



Unraveling the real magnitude of illegal wildlife poisoning to halt cryptic biodiversity loss

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ABSTRACT

Illegal wildlife poisoning is a global threat for biodiversity, yet the magnitude of its impact on ecosystems is largely underestimated as most of poisoning episodes remain undetected. Here, we conducted a large-scale field experiment to better understand the real dimension of the illegal wildlife poisoning in terms of composition and number of species and abundance of impacted individuals, as well as the ecological factors driving it. We used camera traps to monitor simulated poison baits placed in 25 study areas in SW Europe and applied Good–Turing theory to estimate the richness of species of the entire assemblage (observed plus undetected). We recorded 3095 individuals from 39 vertebrate species that consumed 94 % of the baits ($N = 590$). Yet, using sample completeness to estimate the entire species assemblage yielded a total of 47 species exposed to illegal poisoning. The observed assemblage included different trophic and functional groups (from lizards and snakes to apex species among birds and mammals), as well as a 38 % of threatened and near threatened species (according to Spanish and Portuguese vertebrate red list and IUCN list). The size (weight) of the bait outstands as a reliable predictor of the number of species (0–8 species/bait, mean = 2) and individuals (0–99 individuals/bait, mean = 5) susceptible to poisoning. The habitat where the bait was placed modulated the abundance of individuals affected (greater in open than in closed habitats). Type of bait and habitat drove the compositional variation of species. Our approach enables uncover entire species assemblages prone to illegal poisoning and their ecological drivers associated, advancing the understanding of the impact of wildlife poisoning in ecosystems.

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1. Introduction

Wildlife crime is still a global concern for biodiversity conservation (European Union, 2018; Wilson and Boratto, 2020; CITES, 2021), with far-reaching ecological, social and economic consequences (CITES, 2021). Globally, millions of wild animals and plants from thousands of species are poached and captured for illegal wildlife trade annually (European Union, 2018; Scheffers et al., 2019; Traffic, 2019), which is leading iconic species including tigers, elephants, rhinos, and vultures to the brink of extinction (Maxwell et al., 2016; European Union, 2018; Scheffers et al., 2019; Ogada et al., 2016a). The killing of wildlife (poaching) remarkably contributes to one of the major drivers of biodiversity loss: overexploitation of species (Maxwell et al., 2016; European Union, 2018; Scheffers et al., 2019; WWF, 2020).

Along with illegal shots and trapping, poisoning is one of the most frequently used methods for poaching or predator control (Newton, 1979; Woodroffe et al., 2005; Mateo-Tomás et al., 2012; De Lange et al., 2021; Estrada Pacheco et al., 2020). Illegal wildlife poisoning typically consists of the placement of poison-baits in the field (e.g. small meat remains, use of animal carcasses; Rspb, 2009; Ogada et al., 2016b; de la Bodega et al., 2020). This illegal practice typically arises as a response to the real or perceived negative impact of wildlife on humans and their interests (Woodroffe et al., 2005; Carter et al., 2017), such as predation on livestock, damage to crops, competition for game or, rarely, attacks on humans (Redpath et al., 2015). Many cases exemplify the global threat of illegal poisoning to wildlife across the planet (e.g. from vultures and bears in Europe, vultures and lions in Africa, condors and pumas in South America, eagles in Australia, and wolves in North America, to name a few; de Greef, 2019; de la Bodega et al., 2020; Estrada Pacheco et al., 2020; Stafford, 2019; Koulouris, 2020; Diaz, 2021).

Illegal wildlife poisoning is a non-selective practice that affects not only the target species for poachers, but also many other animal species, including domestic pets and even humans (Wobeser et al., 2004; Berny et al., 2015; Mateo-Tomás et al., 2012), and contributing to severe population declines of threatened species (Ogada et al., 2016a; Margalida et al., 2019; Méndez et al., 2021a; African Wildlife Poisoning Database, 2021). Indeed, 2602 animal species (1134 listed as threatened) are considered to be globally threatened by poisoning (IUCN Red List; Mateo-Tomás et al., 2020). Despite these figures, we have still a poor understanding of the real magnitude of wildlife poisoning; i.e., only a tiny fraction of poisoning events are estimated to be detected (5–15 % of cases; Berny, 2007; Cano et al., 2016; European Union, 2018; de la Bodega et al., 2020). This is mainly owing to the sensitive and cryptic nature of illicit activities (Nuno et al., 2013; Gavin et al., 2010; Mateo-Tomás et al., 2012), as well as the difficulty to find poisoned animals despite its active search (e.g. surveillance and search with dogs and rangers, or monitoring the movements of animals equipped with tracking devices: GPS/GSM or satellite; Murgatroyd et al., 2019; Stoyanov et al., 2019; Deák et al., 2020; de la Bodega et al., 2020). Moreover, once the poisoned animals and/or baits are found, there are analytical limitations detecting toxic substances in the carcasses and difficulties in unequivocally assigning the cause of death by poisoning (e.g. fresh corpses are usually required; Berny, 2007; Kohler and Triebeskorn, 2013). The high cryptic mortality of undetected poisoned wildlife jeopardizes an adequate fight against this threat. Although much effort has been put into addressing the problem of illegal killing (e.g. the EU has invested >70 million euros in 43 LIFE projects including measures to fight against wildlife crime, 28 of which dealt with poisoning; European Union, 2018), our understanding of the real dimension of wildlife poisoning is still limited.

For approaching the real magnitude of illegal wildlife poisoning and identifying key drivers affecting it, we conducted a large-scale field experimental study in the Iberian Peninsula: a major biodiversity stronghold in Europe (IUCN, 2010; see also Appendix S1.1) and an area where poison use is relatively common (de la Bodega et al., 2020),

affecting to endangered species (Mateo-Tomás et al., 2020). By combining camera-trapping with simulated baits (590 baits across 25 areas; Fig. 1), we assessed the number and identity of the species susceptible of poisoning by consuming poison-laced baits and quantifying their degree of exposure through determining frequencies and relative abundances of consumption, as well as factors driving it (bait and habitat characteristics). Because many species in an assemblage are often rare (e.g. small population sizes or distributions), they can remain undetected and, as a result, samples of species are mostly incomplete (Magurran and McGill, 2011; Chao et al., 2014). Here, we apply statistical techniques based in Good–Turing theory (Chao et al., 2014; Chao et al., 2017), in order to estimate the richness of species of the entire assemblage (i.e. observed plus undetected) consuming simulated baits and thereby gaining a better picture of the real number of species susceptible of poisoning.

2. Materials and methods

2.1. Study area

We conducted the study in 25 areas across two countries (Spain and Portugal), covering a sampled extension of >8375 km² (Fig. 1) (see more details in Appendices S1 and S2, Table S2.1). The study areas represent the main socio-ecological systems where poisoning cases have been reported in the Iberian Peninsula, and which are often related to human-wildlife conflicts that can trigger the use of poison: areas of free-grazing livestock overlapping with large carnivores, hunting areas with predators of small game species, and farmlands with presence of crop-damaging species (de la Bodega et al., 2020; Santos et al., 2020).

2.2. Monitoring of simulated baits

We used camera traps to monitor 618 baits across 25 areas of the Iberian Peninsula (Fig. 1; see more details in Appendix S1). After removing those baits with incomplete information on consumption or malfunction of the camera-trap (see below), 590 baits were available for analyses. We selected the type of baits according to those more frequently recorded in illegal wildlife poisoning events in two Iberian countries and elsewhere, i.e. mostly meat of varying size and large carcasses (European Union, 2018; Barosa et al., 2020; de la Bodega et al., 2020). Specifically, we used 5 different types of baits: i) small meat pieces (i.e. sausages, meat and grease), ii) chicken carcasses, iii) guts, iv) remains of entire bodies, v) entire bodies (Table 1), which account for 75 % of the typologies of baits recorded in wildlife poisoning events (European Union, 2018; Barosa et al., 2020; de la Bodega et al., 2020).

The smaller baits (i.e. small meat pieces and chicken carcasses, <1.2 kg) were experimentally placed in 23 (92 %) and 24 (96 %) of the study areas, respectively ($N = 371$, Fig. 1). By default, and within the same area, the simulated baits were laid 1–3 km apart from each other to increase as much as possible the independence of samples based on the home ranges of terrestrial species observed frequently at carcasses, like the red fox *Vulpes vulpes* (2–6 km²; i.e. 0.8–1.4 km radius; Cavallini, 1996; Dekker et al., 2001) or martens *Martes* spp. (Zalewski et al., 2004; Wereszczuk and Zalewski, 2019). However, in some cases, it was not possible due to presence of rivers, gorges, fences..., and were placed <1 km apart (46 of 371; 12 %). In these cases, we separated them by geographic landmarks that could limit the movement of wildlife (e.g. different valleys, rivers or slopes separated by mountain tops). Baits were disposed within 500 m of dirt roads, trails, or footpaths, as these are frequently used by poachers to access natural areas (de Matos Dias et al., 2020). We placed baits >500 m away from urban settlements, because we can reasonably assume that illegal offenders would avoid places where their activity could be observed by others. The baits were weighted using portable scales and monitored with camera traps during at least 7 days to record all the species consuming them (see more details in Appendix S1.2).

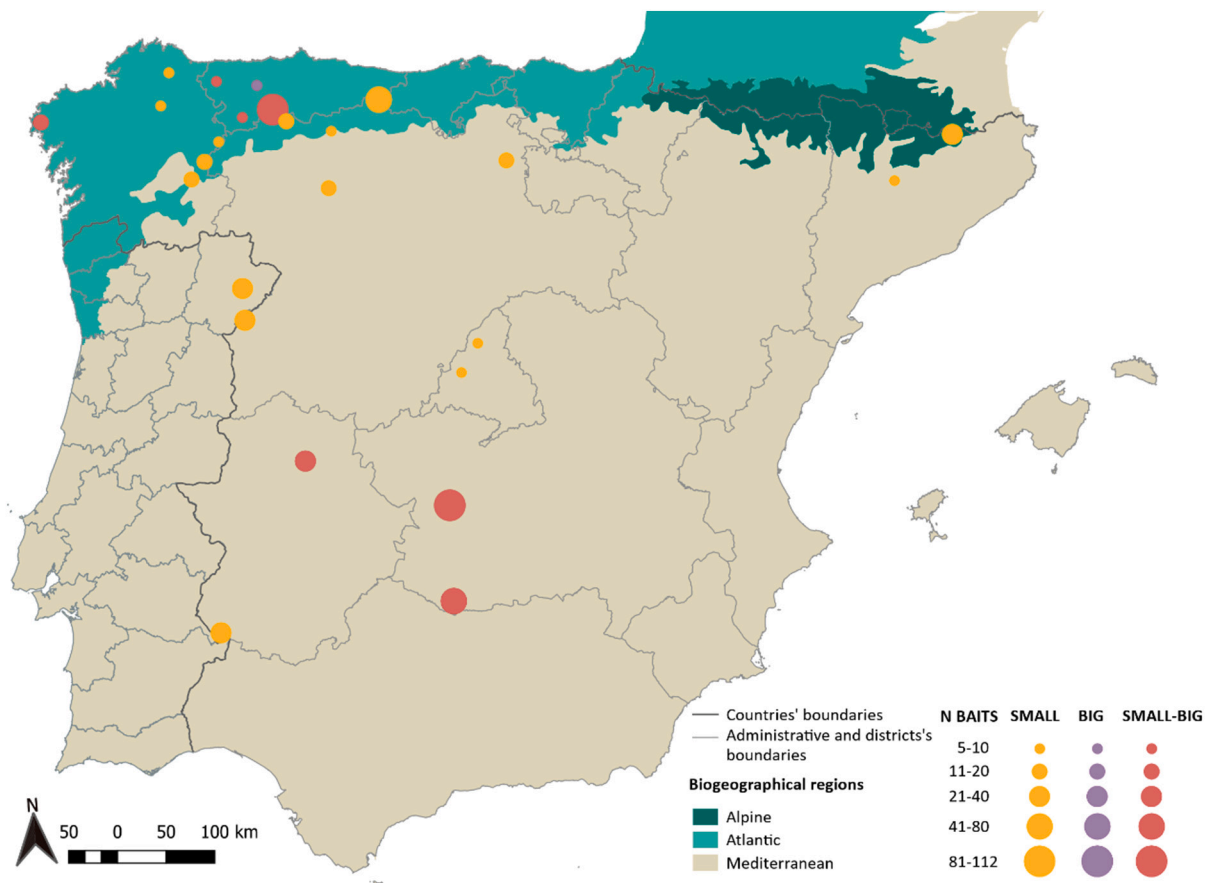


Fig. 1. Map of the Iberian Peninsula (Spain and Portugal) with the 25 study areas (points) where the simulated baits were monitored with camera traps to record the species consuming them, as a proxy of animal poisoning. Size of the circles is proportional to the sample size (number of baits) and colors denote the size of the bait: small (<1.2 kg), large (≥ 2 kg) or both (30 g–650 kg). Different colored areas on the map denote the biogeographical regions. Administrative boundaries of the regional governments in Spain and Portugal are shown.

Table 1

Number of species and individuals consuming the simulated poisoned baits ($N = 590$) placed in 25 study areas in Spain and Portugal. Mean species richness, total number of individuals and mean abundances at each bait type are also shown.

	Bait type	Study areas	Number of total baits (%)	Number of unconsumed baits (%)	Weight (g) mean \pm SE (min-max)	Species observed (min-max)	Species richness mean \pm SE (min-max)	Total number of individuals (%)	Abundance mean \pm SE (min-max)
Small	Small meat pieces	23	158 (26.8)	24 (15.2)	108 \pm 4.9 (30–269)	21 (0–4)	1.24 \pm 0.07 (0–4)	249 (8.0 %)	1.58 \pm 0.12 (0–11)
	Chicken carcasses	24	213 (36.1)	11 (5.2)	389 \pm 14.8 (112–1200)	29 (0–7)	1.46 \pm 0.06 (0–7)	437 (14.2 %)	2.05 \pm 0.14 (0–16)
	Guts	5	137 (25.4)	1 (0.7)	12,312 \pm 674 (2000–45,000)	25 (0–7)	2.54 \pm 0.13 (0–7)	1095 (36.7 %)	7.99 \pm 0.75 (0–61)
Large	Remains	6	37 (6.9)	0 (0)	34,526 \pm 3848 (7700–90,000)	22 (1–7)	3.05 \pm 0.27 (1–7)	415 (13.9 %)	11.22 \pm 1.65 (1–45)
	Entire bodies	4	45 (8.3)	0 (0)	97,922 \pm 1964 (6000–650,000)	21 (1–8)	3.96 \pm 0.27 (1–8)	899 (30.1 %)	19.98 \pm 2.94 (1–99)
	Total	25	590	36 (6.1)	12,752 \pm 2007 (30–650,000)	39 (0–8)	1.94 \pm 0.06 (0–8)	3095	5.25 \pm 0.38 (0–99)

In 8 out of the 25 study areas (32 %; Fig. 1), we also monitored large baits, comprised of guts, entire bodies, or remains of entire bodies (remains hereafter) of livestock and hunted wild ungulates ranging between 2 and 650 kg (Table 1). These baits were camera-trapped until total consumption or until only skin and bones remained (see more details in Appendices S1.2 and S2).

A species was considered as consuming a bait whenever the pictures taken provided unequivocal proof of consumption. When consumption of a bait by a species was suspected (e.g. an individual closely inspecting the bait) but not clearly recorded, we assumed consumption whenever

that species was recorded feeding on another bait of the same type in the study areas (see details in Mateo-Tomás et al. (2017)). Species abundance per bait was calculated as the number of individuals of a given species simultaneously appearing in the picture with the highest number of individuals of that species on that particular bait (i.e. minimum abundance). Individuals with clearly distinct marks, fur patterns, or body sizes were also counted if appeared in different pictures at the same bait (see Mateo-Tomás et al. (2017) for additional details).

We placed baits considering two seasons, spring-summer (March–September) and autumn-winter (October–February). Small meat pieces

and chicken carcasses were placed in 2019–2021. Large baits were set in 2011–2019. We recorded the habitat within 25 m around each bait by classifying it as i) forest, ii) dense tall shrub (>1 m height (tall shrub, hereafter), or iii) open, i.e. sparse low shrub (<1 m high) and/or pasture (shrubland-pasture, hereafter), since these vegetation structures are known to influence the species that locate, access and consume carcasses in the field (e.g. Pardo-Barquín et al., 2019; Turner et al., 2017).

2.3. Data analyses

For each species recorded consuming the simulated poisoned baits, we calculated the frequencies of bait consumption, as the number of consumed baits relative to the total number of monitored baits. Similarly, we calculated relative species abundances, as the minimum number of individuals of a given species recorded consuming baits relative to the total number of individuals of all species recorded consuming all the monitored baits. We also calculated the species richness and minimum abundance per bait (see Appendix S1 for further details).

In the species assemblages recorded at the baits, we calculated the sample completeness (ratio of observed species/true species richness) and sample coverage (proportion of the total number of individuals in the entire assemblage represented in the detected species of the sample), and compared species richness across the five types of baits through estimating coverage-based interpolation and extrapolation sampling curves of Hill numbers (see Chao et al. (2014), Hsieh et al. (2016)). Confidence intervals around the richness estimates were computed through 999 bootstrap replications using the “iNEXT” package in R Core Team (2020). From the observed species frequency, we estimated the species richness of the entire assemblages (i.e. observed plus undetected) (Chao, 1984; Chao and Jost, 2015; Chao et al., 2017).

To test for differences in species richness and abundance among bait types, we built Generalized Linear Mixed Models (GLMMs) with richness and abundance at each monitored bait as response variables. As explanatory variables, we fitted the weight and type of bait (i.e. taking 5 levels: sausages and small meat pieces, chicken carcasses, guts, remains and entire bodies), the type of habitat (3 levels: forest, tall shrub, and small shrub and pasture) and the season (2 levels: spring-summer and autumn-winter). The study area (25 levels) was included as a random factor in all models. We used a Poisson error distribution for modeling species richness, and a negative binomial error distribution for the abundance of individuals, as these error types fit better at each of the two types of response variable. We tested all the two-way interactions of the explanatory variables. We performed all the possible models with the explanatory variables and compared them through AICc using “MuMIn” package. We then fitted an averaged model with all the best models within delta AICc <2 (Bartón, 2020). We considered significant effects of the variables with p -values <0.05. GLMMs were performed using the “lme4” (Bates et al., 2015) package in R software (R Core Team, 2020).

We analyzed the variation in the species composition at each type of bait through distance-based redundancy analyses (dbRDA; Legendre and Anderson, 1999) and PERMANOVA (Anderson, 2001; McArdle and Anderson, 2001). We built a matrix with species in columns and type of bait per area in rows (i.e. 60 rows as not all the bait types were present in all the 25 areas; see above). The value of each element in row i and column j of this matrix was the frequency (i.e. number of baits consumed by a species from the total placed per type and study area) or the presence/absence of each species at all the baits of the same type placed in a study area. By building another matrix of explanatory variables, we tested the effects of the type and weight of bait, type of habitat and season on the species' compositional variation. The bait weight was averaged for all the baits of the same type placed in a given area. As dissimilarity index, we used Bray Curtis for frequency data and Jaccard for presence/absence data. We plotted the best two dimensions (axes) from the dbRDA. To do this, we used the “vegan” package (Oksanen

et al., 2020) in R software.

3. Results

3.1. Species richness and abundance at simulated poisoned baits

We recorded a total of 3095 individuals from 39 species of vertebrates in the 590 simulated baits finally analyzed in this study (Table 1). Estimates of the sample completeness showed that we detected around 83 % of species of the entire species assemblage (observed plus undetected) associated with meat baits: 39 observed of 47 (39–68, 95 % IC) species asymptotically estimated. The sample coverage accounts for the 99.7 % of the individuals in the assemblage; that is, only about 3 in 1000 sampled individuals would belong to rare species undetected (Appendix S3, Fig. S3.1a).

Indeed, the empirical estimate when extrapolated to double the total number of sampled individuals (i.e. 6190 individuals) was of 44 species (37–51; 95 % CI; Appendix S3, Fig. S3.1a). Regarding each bait type, the sample completeness ranged from 58 % (guts, sample coverage: 99.5 %) to 95 % (remains and entire body, 99.3 % and 99.7 %, respectively) (Appendix S3, Fig. S3.1b). Applying the same sample coverage (i.e., 98.8 %) to all the types of bait would yield higher species richness at chicken carcasses ($N = 30$) and small pieces ($N = 25$) than at remains ($N = 21$), guts ($N = 20$), and entire bodies ($N = 17$) (Table 1, Appendix S3, Fig. S3.1b).

At least 94 % of the baits were totally consumed by vertebrates, i.e. only 6 % (36) of the monitored baits were estimated to be unconsumed (Table 1). Between one and eight species were recorded consuming a single bait (mean ≈ 2 species/bait) (Table 1). The mean abundance of individuals per bait was 5.3 individuals (range = 0–99 individuals). The mean number of species recorded consuming the baits varied with the type of meat bait (Table 1), with the highest number of species being observed in entire bodies, and the lowest one in small pieces (Table 1). Yet, the first best model explaining the variation of species richness showed that the number of species potentially poisoned by consuming a given bait increased with the bait weight, irrespective of the bait type (GLMM, $\beta = 0.18 \pm 0.02$ (standard error, SE); χ^2 Wald test: 10.4, $p < 0.001$; model weight = 0.30) (Fig. 2a; Appendix S4, Table S4.1). There was not statistical evidence to support a non-linear (quadratic) relationship of the bait weight on species richness (GLMM: $\beta = -0.003 \pm 0.006$, Wald test: -0.50 , $p = 0.62$; AICc = 1735.2 vs 1736.9). Bait weight explained 16.7 % of the variation in number of species, while the study area (as random factor) accounted for 3.9 %. The averaged model included, besides the bait weight ($\beta = 0.17 \pm 0.02$, $p < 0.001$), season and the interaction season \times weight, yet these two effects were not statistically significant (season: $p = 0.19$, season \times weight: $p = 0.33$) (Appendix S4, Table S4.3).

Concerning the abundance of individuals, the three equivalent best models (delta <2AICc) retained the interaction between the weight of the bait and the habitat (Appendix S5, Table S4.2). The first and third best models included also the variables season and type of bait, but their effects were not significant (Appendix S4, Table S4.4). The averaged model showed a positive effect of the weight of the bait on the mean abundance of individuals in the three habitat types (slopes: $\beta_{\text{shrubland.pasture}} = 0.43 \pm 0.03$ (SE); $\beta_{\text{forest}} = 0.31 \pm 0.05$, $\beta_{\text{tall.shrubland}} = 0.31 \pm 0.06$; $p < 0.001$ in all cases) (Fig. 2b) (Appendix S4, Table S4.4). The increase of abundance with bait weight was significantly higher in more open habitats, i.e. steeper slopes for shrubland-pasture than for forest ($p < 0.001$) and tall shrubland ($p = 0.036$); the slopes of forest and tall shrubland did not differ ($z = 0.10$, $p = 0.92$) (Fig. 2b; Table S4.4). The model including the significant variables weight of the bait, habitat type and its interaction explained 42.6 % of the variation in abundance of individuals at the baits, from which 40.7 % was explained for the fixed effects of bait weight and type of habitat and 1.85 % for the study area effect (random effect).

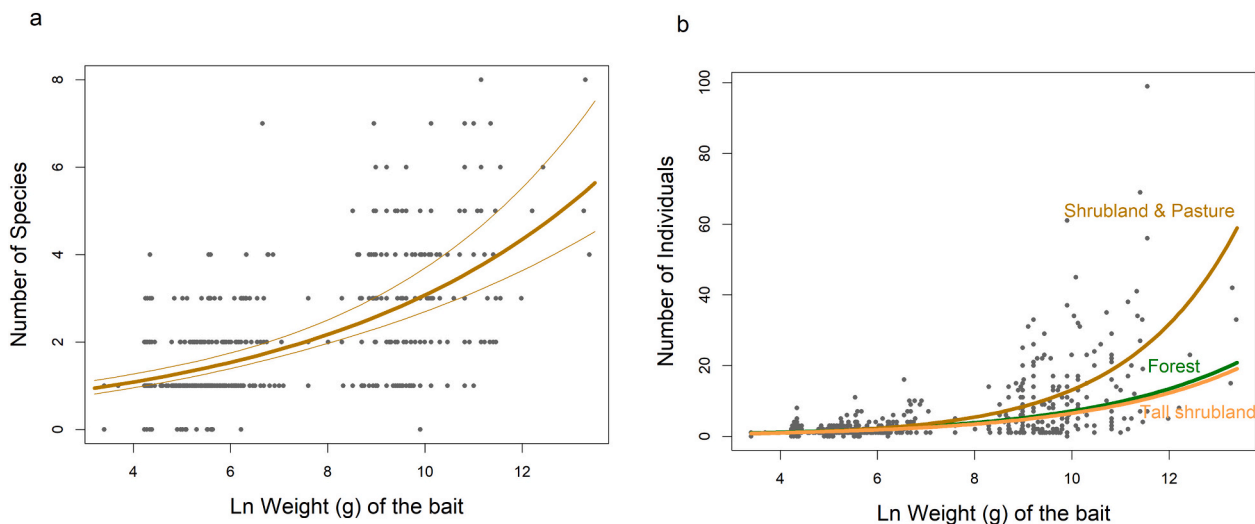


Fig. 2. a) Plot of species richness as a function of bait weight. The only significant variable explaining the number of species at the baits was their weight (16.7 % of the variance explained). Points are observed data. The thick line shows the mean prediction of the averaged GLMM fitted with the best models included within ΔAIC_c , and the two thin lines indicate its 95 % confidence interval. b) Number of individuals consuming the meat baits as a function of the weight of the bait in different habitats. The weight of the bait and the habitat, the only variables significant in the GLMM, explained 40.7 % of the number of individuals recorded at the baits. Points are observed data. The lines show the mean predictions for the weight of the bait in each habitat estimated by the averaged GLMM fitted with the best models included within ΔAIC_c (Table S1).

3.2. Species composition at simulated poisoned baits

More species of birds (22; 56 %) than mammals (15; 38 %) were detected in the simulated baits, whilst reptiles only contributed with 2 species (5 %; a lizard and a snake) (Fig. 3 and Appendix S5, Fig. S5.1). The red fox was by far the species most frequently recorded consuming the baits, being detected in almost half of the total sample (49 %). Common raven *Corvus corax*, griffon vulture *Gyps fulvus*, *Martes* spp., mice, carrion crow *Corvus corone* and wild boar *Sus scrofa* were recorded consuming baits at frequencies ranging from 10 % to 20 %. Five species showed frequencies between 5 % and 9 % (Fig. 3a). The remaining species recorded consuming monitored baits were present in <5 % of the baits (Fig. 3a and Appendix S5, Fig. S5.1a).

In terms of abundance, griffon vulture was the most abundant species (42 % of the total individuals recorded consuming the monitored baits), followed by the red fox (11 %) and raven, carrion crow, and wild boar (>5 %–10 %) (Fig. 3b and Appendix S4, Fig. S4.1b). A 38 % of species consuming the baits were listed as threatened or near threatened ones (33 % were listed after national list, Real Decreto 139, 2011; Cabral et al. (2005) and 18 % according to the IUCN red list, IUCN, 2021; Fig. 3 and Appendix S4, Fig. S4.1). Although most species consumed all the different types of baits, their relative use varied among bait types (Fig. 3 and Appendix S4, Fig. S4.1).

The two first axes of the dbrDA using frequency data explained 17.4 % (full model, $R^2_{\text{adjusted}} = 32.3$ %) of the compositional variation of species across areas and types of baits (first axis: 13.3 %, $F_{1,50} = 9.33$, $p = 0.001$; second axis: 3.9 %, $F_{1,50} = 2.69$, $p = 0.47$). The first axis clearly separated the species assemblages of small from larger baits (Fig. 4a). The PERMANOVA analyses revealed that this difference in species assemblages was indeed driven by the type of meat bait ($F_{4,50} = 1.51$, $p = 0.04$; explained variance = 8.4 %) and habitat ($F_{2,50} = 1.58$, $p = 0.08$; explained variance = 4.4 %). The weight of the bait explained an additional marginally significant portion of the variation in species composition ($F_{1,50} = 1.83$, $p = 0.07$; explained variance = 2.5 %). Species such as mice and *Martes* spp. were associated with smaller baits placed in closed habitats, while vultures, raven, wolf *Canis lupus signatus* and brown bear *Ursus arctos* did so with larger baits in open habitats; wolf and raven were associated with guts and remains, and vultures with entire bodies (Fig. 4a and b). These results were further supported by

post-hoc tests (PERMANOVA; Appendix S6, Table S6.1). Compositional differences were only found between small (small pieces of meat and chicken carcasses) and large (guts, remains and entire body) baits, and between open and the other two habitat types (forest and tall shrubs) (Appendix S6, Table S6.1 and S6.2). Season had not a significant effect on the species compositional variation ($F_{1,50} = 1.31$, $p = 0.18$). The dbrDA with data of incidence (presence/absence) provided very similar results (results not shown).

4. Discussion

We empirically demonstrated that a remarkable diversity of vertebrate species (39 observed, 47 predicted) is prone to illegal poisoning in the Iberian Peninsula and that a high proportion of baits placed in the field are consumed by wildlife (94 %). This set of species potentially impacted by poison represents about 5 % of the total richness of birds, mammals, and reptiles in Spain (Morales and Lizana, 2011) and includes different functional and trophic groups (vultures 8 %, raptors 25 %, large carnivores 5 %, mesocarnivores 21 %, corvids 13 %, rodents 8 %, reptiles 5 %), as well as many species listed as threatened (38 %). This assemblage of species is prone to poisoning to varying extents by their scavenging habits (Fig. 3). Scavenging is known to be widespread in vertebrates from different trophic levels across the planet (up to 3700 species of facultative scavengers; Olea et al., 2019) and, as a result, a significant amount of biodiversity is potentially exposed to the widespread threat of illegal wildlife poisoning. The cascading effects of poisoning-driven defaunation (Dirzo et al., 2014; Ripple et al., 2014) on ecosystem functioning, although expected, remain yet largely unknown (e.g. Ogada et al., 2012).

Our results also indicate that the potential damage of a given bait in terms of the number of species and individuals affected relied on the weight of the bait and the habitat where was placed. The relationships we found between the structure of the assemblage (species richness and abundance) and the characteristics of the monitored baits are consistent with empirical evidence of vertebrate scavenging (e.g. DeVault et al., 2004; Moleón et al., 2015; Turner et al., 2017; Pardo-Barquín et al., 2019). Both a longer time available and higher detectability associated with larger carcasses would enable more species and individuals to gather at them (DeVault et al., 2004; Turner et al., 2017), and thus, as

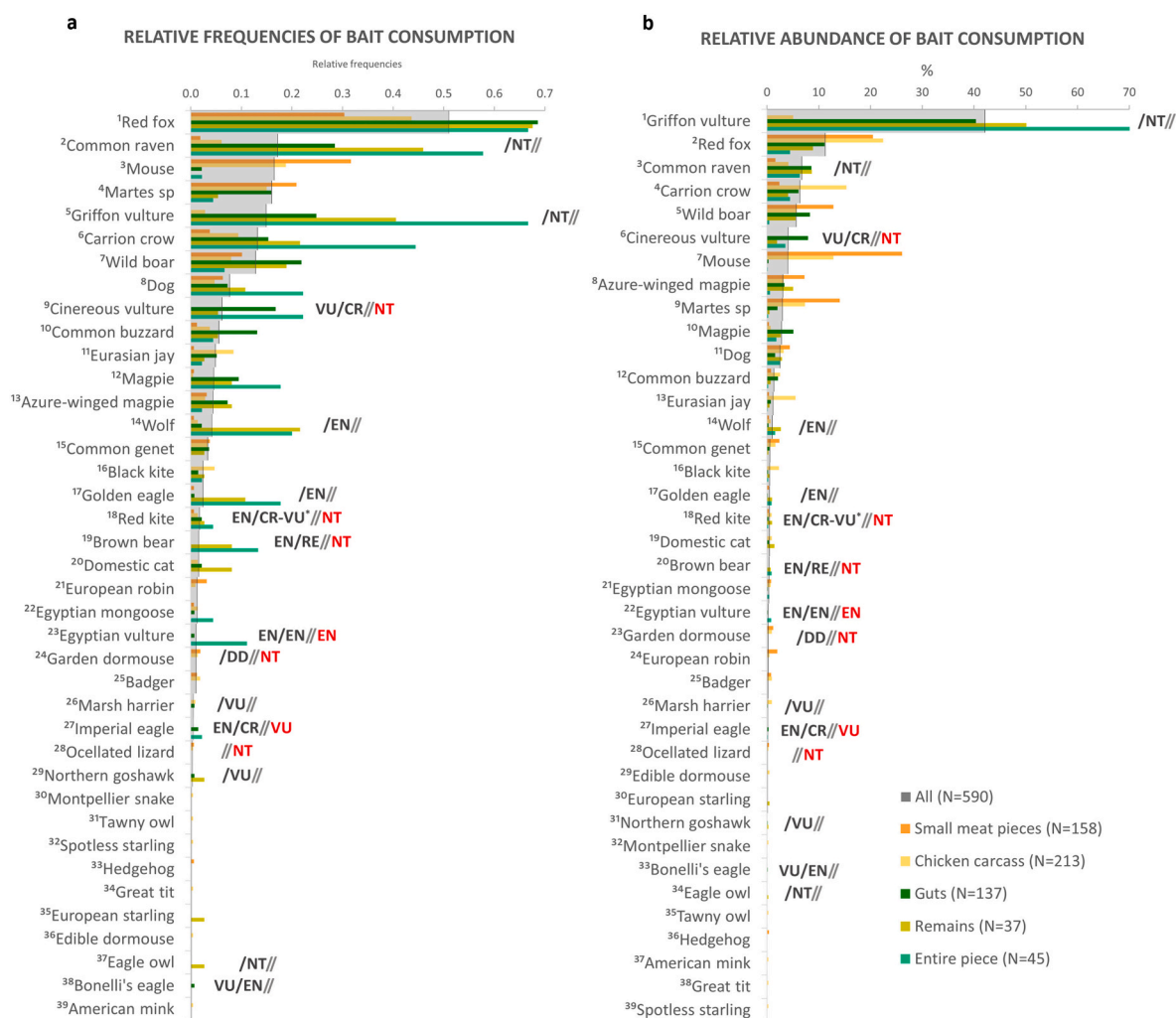


Fig. 3. a) Frequencies of species incidence/occurrence (No. occurrences of species i / No. total baits) in each type of meat bait. Species are ordered ranging from the highest to the lowest frequency of occurrence (correlative numbers in each species indicate that order). Frequencies are calculated for the same type of bait across species. Wide grey bars represent frequencies of occurrence of each species considering all the baits together ($N = 590$); b) Relative abundance (%) of species consuming different types of bait. Species are ordered ranging from highest to lowest relative abundance. Relative abundances were calculated independently for each type of bait across all the recorded species (i.e. n in $\sum_{i=1}^n$ percentage $i = 100$). The wide grey bars represent the relative abundance of each species considering all the baits together ($N = 590$). Bold capital letters after bars indicate the species' conservation status according to national legislation and/or red list (in black before the slash for Spain and Portugal respectively; Real Decreto 139, 2011; Cabral et al., 2005), while red capital letters after the double slash show globally threatened species (IUCN, 2021). *Martes* spp. includes *M. foina* and *M. martes*.

CR: Critically Endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least Concern; DD: Data Deficient; RE: Regionally Extinct. *Denote different status for the wintering and breeding red kite *Milvus milvus* population in Portugal. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

expected, the weight of the bait was the most relevant factor driving species richness and abundance at the baits. Additionally, the identity of the species poisoned also changed with the weight of the baits, likely because large carcasses are usually exploited and dominated by large vertebrates, especially vultures (Moleón et al., 2015; Mateo-Tomás et al., 2017; Pardo-Barquín et al., 2019), whilst small carcasses are first detected by small and medium vertebrates, thereby having a competitive advantage for exploiting them (DeVault et al., 2004). Some of these relationships were also partially modulated by the habitat surrounding the baits (Turner et al., 2017; Pardo-Barquín et al., 2019).

Beyond their ecological implications, these results are particularly interesting to offer guidance to cope with the threat of illegal wildlife poisoning on the ground. The statistical models allow us to reliably predict, regardless of the type of bait, the impact of poisoning on both species richness and abundance of individuals at meat baits within a wide range of weights (0.05–650 kg). For example, only by knowing the size of the meat bait, we could estimate the number of species and

individuals being potentially affected in a given poisoning case even if, as expected, not all the species and individuals involved in such event were found. For example, a threefold increase in the bait weight would result in a 21 % increase in the number of species consuming that bait, while increasing the number of individuals by 41–62 % depending on the habitat. Baits placed in open habitats (i.e. short shrubs interspersed with pasture) gathered more individuals than baits placed in forests and tall shrublands, likely because highly-gregarious species such as the griffon vulture and corvids easily access carcasses located in open areas (Pardo-Barquín et al., 2019). The prominent role of the weight of the bait driving richness and abundance is consistent with massive poisoning events at large carcasses in which highly-gregarious species are disproportionately affected (Ogada et al., 2016b; de la Bodega et al., 2020; Méndez et al., 2021b; Elcacho, 2021; African Wildlife Poisoning Database, 2021). Nonetheless, although demographic models show that a lower number of poisoned animals are involved per poisoning event, a higher frequency (as those expected from regular baiting activities for

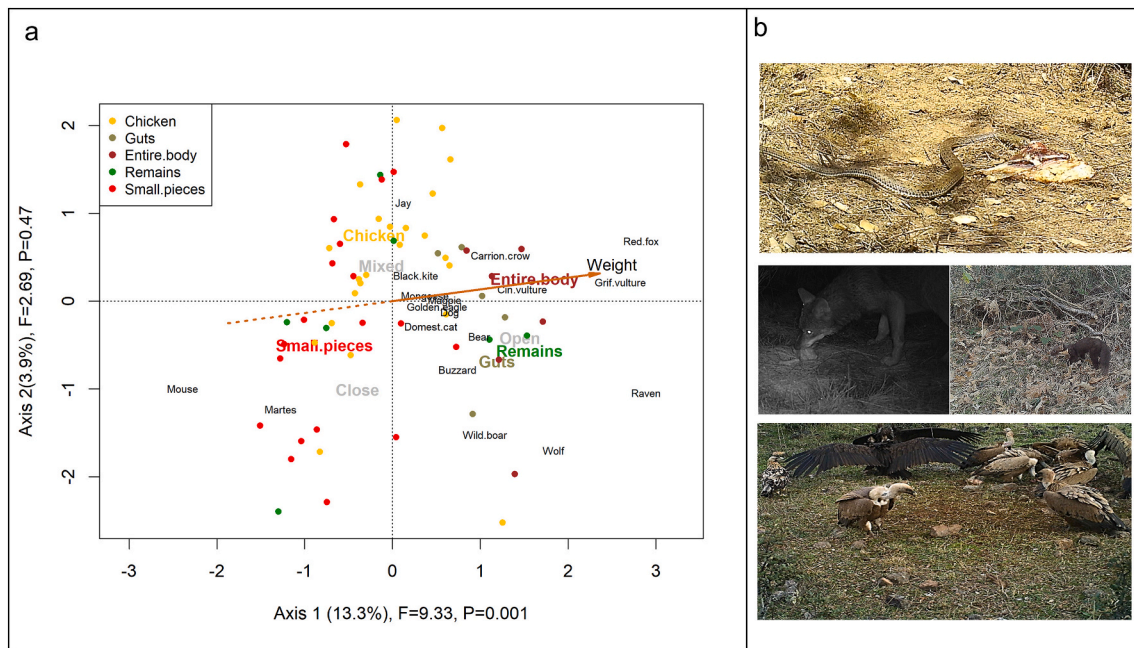


Fig. 4. a) Results of the dBRDA explaining the compositional variation of species recorded in the different types of baits and habitats. Analysis based on Bray Curtis di-similarity index (frequency data). Only species with high loads (>0.10) on the axes are represented. b) Pictures of species recorded in the meat bait study across Spain and Portugal. Fox and griffon vulture (photo) were the most frequent species recorded at the baits. Mice and Marten spp. (photo) were most often recorded at small baits (sausages and chicken) in closed habitats. Vultures, raven, brown bear, and wolf (photo) were associated with larger baits in open habitats; wolf and raven with gut and remains, and vultures with entire bodies. Reptiles such as the Montpellier snake *Malpolon monspessulanus* (photo) was also recorded but in very low frequency.

predator control) could have similar or even more detrimental effects on large avian scavengers than massive, single, and rare poisoning events (Tsiakiris et al., 2021).

But even if the illegal poisoned bait is unknown (e.g. baits were identified only in 17.5 % of the 9750 wildlife poisoning events recorded in the Spanish ANTÍDOTO database in 1993–2017; de la Bodega et al., 2020), our results on the association of species consuming each type of bait might further inform monitoring of illegal wildlife poisoning. Species such as mice, pine and stone martens were more frequently associated with small baits in closed habitats, whilst vultures, raven, wolf, and brown bear were most likely to occur at larger carcasses located in open habitats. From this kind of information, one might infer from the poisoned species found in a place, the type of bait used and even the conflict underlying this illegal practice (Mateo-Tomás et al., 2012; Cano et al., 2008). This information along with the knowledge on the behavior of poachers (Gavin et al., 2010; Nuno et al., 2013) when placing the baits might improve monitoring and surveillance of wildlife poisoning.

We recorded about 3100 animals from 39 species consuming at least 94 % of the 590 monitored baits, but these huge amounts of fauna potentially affected by illegal poisoning could be higher if secondary poisoning (i.e. when an animal feeds upon another poisoned animal; Brakes and Smith, 2005) is taken into account. Our results show that small rodents consumed small baits at relatively high frequencies (i.e. 32.3 % of small pieces and 21 % of chicken carcasses) and abundances (i.e. 26 % of small pieces and 14 % of chicken carcasses), suggesting a role in secondary poisoning of mesocarnivores and raptors that could prey or scavenge upon these or other poisoned species (Fig. 3; Appendix S5, Fig. S5). Indeed, nocturnal raptors and mammalian carnivores are among the functional groups most affected by secondary poisoning (Sánchez-Barbudo et al., 2012).

Although there were a few species highly ubiquitous at our baits (e.g. red fox, griffon vulture and common raven; Fig. 3), most of them occurred in a few baits and with low relative abundance, showing a pattern of long-tailed distribution. As a result, some sampling curves did not stabilize (Appendix S3, Fig. S3.1) even though we monitored 590

baits, and thereby estimates of asymptotic richness represent a minimum species richness (e.g. 47 species for the entire assemblage: observed plus undetected; Chao et al., 2014, 2017). Consequently, it is expected that rarer species at baits are likely to appear in the assemblage with increasing sample size. For example, in our study we did not detect several species susceptible to consume baits, such as bearded vulture *Gypaetus barbatus*, wild cat *Felis sylvestris*, Iberian lynx *Lynx pardinus*, least weasel *Mustela nivalis*, European polecat *Mustela putorius*, and yellow-legged gull *Larus michahellis*. Nonetheless, our extensive study shows that the 39 species we have detected represent 99.7 % of the individuals of the entire assemblage; and thus only 0.3 % would be individuals of undetected species. Therefore, our comprehensive study covering a wide array of sites and types of meat baits would closely reflect the actual magnitude of the biodiversity potentially affected by poison. Furthermore, our study encompassed 25 study areas, which by including them as a random effect in our statistical models, allow robust generalizations to be made of our results (i.e. bait weight and habitat type as underlying factors driving species richness and abundance across areas), while minimizing effects of others non-controlled factors (e.g. among-site differences in land use and other idiosyncratic features of the study areas). Additionally, the major role we found for the weight and type of bait driving richness and composition of species, as well as abundance of individuals (Figs. 2 and 4), advocates for considering all these underlying factors driving the presence and abundance of species in future studies to avoid biased results. For example, studies using only small baits have underestimated the number of vertebrate species prone to be affected by poisoning (26 species recorded at baits of 50–100 g, Gil-Sánchez et al., 2021). Moreover, our results show that habitat acts also as an ecological filter selecting particular species consuming the baits, and thereby this factor would also distort results if overlooked.

Overall, our results are in accordance with evidence showing illegal poisoning as a major driver of wildlife population declines of threatened species such as large vultures, raptors and carnivores around of the world (e.g. Ogada et al., 2016a; European Union, 2018; Mateo-Tomás et al., 2020; Méndez et al., 2021a). Moreover, our approach provides

further insights useful to ascertain the real magnitude of poisoning events. It can help managers to estimate the number of species susceptible to poisoning, as well as their relative abundances and their relationships with characteristics of the bait and habitat to improve the actions against wildlife poisoning, being especially useful in broad regions of the world where poisoned fauna databases are hardly available.

Likewise other illicit human activities, wildlife poisoning is multifaceted and difficult to tackle owing to its cryptic nature, therefore resulting in very low levels of detected cases (Berny, 2007; Cano et al., 2016; European Union, 2018; de la Bodega et al., 2020), and thus challenging the ability to reach effective solutions through, for example, prevention or prosecution. Our results enable to improve the understanding of the extent to which poisoning affects wildlife while providing guidance to reduce the bias and uncertainty associated to monitoring the real impact of these cryptic practices on biodiversity.

CRediT authorship contribution statement

PPO: conceived the idea and conceptualized the study. PMT, JVLB, JV and PPO: designed the field survey, which was coordinated by PMT. All authors performed field work. PPO analyzed the data and MFG and PMT assisted in them. PPO: lead the writing with contributions of PMT, MFG, JVLB, JPVS and JV.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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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.2022.109702>.

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