Most livestock carcasses found in each area corresponded to authorized livestock species and husbandry practices. GPS-tracked scavengers revealed, however, some carcasses from intensive farms, with special concern in the case of pigs consumed regularly by vultures at the collection points of at least four different intensive farms located in Castilla y León, up to >110 km away from the vultures' breeding colonies. Vultures feeding at these farms indicate an additional lack of compliance with regulations that obliges the collection of carcasses from intensive farms by authorized operators to prevent carcass consumption by wildlife. Meanwhile, EU regulations require the maintenance of appropriate containers that prevent wildlife access to carcasses of intensively farmed animals, which are expected to contain toxic substances not authorized for animal consumption (Shore et al., 2014). Our results encourage therefore to reinforce official inspections at intensive farms to prevent wildlife feeding on livestock carcasses treated with drugs not intended for animal consumption.

More of the livestock carcasses found would comply with the age limits set by the regulations, with the lowest values corresponding to those regions with a higher presence of bovine species (i.e. Asturias), since animals older than 48 months are not authorized to be left in the field. The high compliance with age found in Castilla y León and Portugal was due to assuming that all carcasses of ovine and caprine species over 18 months complied with the mandatory testing procedures (4% of the animals); otherwise, compliance with this criterion would drop to 50.9% and 35.2% respectively. While in Galicia most of the carcasses were abandoned in situ, almost half of the carcasses found in Asturias were thrown away from the place where the animal died. Moreover, 54 illegal dumps where livestock carcasses are thrown away on a recurrent basis were found across the study areas, some of them in dangerous places for wildlife and/or people, such as at road borders, windfarms and power lines. The largest proportion of carcass dumps (29.0% of carcass locations) was recorded in Portugal, where the absence of SFZs could facilitate carcasses to be thrown away at dumpsites instead of being left in situ.

Remarkably, non-compliance with distance criteria sharply decreased the total level of compliance across regions. Nonetheless, depending on the distances considered, compliance greatly varied, indicating the indiscriminate nature of many of these criteria. For example, varying the minimum distance from carcasses to windfarms from 200 m (as required in Asturias) to the 4000 m recommended by the Spanish Government (2011) would decrease compliance from 96.9% to 71.9% in Asturias, 100% to 71.3% in Castilla y León and 52.4% to 4.8% in Galicia. In fact, despite not including distance to windfarms in the regulations for authorizing the abandonment of horse carcasses, Galicia was the study region with the largest proportion of carcasses near wind turbines. Instead of setting fixed distances, on-ground monitoring could help to better adapt these criteria regionally, while gathering useful information for better assessment of the actual effectiveness of the EU sanitary regulations in reconciling scavenger conservation and public health and to evaluate the convenience of major modifications of the norms (Mateo-Tomás, Olea, & López-Bao, 2019).

Although out of the scope of this study, the functional complementarity of vultures and wolves would provide information on carrion availability across habitats and for other scavenging vertebrates (Gigante et al., 2021; Mateo-Tomás et al., 2015; Mateo-Tomás, Olea, López-Bao, González-Quirós, et al., 2019; Olea et al., 2022). No major differences were found between vultures and wolves in terms of the carcass species found (>78% were cows and horses in both cases; Appendix S5) or compliance with SFZs (44.4% and 44.1%, respectively), but wolves located more carcasses than vultures in areas with denser vegetation (i.e. 31.6% vs. 10.1%). These results would agree with vultures' major ability to locate and access carcasses in open areas (Pardo-Barquín et al., 2019; Ruxton & Houston, 2004) and would point towards complementarity between vultures and wolves to locate carcasses across habitats. Nonetheless, to what extent the combination of several sentinel species with different functional traits could improve carcass monitoring deserves further investigation.

We show here how GPS-tagged large vertebrates can act as sentinels of compliance with law, but also of other risks for biodiversity. Not in vain, GPS tagging has frequently revealed illegal persecution of wildlife (e.g. poisoning; Surkes, 2021), de facto indicating a lack of compliance with regulations for species conservation (e.g. Weimerskirch et al., 2020). Although the high cost of GPS devices may limit their usefulness, for example, in having enough marked individuals (Fischer et al., 2018), low-cost GPS technologies are increasingly available for tracking more and more species across the globe (Jezt et al., 2022). Meanwhile, advances in movement ecology through, for example, remote identification of species behaviours from GPS sensors (Nathan et al., 2012; Resheff et al., 2014), could significantly reduce the costs of on-ground monitoring GPS-tagged individuals, even allowing data collection from remote areas of difficult access. Even though assessing the effectiveness of GPS-tracked scavengers for locating feeding events is beyond the scope of this study, our approach showed a relatively high ability to detect vulture feeding events (i.e. 70.2%). This score could be increased by coupling the on-ground monitoring of carcasses used here with remote identification of feeding behaviours of GPS-tracked vultures (e.g. Arkumarev et al., 2021; Nathan et al., 2012; Resheff et al., 2014; Rodríguez-Pérez, 2020) to reduce the costs of fieldwork while increasing the precision of the estimates of carcass availability in space and time. Similar approaches should be further evaluated for facultative scavengers like wolves, which can provide complementary information (e.g. from dense vegetation areas), as well as to differentiate livestock carcasses from other feeding resources (e.g. Ciucci et al., 2020; Mohammadi et al., 2019; Planella et al., 2016). This would enhance in turn the usefulness of GPS tracking of wildlife as sentinels for monitoring compliance with EU regulations for wildlife conservation and public health. This information would thus contribute to a more effective adaptive management of the EU sanitary regulations that has been previously claimed (e.g. through on-ground carcass monitoring; Mateo-Tomás, Olea, & López-Bao, 2019). Likewise, given the increasing availability of information from GPS-tagged animals (Jezt et al., 2022), this approach could be used to monitor compliance with different regulations affecting biodiversity conservation almost anywhere on the planet.

AUTHOR CONTRIBUTIONS

Patricia Mateo-Tomás conceived the idea, led the writing and analyses, designed together with José Vicente López-Bao. Both coauthors led vulture GPS tagging, in collaboration with João Pedro Valente e Santos in Portugal. José Vicente López-Bao led wolf GPS collaring. Patricia Mateo-Tomás, José Vicente López-Bao, Jorge Rodríguez-Pérez, María Fernández-García, Emilio J. García, João Pedro Valente e Santos, Pedro P. Olea and Iván Gutiérrez visited GPS clusters. GREFA (Beatriz Rodríguez-Moreno) provided some GPS devices. All authors contributed critically to the drafts and gave final approval for publication.

Statement of inclusion: Our study brings together authors from the countries where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest. Patricia Mateo-Tomás is an Associate Editor of *Journal of Applied Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.fqz612jz4 (Mateo-Tomás et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Livestock farming in the Cantabrian Mountains (NW Spain) and the Douro River at the Portuguese-Spanish border.
Appendix S2: International, national and subnational regulations enforced for the management of livestock carcasses in the study area.
Appendix S3: GPS-tagging of large vertebrates for carcass location.
Appendix S4: Main criteria and levels of compliance with the enforced regulations for carcass disposal.
Appendix S5: Livestock carcasses revealed by sentinel GPS-tagged scavengers.
Appendix S6: Potential compliance under changing scenarios in the study area.

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