HUMAN-SCAVENGER RELATIONS: FROM CONSERVATION CHALLENGES TO CONTRIBUTIONS TO PEOPLE

RELACIONES ENTRE HUMANOS Y CARROÑEROS: DE LOS RETOS DE CONSERVACIÓN A LAS CONTRIBUCIONES A LAS PERSONAS

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A mis padres, hermanos,
a mi abuelo Serafín.

CONTENT

ABBREVIATIONS AND ACRONYMS

CCA	Canonical Correspondence Analysis
GBIF	Global Biodiversity Information Facility
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IUCN	International Union for Conservation of Nature
HF	Human Footprint
NCP	Natures' Contribution to People
PA	Protected Areas

Summary / Resumen

Photo by Pilar Oliva Vidal.
Bearded vulture (*Gypaetus barbatus*) in Pre-Pyrenees of Lleida.

SUMMARY

Human activities are the main driver of global change in the Anthropocene, being responsible for the loss of biodiversity at a global scale. The loss of biodiversity alters the ecosystem functions, impacting on the contributions that nature provides to people, which condition human wellbeing. One of the most threatened functional groups are scavengers, which are related to important regulating functions in ecosystems. This thesis focuses on how human activities affect the conservation of scavenger species, whilst at the same time, delving into the multiple benefits derived from human-scavenger relations. In particular, this thesis aims to assess the following points: the response of scavenger birds to transhumant livestock activity (Chapter 1); the potential biases in the detection of poisoned wildlife (Chapter 2); the role of scavenger species in nature's non-material contributions to people (Chapter 3); and the spatial patterns that determine the provision of non-material contributions (Chapter 4).

Chapter 1 assesses the changes in the abundance of scavenger birds according to the presence of transhumant livestock, in addition to the changes in the foraging behaviour of griffon vultures (*Gyps fulvus*). For this purpose, we conducted field surveys to monitor changes in the abundance of scavenger birds and ungulates according to the season with presence and absence of livestock in a pastureland area of southeaster Spain where transhumant activity is still preserved. In addition, we tracked 30 griffon vultures by GPS devices, which allowed us to analyse their foraging activity in both seasons. In the presence of the livestock, there was an increase in the abundance of obligate scavengers, as well as an increase in the foraging activity of the tracked vultures. These results highlight the importance of traditional agrosystems for the conservation of obligate scavengers.

In Chapter 2, a field experiment, in which animals consuming non-poisoned baits were detected by means of camera traps, was conducted in six study areas to assess potential biases in the records of poisoned wildlife. The results were compared with the poisoning records in an official database in Spain. We found that the detection of poisoned wildlife is species-dependent. Domestic animals and vultures tended to be

over-represented in the database relative to those detected in the experiment, while corvids and small wild mammals were underrepresented. The differences were mediated by species traits such as size and colour. These results can provide guidance to improve strategies in the detection of poisoned wildlife.

In Chapter 3, we explored different indicators to assess the role of the scavenger guild in providing non-material contributions to people in Spain. In particular, we assessed the categories of physical and psychological experiences, learning and inspiration, and the supporting identity. In addition, we explored the ecological traits of species that may determine the capacity to provide these contributions. The results showed associations among the categories, mediated by species traits. Four main groups were identified: aesthetic enjoyment experiences and contribution to knowledge through wildlife observation records, related to common species; recreational experiences and contribution to knowledge for society, related to charismatic species; contribution to scientific knowledge, associated with mesocarnivores; and supporting identity, related to species with dual roles, capable of providing both beneficial and detrimental contributions. The use of different indicators allowed to reveal the interlinkages among contribution categories and species. These findings highlight the importance of scavengers in the contributions to the human well-being.

Chapter 4 explores the spatial patterns that determine the provision of non-material contributions in continental Spain. For this purpose, several indicators that assess aesthetic enjoyment experiences, recreational experiences, and contribution to scientific knowledge were mapped, and we calculated hotspots of contributions. In addition, we explored environmental factors that may condition the provision of these contributions: the presence of protected areas, the human impact index, and the richness of scavenger species. We found that protected areas, especially national parks, have a very important role in the provision of non-material contributions by scavengers, as they are preferentially developed in areas with higher species richness. Recreational experiences were associated to areas with low human impact, while aesthetic enjoyment and contribution to scientific knowledge was developed in areas with some degree of humanization.

Finally, the general discussion addresses the implications of the findings in a context of global change. We also discuss the limitations identified, as well as the insights for future research addressing human-nature relations.

RESUMEN

Las actividades humanas son el principal motor de cambio en la era del Antropoceno, responsables de la pérdida de biodiversidad a nivel global. Esta pérdida de biodiversidad altera las funciones de los ecosistemas repercutiendo en las contribuciones que la naturaleza proporciona a las personas, las cuales condicionan el bienestar humano. Uno de los grupos funcionales más amenazado es el de las especies carroñeras, de cuyos procesos ecológicos dependen importantes funciones de regulación en los ecosistemas. Esta tesis se centra en abordar cómo las actividades humanas afectan a las especies carroñeras, al mismo tiempo que profundiza en los múltiples beneficios que se derivan de las relaciones humanas con estas especies. En particular esta tesis pretende evaluar los siguientes objetivos: la respuesta de las aves carroñeras a la actividad ganadería trashumante (Capítulo 1); los potenciales sesgos en la detección de fauna envenenada (Capítulo 2); el papel que desempeñan las especies carroñeras en las contribuciones no materiales de la naturaleza para las personas (Capítulo 3); cuáles son los patrones espaciales que determinan la provisión de contribuciones no materiales (Capítulo 4).

El Capítulo 1 evalúa los cambios en la abundancia de aves carroñeras según la presencia de ganado trashumante junto a los cambios en los patrones de forrajeo de los buitres leonados (*Gyps fulvus*). Para ello, en una zona de pastizales del sureste de España peninsular, donde aún se conserva la actividad trashumante, se realizaron muestreos de campo para contabilizar los cambios en la abundancia de aves carroñeras y de ungulados acorde a la estación con presencia y ausencia de ganado. Además, 30 buitres leonados fueron equipados con emisores GPS, que permitieron analizar el uso del espacio en ambas estaciones. Ante la presencia de los rebaños, se produjo un incremento en la abundancia de las aves carroñeras obligadas, así como un aumento en el forrajeo de los buitres rastreados. Estos resultados ponen de manifiesto la importancia de los agrosistemas tradicionales para la conservación de estas especies.

En el Capítulo 2 se desarrolla un experimento de campo en seis áreas de estudio para testar los potenciales sesgos en los registros de fauna envenenada, en el cual, mediante cámaras de fototrampeo, se detectaron los animales consumidores de cebos no envenenados. Los resultados se compararon con los registros de envenenamiento de la base de datos oficial. Encontramos que la detección de fauna envenenada es especie-dependiente. Los animales domésticos y los buitres tendieron a estar sobrerreprentados en la base de datos respecto a lo detectado en el experimento, mientras que los córvidos y los pequeños mamíferos silvestres estuvieron infrarepresentados. Estas diferencias estuvieron mediadas por las características de las especies, como el tamaño y la coloración. Estos resultados, pueden servir de guía para mejorar las estrategias de detección de fauna envenenada.

En el Capítulo 3, exploramos diferentes indicadores para evaluar el papel del gremio de especies carroñeras en las categorías de provisión de contribuciones no materiales para las personas en España. En particular, evaluamos las experiencias físicas y psicológicas, el aprendizaje e inspiración, y la base para la construcción de identidades. Además, exploramos las características ecológicas de las especies que pueden determinar la capacidad de provisión de estas contribuciones. Los resultados mostraron asociaciones entre las categorías según las características de las especies. Se identificaron cuatro grupos principales: las experiencias de disfrute estético y la contribución al conocimiento mediante los registros de observación de fauna estuvieron relacionados con especies comunes; las experiencias recreativas y la contribución al conocimiento para la sociedad se relacionó con las especies carismáticas; la contribución al conocimiento científico fue asociada a los mesocarnívoros; y la base para la construcción de identidades estuvo ligada a especies con rol dual capaces de proveer tanto contribuciones beneficiosas como perjudiciales. El uso de diferentes indicadores permitió desvelar las interconexiones entre las categorías de contribuciones y las especies. Estos hallazgos ponen en valor la importancia de las especies para las contribuciones al bienestar de las sociedades.

En el Capítulo 4 se exploran los patrones espaciales que determinan la provisión de contribuciones no materiales en España continental. Para ello, se cartografiaron diferentes indicadores que evalúan las experiencias del disfrute estético, las experiencias recreativas y la contribución al conocimiento científico, y calculamos los puntos calientes de provisión de contribuciones. Además, exploramos las características del paisaje que pueden condicionar la provisión de estas contribuciones: la presencia de áreas protegidas, el índice de impacto humano, y la riqueza de especies carroñeras.

Encontramos que las áreas protegidas, especialmente los parques nacionales tienen un papel muy importante para la provisión de contribuciones no materiales, así como se desarrollan preferentemente en áreas con mayor riqueza de especies. Las experiencias recreativas están asociadas a zonas con bajo impacto humano, mientras que el disfrute estético y la contribución al conocimiento científico puede desarrollarse en áreas con cierto grado de antropización.

Finalmente, en la discusión general se abordan las implicaciones de los resultados obtenidos en un contexto de cambio global, las limitaciones encontradas, así como propuestas para futuras líneas de investigación que aborden las relaciones entre los seres humanos y la naturaleza.

General Introduction

Photo by Pilar Oliva Vidal.
Griffon vultures (*Gyps fulvus*) in Pre-Pyrenees of Lleida.

GENERAL INTRODUCTION

HUMAN-NATURE RELATIONS: A CHANGING WORLD

Increasing human development is having a huge impact on the planet, and one of such magnitude that we are witnessing a new geological era: the Anthropocene. The severe transformation of ecosystems, especially in the last 50 years, to supply the growing human population's increasing high demands has brought about a global biodiversity crisis (Foley et al. 2005; Bellard et al. 2012; Hooper et al. 2012). Habitat fragmentation, pollution, invasive species and climate change are some of the main drivers of the global change (Brook et al. 2008) that has resulted in the extirpation of natural populations, and even species, as well as associated ecological functions (MEA 2005; Díaz et al. 2019; Brauman et al. 2020).

In response, this Global Environmental Change has led to growing awareness of and concern about nature conservation. Several international meetings have been held to establish common planetary objectives to curb biodiversity loss, such as the Aichi Targets adopted from the Convention of Global Diversity (Secretariat of the Convention on Biological Diversity 2010), including the ongoing 2030 Sustainable Development Goals of the United Nations. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) was created to reinforce the integration of scientific knowledge into policy decisions about conservation and the sustainable use of biodiversity (IPBES 2019). In the past century, protected areas have been established to prevent their degradation. Currently, designation of protected areas is one of the most frequently implemented conservation strategies (Chape et al. 2005), together with granting legal protection of endangered species for their conservation and recovery in many areas (Chapron et al. 2014; Johnson et al. 2017).

Thus, humans may trigger both negative and positive effects on wild species and ecosystems. Conversely, humans may receive (or perceive) both benefits and detriments from nature. Therefore, biodiversity conservation must be approached from a broad perspective by acknowledging the complexity and interaction among these pathways (Díaz et al. 2018; see Figure 1).

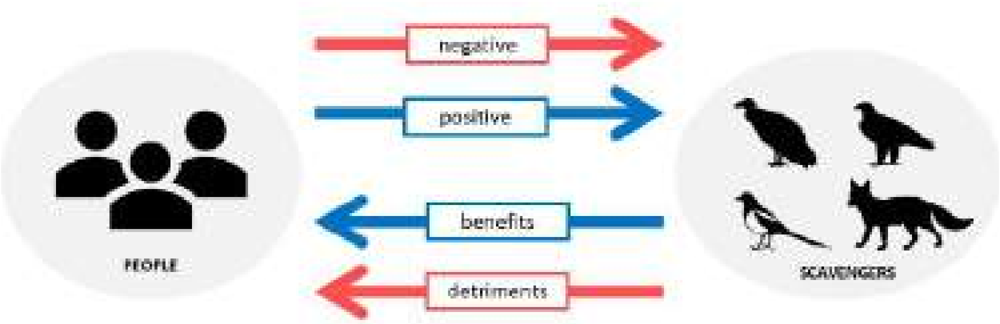


Figure 1. Conceptual map for human-nature relations.

NCP IN A CHANGING WORLD

Given the need to emphasise human dependence on nature, the scientific community has proposed different terminologies. They have evolved into today's nomenclature of Nature's Contributions to People (NCP) (Box 1). NCP is a framework that addresses both the positive and negative effects of living nature on people's quality of life (Díaz et al. 2018). NCP are classified into 18 categories, which are clustered into three main groups: regulating, material and non-material. **Regulating NCP** refer to the ecological processes that sustain environmental conditions for human development and well-being, including both material and non-material contributions (e.g., climate regulation, pollination). **Material NCP** are the physical elements of nature that humans use for consumption (e.g., food, raw materials). **Non-material NCP** are the subjective and psychological effects of nature on human well-being, which comprise the aesthetic enjoyment of nature, recreation experiences, learning and inspiration, and animal or plants that are the basis of spiritual experiences (Díaz et al. 2018). However, NCP categories are not stand-alone because they considerably overlap and are intertwined. They are also context-specific depending on the considered stakeholders (Chan et al. 2016). For example, extensive livestock farmers positively value wild ungulates as alternative prey for the predators that attack their livestock, while researchers do not focus on these positive effects, but on others like the benefits of hunting (Pascual-Rico et al. 2020). The changes in natural habitats in the past century include substantial social changes. A rural exodus to urban areas has taken place in many parts of the world (Parry et al. 2010; Ma et al. 2018; Llorent-Bedmar et al. 2021), which has led to changes in the way we relate to nature (Berenguer et al. 2005). The rural life-urban life dichotomy also affects the perception of nature's contributions (Martín-López et al. 2012).

Box 1. From Nature's Services to Nature's Contributions to People

The many ways in which nature benefit humans have been studied since Westman coined the term *Nature's Services* (Westman 1977). This term resulted from some scientists' emerging concern to adequately define such human dependence on nature given accelerated human population growth and resource exploitation. Shortly afterwards, Ehrlich and Ehrlich (1981) introduced the term *ecosystem services* for the first time. However, it was not until 1997, with the publications of Daily (1997) and Costanza et al. (1997), when this research topic began to flourish. In the Millennium Ecosystem Assessment (MEA) (2005), the term *ecosystem services* (ES) was formalised and defined as the direct or indirect benefits that people obtain from ecosystem functioning. Since then, research on this topic has been on the rise (Costanza et al. 2017). The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) recently established a broader definition of the links between people and nature, termed nature's contribution to people (NCP) (Díaz et al. 2018). This updated conceptualisation considers both the benefits and detriments of living nature for people's quality of life, incorporates indigenous and local knowledge into its assessments, and considers culture to play a transversal role to define the human-nature link. Therefore, the NCP framework allows more integrative analyses than ES to explore complex socio-ecological systems (Dean et al. 2021).

Most research into NCP has focused on material and regulating contributions (Luederitz et al. 2015; Fagerholm et al. 2016; Hevia et al. 2017), whereas non-material contributions are clearly underrepresented in the scientific literature (Daniel et al. 2012; Milcu et al. 2013), which has centred mostly on recreational activities and aesthetic enjoyment (Kosanic and Petzold 2020).

NCP assessments have been made based on numerous indicators. Regulating assessments, such as carbon storage capacity or water regulation, have been assessed by biophysical landscape metrics like land cover (Maes et al. 2016). In these cases, spatial mapping has been a key tool for identifying the provision areas of NCP, which are useful for developing land-use planning and focusing on conservation efforts (Malinga et al. 2015). Some cultural or non-material topics have been addressed by counting users in enjoyment experiences, such as fishing or birdwatching (Maes et al. 2016). Meanwhile according to species distribution, biodiversity-based NCP has been less assessed (Maes et al. 2016) despite being very closely linked with NCP provisions and human well-being (Balvanera et al. 2006; Haines-Young and Potschin 2010; Díaz et al. 2019).

SCAVENGERS IN THE HUMAN SPHERE

Vertebrates have been paid less scientific attention compared to vegetation and invertebrates among the biodiversity groups that have been assessed within an NCP framework, (Hevia et al. 2017). Birds have been identified as providers of all NCP categories (Whelan et al. 2008; Sekercioglu et al. 2016), are an important component of human diet, and also contribute to regulate ecosystems by seed dispersal (Jordano et al. 2007), pest control (Gorosábel et al. 2022) and carrion removal (Moleón et al. 2014a; DeVault et al. 2016). Furthermore, recreational activities like birdwatching have flourished worldwide, and are argued to favour conservation, act as a tool for environmental education, and can even be considered to provide economic local input (Sekercioglu 2002). Regarding mammals, carnivores have predominantly been considered to be detrimental to humans (Lozano et al. 2019; Methorst et al. 2020). Their predatory behaviour has historically been a source of conflict with humans given competition for the same resources (livestock, game animals). But there also many charismatic species (Wolf and Ripple 2018).

The functional guild of terrestrial vertebrate scavengers, which comprises mainly birds and mammals, has also been linked with the provision of all NCP categories (Moleón et al. 2014a; DeVault et al. 2016; O'Bryan et al. 2018), and is closely linked with human well-being. The human-scavengers relation dates back to the Late Pliocene, when early humans followed vultures to find carrions. At the same time, humans competed with scavenging birds and mammals for meat from megaherbivore carcasses (Moleón et al. 2014a; Morelli et al. 2015). Over time, this relation has changed. In a next step, humans became hunters and, thus, providers of hunting leftovers to scavengers. This role as carrion providers expanded with animal domestication, to the point that humans are now the main providers of food for scavenger species in many world regions, especially where native herbivores have been extirpated (Chamberlain et al. 2005; Lambertucci et al. 2009; Margalida et al. 2011a; Lambertucci et al. 2018; Margalida et al. 2018).

Among scavenging species, many birds and mammals exploit carrion opportunistically (facultative scavengers), while vultures are the only ones in terrestrial ecosystems that totally rely on carrion for their survival and reproduction (obligate scavengers) (DeVault et al. 2003). Annually in terrestrial ecosystems, tons of dead biomass are naturally generated (Moleón et al. 2019), and scavengers largely contribute to recirculate this biomass in the ecosystem. Vultures consume large amounts of carrion in very short times (DeVault et al. 2003; Sebastián-González et al. 2016; Morales-Reyes et al. 2017b). This efficient carcass removal performs a regulating function by avoiding long carrion decomposition in the environment, which could otherwise spread infectious diseases, such as anthrax (Den Heever et al. 2021) with negative effects for human well-being. Vultures also have a top-down regulating effect on facultative scavenger populations as they more efficiently compete for carrion resources, which limits access to facultative ones, thus exercising control over their populations (Sebastián-González et al. 2013; Morales-Reyes et al. 2017b). Mammalian scavengers, such as dogs and rats, are reservoirs of zoonotic diseases like rabies, which can have strong detrimental effects on human well-being when their populations increase (Markandya et al. 2008; Ogada et al. 2012b; Den Heever et al. 2021). Top-carnivores also have regulatory top-down effects on ecosystems, whose absence causes a trophic cascade that affects not only herbivores, vegetation and ecosystem dynamics (Boyce 2018; Atkins et al. 2019), but also the structure of scavenger communities (Selva and Fortuna 2007; Moleón et al. 2014b; Sebastián-González et al. 2020).

In addition to the role in ecosystem regulations, scavengers have also been present in cultural spheres of human civilisations. Vultures have taken part in sacred rituals from ancient times, when Neanderthals used avian scavengers feathers and claws as ornaments (Finlayson et al. 2012), and also in current local communities like those in Western and Southern Africa, which employ vulture body parts for traditional medicine purposes (Ogada et al. 2012a; Mashele et al. 2021). Some ethnic groups, such as the Zoroastrians and Tibetan Buddhists, continue to offer the corpses of their dead to scavenger birds as part of their religious practices (DeVault et al. 2016). In addition, ecotourism related to scavenger watching is globally flourishing, and provides a human-wildlife connection that can help to raise awareness of the species conservation of both avian (DeVault et al. 2016) and mammalian (Montag et al. 2005) scavengers. Moreover, economic valuations related to scavengers watching, such as that of Becker et al. (2005) in Israel and García-Jiménez et al. (2021) in the Spanish Pyrenees, point out that this activity provides considerable economic inputs to these areas.

Scavengers can be perceived by humans in a dual sense as either beneficial or detrimental. For example, farmers perceive vultures as beneficial thanks to carrion removal, but mammalian scavengers are perceived as harmful for their potential predatory behaviour (Morales-Reyes et al. 2018). However, some stakeholders have wrongly blamed vultures for attacking livestock, which has generated a negative perception of them (e.g., Andean condors (Vultur gryphus) in South America and griffon vultures (Gyps fulvus) in Europe; Restrepo-Cardona et al. 2019; Lambertucci et al. 2021; Margalida et al. 2011b; Margalida et al. 2014; Duriez et al. 2019), and has led to groundless human-wildlife conflicts.

HUMAN IMPACT ON SCAVENGER POPULATIONS

Despite the numerous benefits that scavengers can provide people with, the global anthropisation of our planet is a serious concern for the conservation of this functional group. Globally, humans are the main drivers of scavenger population decline worldwide (Ogada et al. 2012a). This makes scavenger species richness lower in areas with a stronger human impact (Sebastián-González et al. 2019). Currently, avian scavengers are the most threatened group of birds (Buechley and Şekercioğlu 2016). Of the 23 vulture species that inhabit the world, 12 of them, especially in Eurasia and Africa, are classified as Vulnerable, Endangered or Critically Endangered by the IUCN (2021). There are several reasons for vulture decline, but dietary intoxication and human persecution prominently feature (Botha et al. 2017). Unintentional intoxication caused by consumption of carcasses from livestock treated with non-steroidal anti-inflammatory drugs, particularly diclofenac, has been the cause of 95-99% of vulture populations to plummet in the Indian subcontinent in just over one decade (Prakash et al. 2007). The illegal use of poisoned baits to eliminate carnivores may secondarily kill other scavenger species, which is the main cause of vulture mortality in Europe and Africa (Ogada et al. 2012a). In addition, lead intoxication that derives from hunting activities is of growing concern (Arrondo et al. 2020a). Furthermore, today's African vulture crisis is driven by poachers' direct persecution, who poison large carcasses to eliminate vultures, and to prevent them from bird circling by alerting rangers of their illegal activity (Ogada et al. 2016). Additionally, human industrialisation is leading to an increasing number of collisions with infrastructures, such as wind farms, power lines and railways, which is another cause of mortality for scavenger birds (Botha et al. 2017). For large carnivores, direct persecution and habitat degradation have led to their global decline (Ripple et al. 2014).

Therefore, to prevent scavengers' decline and loss of associated NCP, it is necessary to consider the human factor as a powerful driver that affects their conservation. Generally delving into the humans-wildlife relation could help to highlight the human dependence on nature to develop appropriate management and conservation policies that alleviate misperceptions and conflicts. Improving the human activities that positively and directly impact scavengers' population dynamics is another crucial issue for their conservation. Livestock farming and managing livestock carcasses greatly condition necrophagous species' behaviour, survival and population dynamics (Margalida and Colomer 2012). Traditional livestock practices, rather than modern, intensive livestock rearing, can be particularly important to sustain healthy and functional populations of scavenging species, especially in areas where declining wild ungulate populations ecological functions are being lost. Likewise, it is equally important to address the threats that scavengers face. A proper understanding of the real impact that anthropogenic activities have is necessary to take appropriate mitigation measures. It is only in this way that will we be able to achieve sustainable development as humanity that does not jeopardise nature conservation, including humans.

THE SPANISH CONTEXT

Spain houses the main population of European vultures (Botha et al. 2017), which comprises four breeding species: Eurasian griffon vulture; cinereous vulture (*Aegypius monachus*); Egyptian vulture (*Neophron percnopterus*); bearded vulture (*Gypaetus barbatus*). The Iberian Peninsula also connects European and African populations via the migratory route that crosses the Strait of Gibraltar. In addition, the presence of the critically endangered Rüppell's vulture (*G. rueppelli*) in Spain is increasingly frequent (Garrido et al. 2020). Spain also houses a rich community of facultative scavenger species, including important populations of two large carnivores, the brown bear (*Ursus arctos*) and the grey wolf (*Canis lupus*) (Fernández-Gil et al. 2016), and endangered raptors like the Spanish imperial eagle (*Aquila adalberti*) (BirdLife International 2021).

It is well-known that this diverse scavenger community provides important regulating NCP through carrion consumption in Spain (Sebastián-González et al. 2013; Morales-Reyes et al. 2015; Sebastián-González et al. 2016; Mateo-Tomás et al. 2017; Morales-Reyes et al. 2017a; Morales-Reyes et al. 2017b). That is why livestock farmers recognise the value of scavengers as beneficial species for ecosystems (Morales-Reyes et al. 2018). Otherwise, in a scenario in which scavengers are unable to consume livestock carcasses, industrialised carrion removal entail an economic cost in insurance payments for farmers and high greenhouse gas emissions (Morales-Reyes et al. 2015).

Spain has a long-standing history of livestock farming. The earliest pieces of evidence for livestock activity, including transhumance, date back to the Neolithic (7700 years BP; Zeder 2008; Tejedor-Rodríguez et al. 2021). Transhumance peaked in popularity in the 18th century, when Spain had the European monopoly on merino wool (Oteros-Rozas et al. 2013). Market changes and industrialisation have led to the decline in extensive livestock farming, although the Spanish government has acknowledged transhumance as a representative manifestation of intangible cultural heritage (Spanish Royal Decree 385/2017, of 8 April) to avoid it from disappearing given the great cultural legacy with which it is associated. In recent times, traditional extensive livestock farming continues mainly on grassland and *dehesas* landscapes, where vultures predominantly forage (Martin-Díaz et al. 2020). However, intensive livestock industries are rapidly replacing extensive livestock regimes, including transhumance, and strongly impacts scavengers' ecology and conservation. Intensification implies a change in the carrion distribution on landscapes, which becomes a predictable resource in time and space terms in association with fenced feeding sites and farms (Moreno-Opo and Margalida 2019). Carrion from intensive farming exposes vultures to veterinary drugs and pollutants (Blanco et al. 2019), in addition to being linked with anthropised areas, which expose scavengers to poorer physiological conditions (Gangoso et al. 2021) and to higher risks of human-caused mortality, such as collisions, electrocution and poisoning (Arrondo et al. 2020b). Thus,examining the livestock-scavengers ecological relation in-depth could shed light on how they will be affected by changing future scenarios.

Traditional activities, such as livestock farming or hunting, are performed in nature in a close connection with wildlife. When conflicts arise, stakeholders react in retaliation. Notably, the illegal use of poisoned bait is an ancestral practice that is carried out to eliminate the wildlife that humans consider to be competitors. In Spain, poisoning is promoted mainly by hunters, followed by livestock farmers, to eliminate mammalian carnivores (De la Bodega et al. 2020). Nevertheless, birds of prey and domestic animals are primary victims (De la Bodega et al. 2020). Today poisoning is one of the main mortality risks for Spanish scavengers. This activity has led endangered species like the bearded vulture (Margalida et al. 2008), Egyptian vulture (Hernández and Margalida 2009) and red kite (Mateo-Tomás et al. 2020) to decline. Despite the use of poison being considered a crime according to the Spanish penal code (Organic Law 10/1995 of the Criminal Code), the legal consequences for poisoners have proven largely insufficient. For instance, of all the poisoning episodes that occurred between 1993 and 2018 in Spain, only 1.8% led to legal sentences. Of these, 80.8% resulted in a penalty for perpetrators (Durá Alemañ et al. 2020). These figures undoubtedly promote poisoners' impunity. In addition, monitoring protocols and the quantification of poisoned fauna are managed independently by each Spanish Autonomous Community, with marked heterogeneous efforts and procedures (Cano 2017). So, the number of animals reported to be poisoned should be taken into account as only "the tip of the iceberg". Therefore, research that uncovers the real extent of using poison would be very useful for estimating their impact on wild populations and to, thus, establish appropriate mitigation measures.

To date, however, the non-material NCP associated with scavengers have been hardly explored in Spain, or elsewhere. Recent research conducted in the Spanish Pyrenees has revealed the role of scavenging birds in supporting identities (based on the emotions aroused by watching it) of birding tourists (García-Jiménez et al. 2022), with considerable economic benefits (García-Jiménez et al. 2021). Nevertheless, studies covering other non-material NCP categories (aesthetic enjoyment, contribution to knowledge, etc.) are lacking. In addition, studies performed on larger spatial scales remain completely unexplored, especially for highly mobile species like avian scavengers (Arrondo et al. 2020b). Spatial studies on a national scale could reveal key areas for the human-nature connection.

Spain still houses large populations of scavengers (which attract the attention of national and international ecotourists and other sectors of society), a large number of extensive livestock, and one of the most effective antipoison programmes in Europe.

Thus, Spain plays a crucial role in the conservation of scavengers (Santangeli et al. 2019), and is also an ideal scenario for exploring human-scavenger relations.

AIMS

The present thesis aims to disentangle the interface between human and scavengers in Spain. As a first approach, this thesis addresses in Chapter 1 how traditional human activities impact positively the conservation of scavenger species populations by providing the carrion resource and, in Chapter 2, negatively by jeopardising their populations' viability by the illegal use of poison. As another approach of the human-scavengers relation, this thesis analyses how people benefit from the role that species play in nature and, hence, contributes to people's well-being. Chapter 3 particularly assesses which species are the most significant for humans in the non-material NCP context, as well as the traits that this depends on. Chapter 4 describes how non-material contributions are spatially distributed and their conditioning factors (see Figure 2).

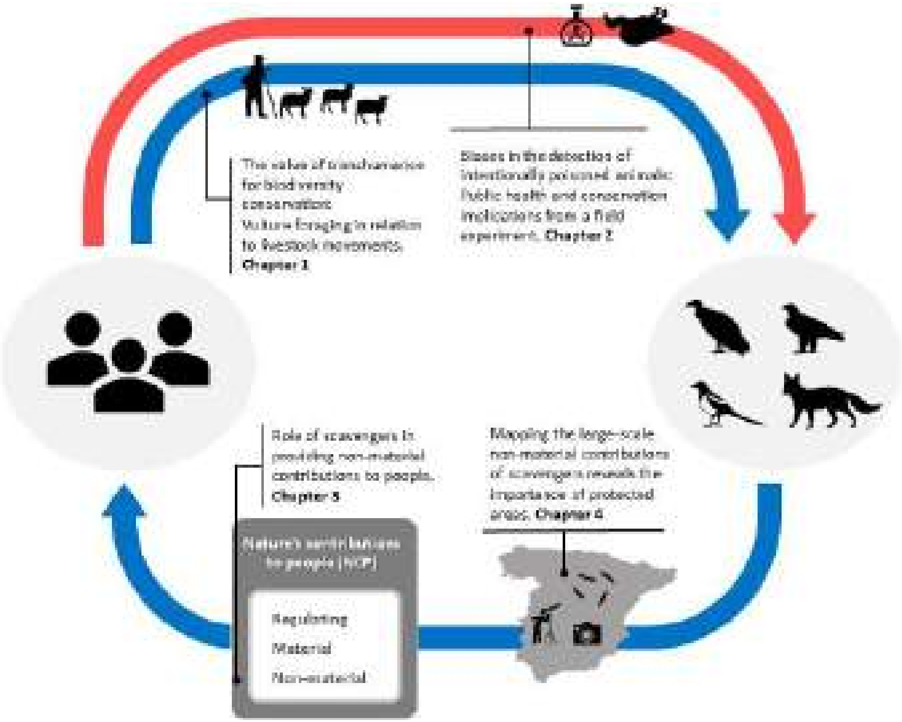


Figure 2. Framework for the present thesis. Blue arrows: positive effects. Red arrow: negative effect.

Specific aims:

Chapter 1: to assess avian scavengers' response to transhumant herds at two levels: landscape and individuals

Chapter 2: to identify the potential biases for detecting poisoned fauna by a field experiment and the traits on which it depends

Chapter 3: to assess the role played by vertebrate scavengers in the provision of non-material NCP, and to identify which ecological variables determine scavengers' capacity to provide non-material NCP

Chapter 4: to describe how scavengers' non-material NCP are spatially distributed, and to explore which landscape features condition this spatial pattern

REFERENCES

Arrondo, E., J. Navarro, J. M. Perez-García, R. Mateo, P. R. Camarero, R. C. R. Martin-Doimeadios, M. Jiménez-Moreno, A. Cortés-Avizanda, et al. 2020a. Dust and bullets: Stable isotopes and GPS tracking disentangle lead sources for a large avian scavenger. *Environmental Pollution* 266. doi:10.1016/j.envpol.2020.115022.

Arrondo, E., A. Sanz-Aguilar, J. M. Pérez-García, A. Cortés-Avizanda, J. A. Sánchez-Zapata, and J. A. Donázar. 2020b. Landscape anthropization shapes the survival of a top avian scavenger. *Biodiversity and Conservation*. Springer Netherlands. doi:10.1007/s10531-020-01942-6.

Atkins, J. L., R. A. Long, J. Pansu, J. H. Daskin, A. B. Potter, M. E. Stalmans, C. E. Tarnita, and R. M. Pringle. 2019. Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science* 364: 173–177.

Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9: 1146–1156. doi:10.1111/j.1461-0248.2006.00963.x.

Becker, N., M. Inbar, O. Bahat, Y. Choresh, G. Ben-Noon, and O. Yaffe. 2005. Estimating the economic value of viewing griffon vultures *Gyps fulvus*: A Travel Cost Model study at Gamla Nature Reserve, Israel. *Oryx* 39: 429–434. doi:10.1109/SENSOR.2007.4300616.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. *Ecology Letters* 15: 365–377. doi:10.1111/j.1461-0248.2011.01736.x.

Berenguer, J., J. A. Corraliza, and R. Martin. 2005. Rural-Urban differences in environmental concern, attitudes, and actions. *European Journal of Psychological Assessment* 21: 128–138. doi:10.1027/1015-5759.21.2.128.

BirdLife International. 2021. The IUCN Red List of Threatened Species 2021.

Blanco, G., A. Cortés-Avizanda, Ó. Frías, E. Arrondo, and J. A. Donázar. 2019. Livestock farming practices modulate vulture diet-disease interactions. *Global Ecology and Conservation* 17. doi:10.1016/j.gecco.2018.e00518.

Botha, A., J. Andevski, C. G. R. Bowden, M. Gudka, R. J. Safford, J. Tavares, and N. P. Williams. 2017. *Multi-species Action Plan to Conserve African- Eurasian Vultures*. Abu Dhabi, United Arab Emirates.

Boyce, M. S. 2018. Wolves for Yellowstone: dynamics in time and space. *Journal of Mammalogy* 99: 1021–1031. doi:10.1093/jmammal/gyy115.

Brauman, K. A., L. A. Garibaldi, S. Polasky, Y. Aumeeruddy-Thomas, P. H. S. Brancalion, F. DeClerck, U. Jacob, M. E. Mastrangelo, et al. 2020. Global trends in nature's contributions to people. *Proceedings of the National Academy of Sciences of the United States of America* 117: 32799–32805. doi:10.1073/pnas.2010473117.

Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends in Ecology and Evolution* 23: 453–460. doi:10.1016/j.tree.2008.03.011.

Buechley, E. R., and Ç. H. Şekercioğlu. 2016. The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions. *Biological Conservation* 198: 220–228. doi:10.1016/j.biocon.2016.04.001.

Cano, C. 2017. *La lucha contra el veneno en España (2011-2016). Clasificación por Comunidades Autónomas*. Madrid: WWF.

Chamberlain, C. P., J. R. Waldbauer, K. Fox-Dobbs, S. D. Newsome, P. L. Koch, D. R. Smiths, M. E. Church, S. D. Chamberlain, et al. 2005. Pleistocene to recent dietary shifts in California condors. *Proceedings of the National Academy of Sciences of the United States of America* 102: 16707–16711. doi:10.1073/pnas.0508529102.

Chan, K. M. A., P. Balvanera, K. Benessaiah, M. Chapman, S. Díaz, E. Gómez-Baggethun, R. Gould, N. Hannahs, et al. 2016. Why protect nature? Rethinking values and the environment. *Proceedings of the National Academy of Sciences of the United States of America* 113: 1462–1465. doi:10.1073/pnas.1525002113.

Chape, S., J. Harrison, M. Spalding, and I. Lysenko. 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society B* 360: 443–455. doi:10.1098/rstb.2004.1592.

Chapron, G., P. Kaczensky, J. D. C. Linnell, M. Von Arx, D. Huber, H. Andrén, J. V. López-Bao, M. Adamec, et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346: 1517–1519. doi:10.1126/science.1257553.

Costanza, R., R. D'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.

Costanza, R., R. de Groot, L. Braat, I. Kubiszewski, L. Fioramonti, P. Sutton, S. Farber, and M. Grasso. 2017. Twenty years of ecosystem services: How far have we come and how far do we still need to go? *Ecosystem Services* 28. Elsevier B.V.: 1–16. doi:10.1016/j.ecoser.2017.09.008.

Daily, G. C. 1997. *Nature's Services: Societal Dependence on Natural Ecosystems*. Washington D.C.: Island Press.

Daniel, T. C., A. Muhar, A. Arnberger, O. Aznar,

J. W. Boyd, K. M. A. Chan, R. Costanza, T. Elmqvist, et al. 2012. Contributions of cultural services to the ecosystem services agenda. *Proceedings of the National Academy of Sciences USA* 109: 8812–8819. doi:10.1073/pnas.1114773109.

Dean, G., M. G. Rivera-Ferre, M. Rosas-Casals, and F. Lopez-i-gelats. 2021. Nature's contribution to people as a framework for examining socioecological systems : The case of pastoral systems. *Ecosystem Services* 49. Elsevier B.V.: 101265. doi:10.1016/j.ecoser.2021.101265.

DeVault, T. L., O. E. Rhodes, and J. A. Shivik. 2003. Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102: 225–234. doi:10.1034/j.1600-0706.2003.12378.x.

DeVault, T. L., J. C. Beasley, Z. H. Olson, M. Moleón, M. Carrete, A. Margalida, and J. A. Sánchez-Zapata. 2016. Ecosystem Services Provided by Avian Scavengers. In *Why Birds Matter: Avian Ecological Function and Ecosystem Services*, ed. Ş. C.H., W. D.G., and W. C.J., 235–270. Chicago: University of Chicago Press.

Díaz, S., U. Pascual, M. Stenseke, B. Martín-López, R. T. Watson, Z. Molnár, R. Hill, K. M. A. Chan, et al. 2018. Assessing nature's contributions to people. *Science* 359: 270–272. doi:10.1126/science.aap8826.

Díaz, S., J. Settele, E. S. Brondízio, H. T. Ngo, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, et al. 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science* 366. doi:10.1126/science.aax3100.

Durá Alemañ, C. J., Z. Morales-Reyes, P. Ayerza, D. De la Bodega, N. Aguilera-Alcalá, F. Botella, J. Jiménez-Peinado, J. Jiménez, et al. 2020. La responsabilidad por el daño ambiental generado en el caso de la lucha contra el uso del veneno en España. *Actualidad Jurídica Ambiental* 102: 564–576.

Duriez, O., S. Descaves, R. Gallais, R. Neouze, J. Fluhr, and F. Decante. 2019. Vultures attacking livestock: a problem of vulture behavioural change or farmers' perception ? *Bird Conservation International* 29: 437–453. doi:10.1017/S0959270918000345.

Ehrlich, P., and A. Ehrlich. 1981. *Extinction: the causes and consequences of the disappearance of species*. New York.

Fagerholm, N., M. Torralba, P. J. Burgess, and T. Plieninger. 2016. A systematic map of ecosystem services assessments around European agroforestry. *Ecological Indicators* 62. Elsevier Ltd: 47–65. doi:10.1016/j.ecolind.2015.11.016.

Fernández-Gil, A., J. Naves, A. Ordiz, M. Quevedo, E. Revilla, and M. Delibes. 2016. Conflict misleads large carnivore management and conservation: Brown bears and wolves in Spain. *PLoS ONE* 11. doi:10.1371/journal.pone.0151541.

Finlayson, C., K. Brown, R. Blasco, J. Rosell, J. J. Negro, G. R. Bortolotti, G. Finlayson, A. Sánchez Marco, et al. 2012. Birds of a Feather: Neanderthal Exploitation of Raptors and Corvids. *PLoS ONE* 7: 1–9. doi:10.1371/journal.pone.0045927.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, et al. 2005. Global consequences of land use. *Science* 309: 570–574. doi:10.1126/science.1111772.

Gangoso, L., A. Cortés-Avizanda, A. Sergiel, B. Pudifoot, F. Miranda, J. Muñoz, A. Delgado-González, M. Moleón, et al. 2021. Avian scavengers living in anthropized landscapes have shorter telomeres and higher levels of glucocorticoid hormones. *Science of* *the Total Environment* 782. Science of the Total Environment: 146920. doi:10.1016/j.scitotenv.2021.146920.

García-Jiménez, R., Z. Morales-Reyes, J. M. Pérez-García, and A. Margalida. 2021. Economic valuation of non-material contributions to people provided by avian scavengers: Harmonizing conservation and wildlife-based tourism. *Ecological Economics* 187. Elsevier B.V.: 107088. doi:10.1016/j.ecolecon.2021.107088.

García-Jiménez, R., J. M. Pérez-García, A. Margalida, and Z. Morales-Reyes. 2022. Avian scavengers' contributions to people: The cultural dimension of wildlife-based tourism. *Science of the Total Environment* 806. The Authors: 150419. doi:10.1016/j.scitotenv.2021.150419.

Garrido, J. R., J. Martín-Martín, and H. C. Sousa. 2020. An overview of the first international symposium on the Rüppell' s Vulture in the Mediterranean region, 24 th March 2021. *Vulture News* 79. doi:http://dx.doi.org/10.4314/vulnew.v79i1.4.

Gorosábel, A., L. Bernad, S. D. Muñoz, and J. Pedrana. 2022. Using the ecosystem services approach to link raptors with human well-being in the Southeast Pampas of Argentina. *Biodiversity and Conservation*. Springer Netherlands. doi:10.1007/s10531-022-02372-2.

Haines-Young, T., and M. Potschin. 2010. The links between biodiversity, ecosystem services and human well-being. In *Ecosystem Ecology: a new synthesis*, ed. D. Raffaelli and C. Frid. Cambridge: BES Ecological Review Series. doi:10.1029/JB087iB10p08501.

Den Heever, L. Van, L. J. Thompson, W. W. Bowerman, H. Smit-Robinson, L. J. Shaffer, R. M. Harrell, and M. A. Ottinger. 2021. Reviewing the role of vultures at the human-wildlife-livestock disease interface: An African perspective. *Journal of Raptor Research* 55: 311–327. doi:10.3356/JRR-20-22.

Hernández, M., and A. Margalida. 2009. Poison-related mortality effects in the endangered Egyptian vulture (*Neophron percnopterus*) population in Spain. *European Journal of Wildlife Research* 55: 415–423. doi:10.1007/s10344-009-0255-6.

Hevia, V., B. Martín-López, S. Palomo, M. García-Llorente, F. de Bello, and J. A. González. 2017. Trait-based approaches to analyze links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges. *Ecology and Evolution* 7: 831–844. doi:10.1002/ece3.2692.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, et al. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486. Nature Publishing Group: 105–108. doi:10.1038/nature11118.

IPBES, D. S. 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. *IPBES secretariat*. Bonn Germany.

Johnson, C. N., A. Balmford, B. W. Brook, J. C. Buettel, M. Galetti, L. Guangchun, and J. M. Wilmshurst. 2017. Biodiversity losses and conservation responses in the Anthropocene. *Science* 356: 270–275. doi:10.1126/science.aam9317.

Jordano, P., C. Garcia, J. A. Godoy, and J. L. Garcia-Castano. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences USA* 104: 3278–3282. doi:10.1073/pnas.0606793104.

Kosanic, A., and J. Petzold. 2020. A systematic review of cultural ecosystem services and human wellbeing. *Ecosystem Services* 45. Elsevier B.V.: 101168. doi:10.1016/j.ecoser.2020.101168.

De la Bodega, D., C. Cano, and E. Mínguez. 2020. *El veneno en España. Evolución del envenenamiento de fauna silvestre (1992-2017)*. Edited by SEO/BirdLife and WWF. Madrid.

Lambertucci, S. A., A. Trejo, S. Di Martino, J. A. Sánchez-zapata, J. A. Donázar, and F. Hiraldo. 2009. Spatial and temporal patterns in the diet of the Andean condor: Ecological replacement of native fauna by exotic species. *Animal Conservation* 12: 338–345. doi:10.1111/j.1469-1795.2009.00258.x.

Lambertucci, S. A., J. Navarro, J. A. Sanchez Zapata, K. A. Hobson, P. A. E. Alarcón, G. Wiemeyer, G. Blanco, F. Hiraldo, et al. 2018. Tracking data and retrospective analyses of diet reveal the consequences of loss of marine subsidies for an obligate scavenger, the andean condor. *Proceedings of the Royal Society B: Biological Sciences* 285. doi:10.1098/rspb.2018.0550.

Lambertucci, S. A., A. Margalida, K. L. Speziale, A. Amar, F. Ballejo, K. L. Bildstein, G. Blanco, A. J. Botha, et al. 2021. Presumed killers? Vultures, stakeholders, misperceptions, and fake news. *Conservation Science and Practice* 3: e415. doi:10.1111/csp2.415.

Llorent-Bedmar, V., V. C. Cobano-Delgado Palma, and M. Navarro-Granados. 2021. The rural exodus of young people from empty Spain. Socio-educational aspects. *Journal of Rural Studies* 82: 303–314. doi:10.1016/j.jrurstud.2021.01.014.

Lozano, J., A. Olszańska, Z. Morales-Reyes, A. A. Castro, A. F. Malo, M. Moleón, J. A. Sánchez-Zapata, A. Cortés-Avizanda, et al. 2019. Human-carnivore relations: A systematic review. *Biological Conservation* 237: 480–492. doi:10.1016/j.biocon.2019.07.002.

Luederitz, C., E. Brink, F. Gralla, V. Hermelingmeier, M. Meyer, L. Niven, L. Panzer, S. Partelow, et al. 2015. A review of urban ecosystem services: Six key challenges for future research. *Ecosystem Services* 14. Elsevier: 98–112. doi:10.1016/j.ecoser.2015.05.001.

Ma, T., R. Lu, N. Zhao, and S.-L. Shaw. 2018. An estimate of rural exodus in China using location-aware data. *PLoS one* 13. Public Library of Science San Francisco, CA USA: e0201458.

Maes, J., C. Liquete, A. Teller, M. Erhard, M. L. Paracchini, J. I. Barredo, B. Grizzetti, A. Cardoso, et al. 2016. An indicator framework for assessing ecosystem services in support of the EU Biodiversity Strategy to 2020. *Ecosystem Services* 17: 14–23. doi:10.1016/j.ecoser.2015.10.023.

Malinga, R., L. J. Gordon, G. Jewitt, and R. Lindborg. 2015. Mapping ecosystem services across scales and continents - A review. *Ecosystem Services* 13. Elsevier: 57–63. doi:10.1016/j.ecoser.2015.01.006.

Margalida, A., and M. À. Colomer. 2012. Modelling the effects of sanitary policies on European vulture conservation. *Scientific Reports* 2. doi:10.1038/srep00753.

Margalida, A., R. Heredia, M. Razin, and M. Hernández. 2008. Sources of variation in mortality of the Bearded Vulture *Gypaetus barbatus* in Europe. *Bird Conservation International* 18: 1–10. doi:10.1017/S0959270908000026.

Margalida, A., M. À. Colomer, and D. Sanuy. 2011a. Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model.

PLoS ONE 6: e20248. doi:10.1371/journal.pone.0020248.

Margalida, A., D. Campión, and J. A. Donázar. 2011b. Scavenger turned predator: European vultures' altered behaviour. *Nature* 480: 457. doi:10.1038/480457b.

Margalida, A., D. Campión, and J. A. Donázar. 2014. Vultures vs livestock: Conservation relationships in an emerging conflict between humans and wildlife. *ORYX* 48: 172–176. doi:10.1017/S0030605312000889.

Margalida, A., P. Oliva-Vidal, A. Llamas, and M. À. Colomer. 2018. Bioinspired models for assessing the importance of transhumance and transboundary management in the conservation of European avian scavengers. *Biological Conservation* 228. Elsevier: 321–330. doi:10.1016/j.biocon.2018.11.004.

Markandya, A., T. Taylor, A. Longo, M. N. Murty, S. Murty, and K. Dhavala. 2008. Counting the cost of vulture decline-An appraisal of the human health and other benefits of vultures in India. *Ecological Economics* 67: 194–204. doi:10.1016/j.ecolecon.2008.04.020.

Martin-Díaz, P., A. Cortés-Avizanda, D. Serrano, E. Arrondo, J. A. Sánchez-Zapata, and J. A. Donázar. 2020. Rewilding processes shape the use of Mediterranean landscapes by an avian top scavenger. *Scientific Reports* 10: 1–12. doi:10.1038/s41598-020-59591-2.

Martín-López, B., I. Iniesta-Arandia, M. García-Llorente, I. Palomo, I. Casado-Arzuaga, D. G. Del Amo, E. Gómez-Baggethun, E. Oteros-Rozas, et al. 2012. Uncovering ecosystem service bundles through social preferences. *PLoS ONE* 7. doi:10.1371/journal.pone.0038970.

Mashele, N. M., L. J. Thompson, and C. T. Downs. 2021. Uses of vultures in traditional medicines in the Kruger to Canyons Biosphere Region, South Africa. *Journal of Raptor Research* 55: 328–339. doi:10.3356/JRR-20-36.

Mateo-Tomás, P., P. P. Olea, M. Moleón, N. Selva, and J. A. Sánchez-Zapata. 2017. Both rare and common species support ecosystem services in scavenger communities. *Global Ecology and Biogeography* 26: 1459–1470. doi:10.1111/geb.12673.

Mateo-Tomás, P., P. P. Olea, E. Mínguez, R. Mateo, and J. Viñuela. 2020. Direct evidence of poison-driven widespread population decline in a wild vertebrate. *Proceedings of the National Academy of Sciences of the United States of America* 117: 16418–16423. doi:10.1073/pnas.1922355117.

Methorst, J., U. Arbieu, A. Bonn, K. Böhning-Gaese, and T. Müller. 2020. Non-material contributions of wildlife to human well-being: A systematic review. *Environmental Research Letters* 15. IOP Publishing: 093005. doi:10.1088/1748-9326/ab9927.

Milcu, A. I., J. Hanspach, D. Abson, and J. Fischer. 2013. Cultural Ecosystem Services: A Literature Review and Prospects for Future Research. *Ecology and Society* 18. doi:10.5751/ES-05790-180344.

Millennium Ecosystem Assessment (MEA). 2005. *Ecosystems and Human Well-being: Synthesis*. Washington: Island Press. doi:10.1196/annals.1439.003.

Moleón, M., J. A. Sánchez-Zapata, A. Margalida, M. Carrete, N. Owen-Smith, and J. A. Donázar. 2014a. Humans and scavengers: The evolution of interactions and ecosystem services. *BioScience* 64: 394–403. doi:10.1093/biosci/biu034.

Moleón, M., J. A. Sánchez-Zapata, N. Selva, J. A. Donázar, and N. Owen-Smith. 2014b. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews* 89: 1042–1054. doi:10.1111/brv.12097.

Moleón, M., N. Selva, M. M. Quaggiotto, D. M. Bailey, A. Cortés-Avizanda, and T. L. DeVault. 2019. Carrion availability in space and time. In *Carrion Ecology and Management*, ed. P. P. Olea, P. Mateo-Tomás, and J. A. Sánchez-Zapata, 23-44. Springer. doi:https://doi.org/10.1007/978-3-030-16501-7_2.

Montag, J. M., M. E. Patterson, and W. A. Freimund. 2005. The Wolf Viewing Experience in the Lamar Valley of Yellowstone National Park. *Human Dimensions of Wildlife* 10: 273–284. doi:10.1080/10871200500292843.

Morales-Reyes, Z., J. M. Pérez-García, M. Moleón, F. Botella, M. Carrete, C. Lazcano, R. Moreno-Opo, A. Margalida, et al. 2015. Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. *Scientific Reports* 5: 7811. doi:10.1038/srep07811.

Morales-Reyes, Z., J. M. Pérez-García, M. Moleón, F. Botella, M. Carrete, J. A. Donázar, A. Cortés-Avizanda, E. Arrondo, et al. 2017a. Evaluation of the network of protection areas for the feeding of scavengers in Spain: from biodiversity conservation to greenhouse gas emission savings. *Journal of Applied Ecology* 54: 1120–1129. doi:10.1111/1365-2664.12833.

Morales-Reyes, Z., J. A. Sánchez-Zapata, E. Sebastián-González, F. Botella, M. Carrete, and M. Moleón. 2017b. Scavenging efficiency and red fox abundance in Mediterranean mountains with and without vultures. *Acta Oecologica* 79: 81–88. doi:10.1016/j.actao.2016.12.012.

Morales-Reyes, Z., B. Martín-López, M. Moleón, P. Mateo-Tomás, F. Botella, A. Margalida, J. A. Donázar, G. Blanco, et al. 2018. Farmer Perceptions of the Ecosystem Services Provided by Scavengers: What, Who, and to Whom. *Conservation Letters* 11: 1–11. doi:10.1111/conl.12392.

Morelli, F., A. M. Kubicka, P. Tryjanowski, and E. Nelson. 2015. The vulture in the sky and the hominin on the land: Three million years of human–vulture interaction. *Anthrozoos* 28: 449–468. doi:10.1080/08927936.2015.1052279.

Moreno-Opo, R., and A. Margalida. 2019. Human-Mediated Carrion: Effects on Ecological Processes. In *Carrion Ecology and Management*, ed. P. P. Olea, P. Mateo-Tomás, and J. A. Sánchez-Zapata. Springer.

O'Bryan, C. J., A. R. Braczkowski, H. L. Beyer, N. H. Carter, J. E. M. Watson, and E. McDonald-Madden. 2018. The contribution of predators and scavengers to human well-being. *Nature Ecology and Evolution* 2. Springer US: 229–236. doi:10.1038/s41559-017-0421-2.

Ogada, D., A. Botha, and P. Shaw. 2016. Ivory poachers and poison: Drivers of Africa's declining vulture populations. *Oryx* 50: 593–596. doi:10.1017/S0030605315001209.

Ogada, D. L., F. Keesing, and M. Z. Virani. 2012a. Dropping dead: causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences* 1249: 57–71. doi:10.1111/j.1749-6632.2011.06293.x.

Ogada, D. L., M. E. Torchin, M. F. Kinnaird, and V. O. Ezenwa. 2012b. Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission. *Conservation Biology* 26: 453–460. doi:10.1111/j.1523-1739.2012.01827.x.

Oteros-Rozas, E., B. Martín-López, C. A. López, I. Palomo, and J. A. González. 2013. Envisioning the future of transhumant pastoralism through participatory scenario planning: a case study in Spain. *The Rangeland Journal* 35: 251–272. doi:http://dx.doi.org/10.1071/RJ12092.

Parry, L., B. Day, S. Amaral, and C. A. Peres. 2010.

Drivers of rural exodus from Amazonian headwaters. *Population and environment* 32. Springer: 137–176.

Pascual-Rico, R., B. Martín-López, J. A. Sánchez-Zapata, and Z. Morales-Reyes. 2020. Scientific priorities and shepherds' perceptions of ungulate's contributions to people in rewilding landscapes. *Science of the Total Environment* 705. Elsevier B.V.: 135876. doi:10.1016/j.scitotenv.2019.135876.

Prakash, V., R. Green, D. Pain, S. Ranade, S. Saravanan, N. Prakash, R. Venkitachalam, R. Cuthber, et al. 2007. Recent Changes in Populations of Resident *Gyps* Vultures in India. *The journal of the Bombay Natural History Society* 104: 127–133.

Restrepo-Cardona, J. S., F. Sáenz-Jiménez, and A. A. Lieberman. 2019. Traditional knowledge and perceptions towards the andean condor (*Vultur gryphus* Linnaeus, 1758) in the central andes of Colombia. *ethnoscientia* 4: 1–7. doi:10.22276/ethnoscientia.v4i1.211.

Ripple, W. J., J. a Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, et al. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343: 1241484. doi:10.1126/science.1241484.

Santangeli, A., M. Girardello, E. Buechley, A. Botha, E. Di Minin, and A. Moilanen. 2019. Priority areas for conservation of Old World vultures. *Conservation Biology* 33: 1056–1065. doi:10.1111/cobi.13282.

Sebastián-González, E., J. A. Sánchez-Zapata, J. A. Donázar, N. Selva, A. Cortés-Avizanda, F. Hiraldo, M. Blázquez, F. Botella, et al. 2013. Interactive effects of obligate scavengers and scavenger community richness on lagomorph carcass consumption patterns. *Ibis* 155: 881–885. doi:10.1111/ibi.12079.

Sebastián-González, E., M. Moleón, J. P. Gibert, F. Botella, P. Mateo-Tomás, P. P. Olea, P. R. Guimarães Jr., and J. A. Sánchez-Zapata. 2016. Nested species-rich networks of scavenging vertebrates support high levels of interspecific competition. *Ecology* 97: 95–105. doi:10.1890/15-0212.1.

Sebastián-González, E., J. M. Barbosa, J. M. Pérez-García, Z. Morales-Reyes, F. Botella, P. P. Olea, P. Mateo-Tomás, M. Moleón, et al. 2019. Scavenging in the Anthropocene: Human impact drives vertebrate scavenger species richness at a global scale. *Global Change Biology* 25: 3005–3017. doi:10.1111/gcb.14708.

Sebastián-González, E., Z. Morales-Reyes, F. Botella, L. Naves-Alegre, J. M. Pérez-García, P. Mateo-Tomás, P. P. Olea, M. Moleón, et al. 2020. Network structure of vertebrate scavenger assemblages at the global scale: drivers and ecosystem functioning implications. *Ecography* 43: 1143–1155. doi:10.1111/ecog.05083.

Secretariat of the Convention on Biological Diversity. 2010. *Strategic Plan for Biodiversity 2011–2020 and the Aichi Targets. "'Living in Harmony with Nature.'"* Quebec: CBD, UNEP.

Sekercioglu, C. H. 2002. Impacts of birdwatching on human and avian communities. *Environmental conservation* 29. Cambridge University Press: 282–289.

Sekercioglu, Ç. H., D. G. Wenny, and C. J. Whelan. 2016. *Why birds matter: avian ecological function and ecosystem services*. University of Chicago Press.

Selva, N., and M. A. Fortuna. 2007. The nested structure of a scavenger community. *Proceedings of the Royal Society B: Biological Sciences* 274: 1101–1108. doi:10.1098/rspb.2006.0232.

Tejedor-Rodríguez, C., M. Moreno-García, C. Tornero, A. Hoffmann, Í. García-Martínez de Lagrán, H. Arcusa-Magallón, R. Garrido-Pena, J. I. Royo-Guillén, et al. 2021. Investigating Neolithic caprine husbandry in the Central Pyrenees: Insights from a multi-proxy study at Els Trocs cave (Bisaurri, Spain). *Plos One* 16: e0244139. doi:10.1371/journal.pone.0244139.

Westman, W. E. 1977. How much are Nature's Services worth? *Science* 197: 960–964. doi:10.1126/science.197.4307.960.

Whelan, C. J., D. G. Wenny, and R. J. Marquis. 2008. Ecosystem services provided by birds. *Annals of the New York Academy of Sciences* 1134: 25–60. doi:10.1196/annals.1439.003.

Zeder, M. A. 2008. Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. *PNAS* 105: 11597–11604.

Summary of Materials and Methods

Photo by Pilar Oliva Vidal.
Commons ravens (*Corvus corax*) in Pre-Pyrenees of Lleida.

SUMMARY OF MATERIALS AND METHODS

The present thesis benefits from diverse methods associated with ecology and social sciences, as briefly explained below and separately for each chapter.

Chapter 1 were developed in Los Campos de Hernán-Perea (located in the Sierras de Cazorla, Segura y Las Villas Natural Park, SE Spain), where traditional transhumant livestock practices are still frequent. We carried out field surveys to estimate the seasonal abundance of avian scavengers, livestock and wild ungulates, and used non-parametric Wilcoxon rank tests to assess how the abundance of these faunal groups changes during the seasonal cycle. We also performed GLMMs to explore the influence of the presence of transhumant livestock on griffon vulture abundance on the landscape level. We GPS-tracked 30 adult griffon vultures over a 4-year period. This allowed us to obtain the flying fixes that fell inside and outside the study area, and to assess by GLMMs how griffon vultures' individual foraging behaviour changed according to transhumant livestock's seasonal movements.

In **Chapter 2**, we compared the official database of poisoned wildlife in peninsular Spain, compiled by WWF and SEO/BirdLife, with the information obtained from a field experiment, which was designed to detect species that could potentially be vulnerable to poisoning. For this purpose, by means of camera-trapping, we firstly monitored the consumption patterns of three bait types: eggs, sausages, and chicken (all frequently used to poison wildlife) in six study areas across peninsular Spain: Sierra de Cabrera; Sabinar de Calatañazor-Sierra de Cameros; Pre-Pyrenees of Lleida; Sierra Harana; the Sierras de Cazorla, Segura y Las Villas Natural Park; Sierra Escalona. Then we took those animal species that had been recorded as poisoned in each experimental area according to the official poisoning database. Afterwards, we classified all the species in the poisoning database and the field experiments into nine group: wild carnivores; domestic carnivores;

suids; small mammals; corvids; vultures; other raptors; other birds; reptiles. Next, we compared the frequency of occurrence of each group in both data sources by means of c2 tests, and separately for each study area. Finally, we used GLMMs to explore the species traits that could explain the dissimilarities in both data sources, such as: body mass, colour pattern, mobility, sociality and conservation status.

In **Chapter 3**, we used data about scavengers and their provision of non-material NCP in Spain. Based on previous studies about carrion consumption in Spain (García-Heras et al. 2013; Mateo-Tomás et al. 2015; Sebastián-González et al. 2016), we considered the terrestrial vertebrate scavenger guild to be composed mainly of 22 species: four vultures, six raptors other than vultures, three corvids and nine mammals (Figure 1). We firstly used several Internet data sources to obtain indices that represent the provision of non-material NCP by each species.

- *Aesthetic enjoyment* was assessed by examining photographs of scavengers posted on a social media platform by nature photographers

- *Recreational experiences* were obtained from the wildlife-watching touristic offer related to scavengers

- *Contribution to knowledge* was evaluated from two perspectives: firstly, contribution to knowledge acquired by citizens was assessed with the occurrence of scavenger species in the Spanish outreach magazine *Quercus*; secondly, contribution to knowledge acquired by scientists was assessed by collecting the records of scavenger species' observations from the Global Biodiversity Information Facility (GBIF), and by examining the species studied in scientific publications

- *Supporting identities*, particularly people's satisfaction of knowing that a particular scavenger species exists, were approached according to the prominence of each scavenger species in Google searches

We secondly conducted median and mean comparison tests to explore whether taxonomic group determined the occurrence in each data source. We also performed a canonical correspondence analysis (CCA) to identify the ecological traits of the species that underpinned scavengers' capacity to provide non-material NCP: body mass, foraging activity, home range, fecundity, diel activity, conservation status and taxonomic group.

Figure 1. Scavenger community addressed in Chapter 3 & 4. Left to right, and from top to bottom. Blue line, obligate scavengers: griffon vulture (*Gyps fulvus*), black vulture (*Aegypius monachus*), bearded vulture (*Gypaetus barbatus*), Egyptian vulture (*Neophron percnopterus*). Red line, facultative scavengers' raptors: Spanish imperial eagle (*Aquila adalberti*), golden eagle (*Aquila chrysaetos*), western marsh harrier (*Circus aeruginosus*), common buzzard (*Buteo buteo*), red kite (*Milvus milvus*), black kite (*Milvus migrans*). Yellow line, corvids: common raven (*Corvus corax*), carrion crow (*Corvus corone*), Eurasian magpie (*Pica pica*). Green line, mammals: grey wolf (*Canis lupus*), brown bear (*Ursus arctos*), red fox (*Vulpes vulpes*), stone marten (*Martes foina*), pine marten (*Martes martes*), common genet (*Genetta genetta*), Eurasian badger (*Meles meles*), Egyptian mongoose (*Herpestes ichneumon*), wild boar (*Sus scrofa*). Photo credit: Pilar Oliva Vidal; Shutterstock.

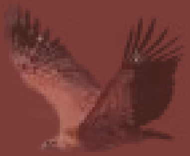
Finally in **Chapter 4**, we mapped the indicators of photography, tourism activities and wildlife observation records, obtained from the previous chapter, to reveal spatial patterns in the provision of non-material NCP by scavengers in peninsular Spain. With the QGIS software, we generated hotspots for these non-material NCPs. We also used generalised linear models (GLMs) to explore the landscape features (presence of protected areas, human footprint, scavenger species richness) that could explain the spatial distribution of the non-material NCP provided by scavengers.

REFERENCES

García-Heras, M. S., A. Cortés-Avizanda, and J. A. Donázar. 2013. Who are we feeding? Asymmetric individual use of surplus food resources in an insular population of the endangered Egyptian vulture Neophron percnopterus. *PLoS ONE* 8: 1–7. doi:10.1371/journal.pone.0080523.

Mateo-Tomás, P., P. P. Olea, M. Moleón, J. Vicente, F. Botella, N. Selva, J. Viñuela, and J. A. Sánchez-Zapata. 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. *Diversity and Distributions* 21: 913–924. doi:10.1111/ddi.12330.

Sebastián-González, E., M. Moleón, J. P. Gibert, F. Botella, P. Mateo-Tomás, P. P. Olea, P. R. Guimarães Jr., and J. A. Sánchez-Zapata. 2016. Nested species-rich networks of scavenging vertebrates support high levels of interspecific competition. *Ecology* 97: 95–105. doi:10.1890/15-0212.1.



CHAPTER 1.

The value of transhumance for biodiversity conservation: Vulture foraging in relation to livestock movements

Photo by Toni Sánchez Zapata.
Transhumant livestock herds in Los Campos de Hernán Perea (Jaén).

This chapter corresponds to the article:

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ABSTRACT

In recent decades, intensive techniques of livestock raising have flourished, which has largely replaced traditional farming practices such as transhumance. These changes may have affected scavengers' behaviour and ecology, as extensive livestock is a key source of carrion. This study evaluates the spatial responses of avian scavengers to the seasonal movements of transhumant herds in south-eastern Spain. We surveyed the abundance of avian scavengers and ungulates, and analysed the factors affecting the space use by 30 GPS-tracked griffon vultures (*Gyps fulvus*). Griffons' foraging activity increased in the pasturelands occupied by transhumant herds, which implied greater vulture abundance at the landscape level during the livestock season. In contrast, facultative scavengers were more abundant without transhumant livestock herds, and the abundance of wild ungulates did not change in relation to livestock presence. We conclude that fostering transhumance and other traditional farming systems, to the detriment of farming intensification, could favour vulture conservation.

Keywords: farming intensification, GPS-tracking, livestock, traditional farming practices, vultures, wild ungulates.

INTRODUCTION

Humans and scavengers have maintained a close and changing relationship since our origins (Moleón et al. 2014). With the first hunters and, especially, shepherds, humans became key carrion suppliers to scavenging animals, while scavengers provided humans with an important hygienic service by efficiently removing animal debris (Moleón et al. 2014). In particular, extensive livestock carcasses from traditional exploitations became a staple food source for vultures and other scavengers in many areas (Margalida et al. 2011), and even exceeded the contribution of wild ungulates (Margalida et al. 2018). Thus, traditional extensive livestock farming has helped to sustain scavenger populations in many regions of the world, such as Eurasian griffon vultures (*Gyps fulvus*; Parra and Tellería, 2004) and Egyptian vultures (*Neophron percnopterus*; Mateo-Tomás and Olea, 2010) in south-western Europe.

However, the profound change in livestock products demand and management in the last few years could strongly influence scavenger behaviour and conservation. Both economic development and human population growth have led to an increasing demand in livestock products and a shift towards industrialization ("livestock revolution"; Seré et al., 2008). This change has involved the stabling of livestock (i.e., intensive farming) and a decline in extensive farming practices, particularly transhumance, which consists of the seasonal movement of herds to take advantage of the availability of natural pastures (Bunce et al. 2004). Transhumant livestock movement takes place twice a year, from wintering to summering areas and back, and is usually based on either latitudinal (north to south in the Northern Hemisphere) or altitudinal travels (generally, from mountains to lowland areas). There is evidence that this farming system has been practised in the Mediterranean region since the Neolithic (6000 yrs BC; Tejedor-Rodríguez et al., 2021). In Spain, a Mediterranean country with marked historic transhumance activity (MARM, 2011), there were 3.5 million transhumant sheep in the 18th century, linked with Europe's wool demand and the Spanish monopoly on merino wool production (Oteros-Rozas et al. 2013a). After the breakdown of this monopoly, transhumance underwent a continuous decline. Today, fewer than 0.5 million of the c. 15.5 million sheep in Spain perform transhumance (MAPA, 2019). In parallel, the main market product of transhumant livestock has changed from wool to meat. Among the causes of the current decline of transhumant livestock numbers are the loss of economic profitability compared to intensive systems, rural abandonment and lack of generational relay (Oteros-Rozas et al. 2013a). In order to protect transhumance from disappearing, the Spanish government declared it to be a representative manifestation of intangible cultural heritage (Spanish Royal Decree 385/2017, of 8 April). The United Nations Educational, Scientific and Cultural Organization (UNESCO) also inscribed transhumance on the Representative List of the Intangible Cultural Heritage of Humanity in 2019 (https://ich.unesco.org/en/decisions/14.COM/10.B.2).

Moreover, the abandonment of transhumance and other traditional livestock practices leads to landscape transformation. Lack of livestock grazing may entail vegetation succession, which promotes a landscape change from grassland to shrub and forest by means of a passive rewilding process (Navarro and Pereira 2015; Corlett 2016). Rewilding triggers an effect on the entire ecosystem, from primary producers to tertiary consumers, such as scavengers (Cortés-Avizanda et al. 2015). Shrub and forest landscape has favoured the expansion of wild ungulates in many European countries (Apollonio et al. 2010), such as Spain (Acevedo et al. 2011). However, for vultures and other avian scavengers, finding carcasses in more heterogeneous habitats with greater vegetation cover takes longer than in the open grazing areas occupied by livestock (Arrondo et al. 2019). In addition, intensive livestock farms substantially change the feeding paradigm for vertebrate scavengers by providing more predictable food in both space and time (Moleón et al. 2019). In turn, the food provided by these highly-predictable resources is of low-quality, as it contains veterinary drugs and other pollutants to which scavengers are exposed (Blanco et al. 2019). Thus, vultures inhabiting anthropized areas with intensive livestock farming have poorer physiological conditions (Gangoso et al. 2021) and lower survival rates due to human-cause mortality than those inhabiting more natural areas with more traditional farming systems (Arrondo et al. 2020a). Given vultures' poor conservation status worldwide (Ogada et al. 2012), investigating the livestock-vulture ecological relationship in the current scenario of rapid global environmental change is an urgent task.

Unlike most avian scavenger species, which are considered facultative or opportunistic scavengers, vultures are obligate scavengers (DeVault et al. 2003), which means that they completely rely on carrion to survive and reproduce. Thus, their foraging and distribution are greatly conditioned by carrion availability (Arrondo et al. 2018). Previous studies based on field surveys provided some evidence that vultures respond to the presence of transhumant livestock, with increased griffon vulture occurrence in roosts close to transhumant herds (Olea and Mateo-Tomás 2009). However, vultures are extremely mobile species (Ruxton and Houston 2004), which challenges in depth investigation of causes and consequences of vulture movement. In recent years, there has been an increase in the use of GPS devices to track large bird movements (Alarcón and Lambertucci 2018). Thus, combining GPS-tracking techniques and field surveys could help to obtain a wide understanding of the ecological processes that shape vulture foraging, at spatial scales ranging from individuals to landscapes.

The present study aims to evaluate the space use by avian scavengers in response to the seasonal movements of transhumant herds in Sierra de Cazorla, Segura y Las Villas Natural Park (Spain), an area that houses the largest number of transhumant sheep in western Europe. To address this, we firstly explored the relationship between the abundance of avian scavengers (both obligate and facultative) and the abundance of wild and domestic ungulates at the landscape level, as inferred by field surveys. We secondly analysed the individual spatial responses of GPS-tracked griffon vultures to the presence and absence of transhumant herds. We focused on the griffon vulture because it is the most abundant vulture species in Europe (Margalida et al. 2010) and the most efficient consumer of ungulate carcasses in Mediterranean habitats (Mateo-Tomás et al. 2017). Our general hypothesis is that avian scavengers, especially vultures, will arrange their space use according to carrion availability. In particular, we expect that vultures will increase their use of transhumant livestock areas in the season in which transhumant herds are present, while avian facultative scavengers will show a weaker response due to their reliance on alternative food sources.

METHODS

STUDY AREA

This study was carried out in one of Europe's largest protected areas (the Sierras de Cazorla, Segura y Las Villas Natural Park; 2143 km^2), a mountain region in south-eastern Spain. The climate is Mediterranean, with annual rainfall ranging between 300 and 1600 mm, and a mean annual temperature of 12-16ºC. The area is covered mainly by pine (*Pinus halepensis*, *P. nigra*, *P. pinaster* and *P. sylvestris*) and oak (*Quercus ilex* and

Q. faginea) forests (Rivas-Martínez 1987). The natural park hosts a rich community of vertebrate scavengers. Obligate scavengers include four vulture species: three resident species (griffon, bearded *Gypaetus barbatus* and Egyptian vultures) and one species that is occasionally present (cinereous vultures *Aegypius monachus*) (Morales-Reyes et al. 2017). The griffon vulture is the most abundant vulture in this area, with more than 300 breeding pairs (Del Moral and Molina 2018). Major facultative scavengers include birds like golden eagles (*Aquila chrysaetos*), common ravens (*Corvus corax*), carrion crows (*C. corone*), Eurasian magpies (*Pica pica*) and Eurasian jays (*Garrulus glandarius*), and also mammals like red fox (*Vulpes vulpes*) and wild boar (*Sus scrofa*) (Arrondo et al. 2019). Apart from wild boar, the wild ungulates community includes red deer (*Cervus elaphus*), fallow deer (*Dama dama*), mouflon (*Ovis orientalis*) and Iberian ibex (*Capra pyrenaica*) (Martínez-Martínez 2002).

In the highest part of this natural park, there is a plateau called "Campos de Hernán Perea" (150 km^2; 1,600-1,700 m a.s.l.; **Fig. 1**). This plateau is covered by communal pastures where transhumant herds from different lowland ranges in the Sierra Morena mountains (located 50-200 km away) arrive at the end of May and stay until the end of November (Morales-Reyes et al. 2018). This denotes two clearly delimited seasons in relation to the presence (June-November; hereafter "livestock season") or absence of livestock (December-May; hereafter "no livestock season"). Transhumant herds include c. 35 000 animals (Arrondo et al. 2019) (7% of the total transhumant livestock in Spain; Oteros-Rozas et al. 2013a), mostly (>90%) sheep (*Ovis aries*), but also goats (*Capra aegagrus hircus*), cattle (*Bos taurus*) and horses (*Equus ferus caballus*).

ABUNDANCE OF AVIAN SCAVENGERS, LIVESTOCK AND WILD UNGULATES

To determine if transhumance practices affect avian scavengers' space use, we assessed the differences in the abundance of avian scavengers (both obligate –vultures– and facultative scavengers –other raptors and corvids–) and ungulates (both domestic and wild species) between the seasons with and without transhumant livestock. For birds, we conducted 75 systematic 30-minute point counts (for a similar approach, see Moleón et al. 2020). We surveyed 37 points during the livestock season (17 in September-October 2019, 20 in July 2020) and 38 during the no livestock season (18 in January, 20 in February 2020). Point counts were separated by at least 1.2 km from one another (**Fig. 1**). Surveys were conducted with the help of binoculars (x12) and field scopes (20-60x) from 2 hours after sunrise to 2 pm (UTC+1) in winter and 3 pm (UTC+2) in summer to, thus, cover soaring birds' main active period (Vergara 2010). For each point count, we recorded the observed species and the number of observed individuals. To minimize recounting birds within and among points, we also recorded observation time, distance from the birds to the observer, and their flight direction (Bibby et al. 2000).

In order to quantify seasonal changes in the relative abundance of wild and domestic ungulates, we conducted 40 systematic 3 kilometre-long transects (Putman et al. 2011): 20 during the livestock season (10 in September-October 2019, 10 in July 2020) and 20 during the no livestock season (10 in January, 10 in February 2020). Transects were done by walking on the unpaved roads distributed across the study area (**Fig. 1**). Transects were carried out at dawn or dusk when ungulates are more active (Pérez et al. 2014). For each transect, we recorded the observed species and number of individuals. To avoid double counting among transects, we also recorded observation time, location of the observed ungulates, and their direction, and their age and sex whenever possible. We expressed the relative abundance of both wild and domestic ungulates according to the Kilometric Abundance Index (KAI), i.e., the number of individuals observed per km walked (Vincent et al. 1991).

Both point counts and transects were distributed throughout the area mostly used by transhumant herds, i.e., the grassland plateau (**Fig. 1**). The average bird and ungulate abundances were calculated separately for each season (livestock and no livestock).

VULTURE GPS TRACKING

Using a baited cannon-net, we captured 30 adult griffon vultures in the natural park in December 2014. Each vulture was equipped with 90 g GPS/GPRS-GSM devices from e-obs digital telemetry (http://www.e-obs.de), which were attached using a backpack harness. These devices were configured according to weather conditions (see **Table S1**). Birds were monitored between January 2015 and December 2018, unless they died or the device technically failed (Table S2). All the individuals were sexed by molecular procedures (Wink et al. 1998). For each monitored year, the breeding status of all the tracked individuals was determined (breeding vs. non-breeding; see Table S2 for details) and the nest location of all the breeding birds. Breeding status was firstly identified by the accumulation of GPS fixes on cliffs suitable for nesting during vultures' nestling period (from March to August; Donázar, 1993), and was then confirmed by field observations. The number of flying fixes (a proxy for foraging activity) located both inside and outside the plateau used by transhumant herds (see **Fig. 1**) was identified for this period. Flying fixes were considered those locations with a ground speed > 5 m/s (see Arrondo et al. 2018 for more details).

STATISTICAL ANALYSES

We firstly used non-parametric Wilcoxon rank tests to explore changes in the abundance of avian scavengers and ungulates between seasons. The absence of normality in these variables was confirmed by the Shapiro-Wilk test ($\alpha = 0.05$).

In order to analyse the influence of transhumant herds on griffon vultures' use of the study area, we followed two different approaches: one focused on the landscape level and another on the individual level. In the first approach, the aim was to explore whether griffon vultures were more frequently observed in the livestock area during the livestock season. For this purpose, we used generalized linear mixed models (GLMMs; Zuur et al. 2009) with Poisson error distributions and log link functions. We considered as response variable the "abundance" of griffon vultures observed per point count. The explanatory variables in the fixed term were the livestock "season" (yes/no) and the "nestling" period of griffon vultures (yes/no). To avoid pseudoreplication, we included "point" counts as a random term. We firstly constructed a full model with all the explanatory variables (no interactions among variables were considered due to low sample size). We secondly constructed the set of alternative models with different combinations of the random structure (i.e., one model with a "point" count as a random factor and another with no random term). We used the glmer() function of the *lme4* package in R (Bates et al. 2015). We thirdly selected the model with the most appropriate random structure. Model selection was based on Akaike's Information Criterion (AIC). After selecting the most appropriate random structure (with a random term in our case), we selected the model with the most appropriate fixed structure by exploring the complete set of alternative models using the dredge() function of the *MuMIn* package in R (Barton 2013). The models with delta-AIC < 2 in relation to the best model (i.e., the model with the lowest AIC) were considered to have similar support (Burnham and Anderson 2002). We finally explored candidate model's performance by means of marginal R^2, which measures how much variability in the response variable is explained by the model's fixed term (Nakagawa and Schielzeth 2013). For this purpose, we used the r.squaredGLMM() function of the *MuMIn* package in R (Barton 2013).

In the second approach, which aimed to assess individual griffon vulture foraging activity changes, we explored whether the GPS-tracked griffon vultures used the study area more during the livestock season, and which factors made some griffon vultures to use the area more than others. We applied GLMMs with binomial error distributions and logit link functions. We modelled the response variable as the proportional data with a binomial denominator of the total "GPS fixes" that fell within vs. beyond the study area limits each month per griffon vulture individual. The explanatory variables in the fixed term were livestock "season" (yes/no), "breeding" status (breeding/non-breeding), "sex" (male/female) and "year" (as a factor, one for each tracked year). The individual ("ind.") was included as a random term. The process for model construction and selection, and for calculating the candidate models' performance, was like that described above.

All the analyses were done in R software, version 3.6.1 (R Core Team 2019) (https://cran.r-project.org/).

RESULTS

ABUNDANCE OF AVIAN SCAVENGERS, LIVESTOCK AND WILD UNGULATES

Obligate scavengers were more abundant during the livestock season (Wilcoxon rank test ($p < 0.05$); **Fig. 2**). We observed avian scavengers in 95.9% of the point counts, and totalled 1728 observed birds (range: 0-154 per point; mean ± SD: 23.4 ± 28.0; **Table 1**). We detected three species of obligate scavengers (griffon, black and bearded vultures) and five species of facultative scavengers. Griffon was by far the most abundant vulture (89.1% of all the observed birds), with 1106 individuals observed during the livestock season and 434 during the no livestock season (**Table 1**). In general, vultures were c. 2.5-fold more abundant during the livestock season than during the no livestock season (**Fig. 2**). In contrast, avian facultative scavengers were more abundant during the no livestock season (**Fig. 2**), with the carrion crow being the most frequently observed species, followed by common raven and golden eagle (**Table 1**).

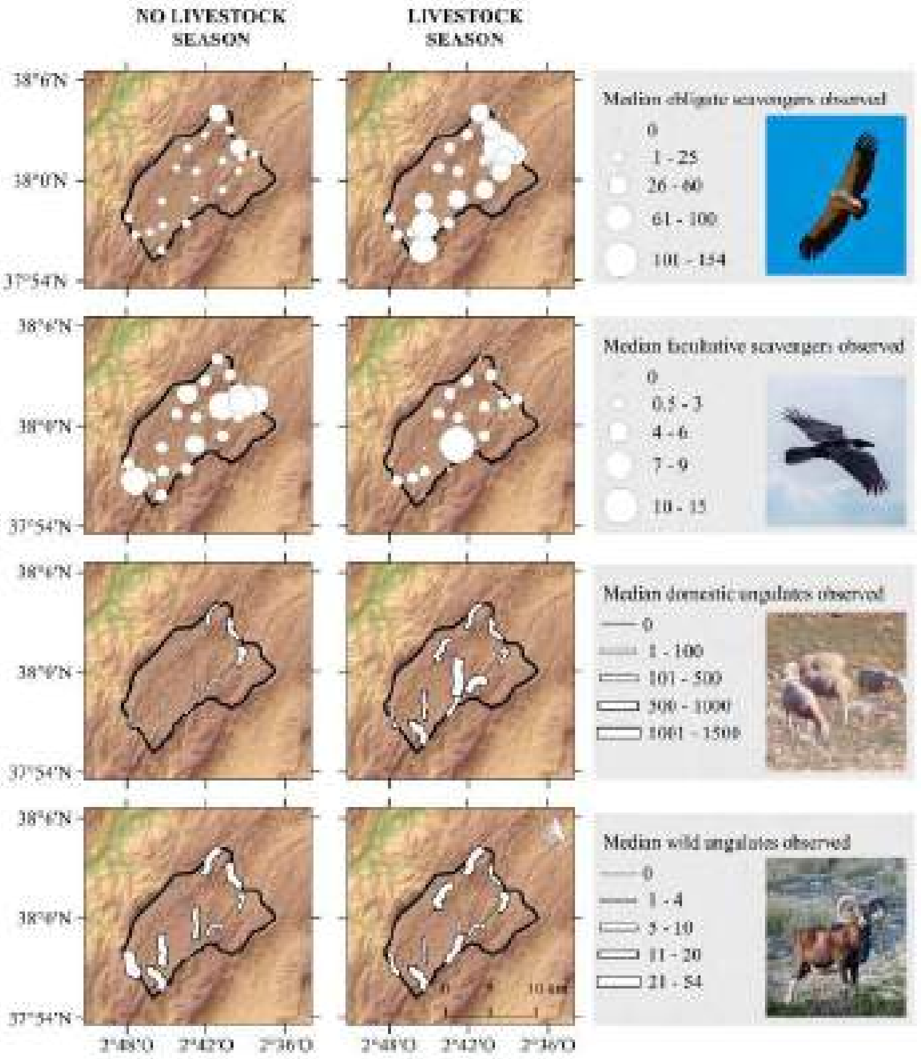

Figure 1. Location of the study area (i.e., the high plateau called "Campos de Hernán Perea") in the Sierra de Cazorla, Segura y Las Villas Natural Park, south-eastern Spain. Point counts for avian scavengers and transects for ungulates are shown per season (livestock and no livestock). The size of the point counts (circles) and transects (lines) are proportional to the median number of observed individuals.

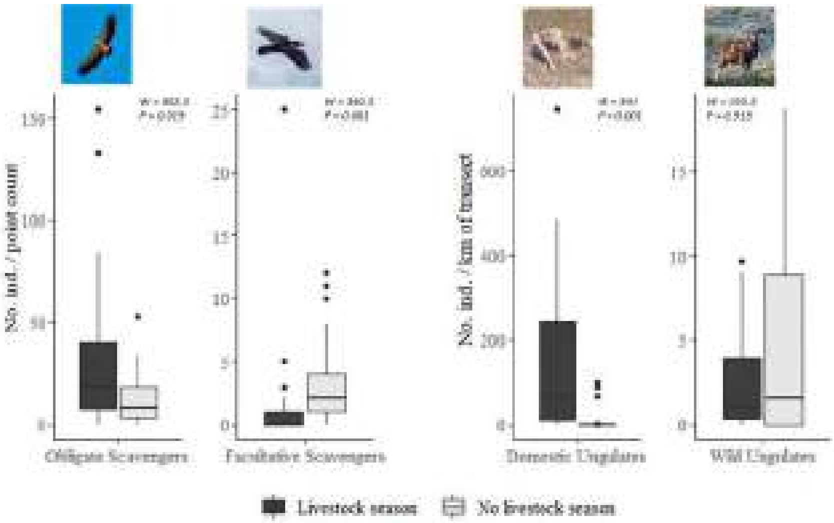

Figure 2. Abundance comparisons of (obligate and facultative) avian scavengers and (domestic and wild species) ungulates between seasons (livestock vs. no livestock) in the study area. Boxes include from the first to the third data quartiles; the median is represented by a horizontal line; thin lines extend from the hinge to the largest and smallest value no further than 1.5 * IQR (the interquartile range); points show outliers. Differences between seasons were calculated by the non-parametric Wilcoxon rank test (α = 0.05).

Domestic ungulates were found in 55.0% of the transects, and totalled 10 046 animals (range: 0-2228 per transect; mean ± SD: 251.2 ± 479.3; **Table 2**). Sheep represented the bulk of the observed livestock species, followed far behind by goats. Cattle and horses were occasionally recorded. During the livestock season, domestic ungulates were c. 12-fold more abundant than during the no livestock season (**Fig. 2**). In contrast, wild ungulates were observed in more transects (70.0%), but total abundance (418 individuals; range: 0-56 per transect; mean ± SD: 10.45 ± 14.70) was much lower than that of domestic ungulates, and was similar between seasons (**Fig. 2**). Mouflons were the most abundant species during both seasons, followed by red and fallow deer, Iberian ibex and wild boar (**Table 2**).

Table 1. Results of the 30-minute point counts conducted to survey avian scavengers' abundance in the study area according to season (livestock and no livestock).

		Livestock season				**No livestock season**			
	Species	**% Occurrence in points (n=37)**	**Total individuals**	**Mean no. of ind./ point**	**SD**	**% Occurrence in points (n=38)**	**Total individuals**	**Mean no. of ind./ point**	**SD**
Obligate scavengers	Griffon vulture *Gyps fulvus*	91.89	1106	29.89	36.01	94.74	434	11.72	11.70
	Bearded vulture *Gypaetus barbatus*	10.81	9	0.24	0.89	15.79	6	0.16	0.37
	Cinereous vulture *Aegypius monachus*	2.70	1	0.03	0.16	2.63	1	0.03	0.16
Facultative scavengers	Golden eagle *Aquila chrysaetos*	0	0	0	-	23.68	10	0.27	0.51
	Common raven *Corvus corax*	16.22	8	0.22	0.53	23.68	16	0.43	0.90
	Carrion crow *Corvus corone*	35.14	41	1.11	3.78	63.16	93	2.51	3.18
	Eurasian jay *Garrulus glandarius*	2.70	1	0.03	0.16	0	0	0	-
	Eurasian magpie *Pica pica*	2.70	2	0.05	0.33	0	0	0	-
	Total	**91.89**	**1168**	**31.57**	**36.00**	**100**	**560**	**15.14**	**12.41**

Table 2. Results of the transects conducted to survey ungulates' abundance in the study area according to season (livestock and no livestock). KAI: Kilometric Abundance Index.

		Livestock season			**No livestock season**		
	Species	**% Occurrence in transects (n=20)**	**Total individuals**	**KAI**	**% Occurrence in transects (n=20)**	**Total individuals**	**KAI**
Domestic	Sheep *Ovis aries*	70	9038	150.63	15	760	12.67
	Goat *Capra aegagrus hircus*	35	194	2.73	5	1	0.02
	Cattle *Bos Taurus*	10	42	0.70	5	2	0.03
	Horse *Equus ferus caballus*	10	9	0.15	0	0	0
Wild	Mouflon *Ovis orientalis*	55	113	1.88	50	195	3.25
	Red deer *Cervus elaphus*	30	18	0.30	20	26	0.43
	Fallow deer *Dama dama*	10	13	0.22	20	37	0.62
	Iberian ibex *Capra pyrenaica*	10	2	0.03	5	1	0.02
	Wild boar *Sus scrofa*	5	13	0.22	0	0	0
	Total	**100**	**9442**	**157.47**	**65**	**1022**	**17.03**

The GLMM with higher performance included livestock season (**Table 3**), and supported the notion that griffon vulture abundance increased during the livestock season (**Table 4**). According to R^2, season explained c. 33.0% of the variability in the number of observed griffon vultures on the plateau. Adding "nestling" period to the previous model did not improve R^2 (**Table 3**), which suggests that the increased abundance of griffon vultures in the study area during the livestock season was not related to changes in breeder behaviour in relation to either the nesting season or movements of young vultures.

Table 3. Generalized linear mixed models (GLMMs) obtained from the AIC-based model selection to assess the factors influencing the changes in: a) the number of griffon vultures observed in the study area per point count ("abundance"); b) the GPS fixes per griffon vulture individual that fell within vs. beyond the study area limits ("GPS fixes"; see Methods for details on the explanatory variables). Number of estimated parameters (k), AIC values, AIC differences (delta-AIC) with the highest ranked model (that with the lowest AIC) and the variability of the response variable explained by the predictors (R2) are shown. Bold: the selected models.

Response variable	**Model**	**k**	**AICc**	**delta-AIC**	**R2**
Abundance	**season + (1|point)**	**1**	**1334.2**	**0**	**0.330**
	season + nestling + (1|point)	**2**	**1334.2**	**0.02**	**0.328**
	nestling + (1|point)	1	1507.2	172.97	
	(1|point)	0	1679.6	345.40	
GPS fixes	**breeding + season + year + (1|ind.)**	**5**	**8468.5**	**0**	**0.014**
	breeding + season + sex + year + (1|ind.)	**6**	**8468.7**	**0.17**	**0.040**
	season + year + (1|ind.)	4	8498.5	30.00	
	season + sex + year + (1|ind.)	5	8499.1	30.55	
	breeding + year + (1|ind.)	4	8735.2	266.70	
	breeding + sex + year + (1|ind.)	5	8735.3	266.79	
	year + (1|ind.)	3	8764.8	296.25	
	sex + year + (1|ind.)	4	8765.3	296.73	
	season + (1|ind.)	1	8795.4	326.89	
	season + sex + (1|ind.)	2	8796.0	327.48	
	breeding + season + (1|ind.)	2	8796.9	328.40	
	breeding + season + sex + (1|ind.)	3	8797.5	328.95	
	(1|ind.)	0	9099.5	631.00	
	sex + (1|ind.)	1	9100.1	631.51	
	breeding + (1|ind.)	1	9101.5	632.99	
	breeding + sex + (1|ind.)	2	9102.0	633.51	

Table 4. Selected generalized linear mixed models (GLMMs) showing the relation among season, nestling, breeding status and sex of griffon vultures, and year (see the text for details on the explanatory variables) and changes in: a) the number of griffon vultures observed in the study area per point count ("abundance"); b) the GPS fixes per griffon vulture individual that fell within vs. beyond the study area limits ("GPS fixes"). Only the models with the highest R**2** are shown. The estimate of the parameters (including the sign), the standard error of the parameters (SE) and the degrees of freedom of the models (df) are shown.

Response variable	**Model**	**Parameter**	**Estimate**	**SE**	**df**
Abundance	season + (1|point)	Intercept	2.188	0.161	3
		Season (livestock)	1.017	0.057	
	season + nestling + (1|point)	Intercept	2.194	0.161	4
		Season (livestock)	0.955	0.071	
		Nestling (yes)	0.097	0.065	
GPS fixes	breeding + season + year + (1|ind.)	Intercept	-5.161	0.357	7
		Breeding (yes)	-0.325	0.057	
		Season (livestock)	0.412	0.026	
		Year (2016)	0.317	0.027	
		Year (2017)	0.357	0.028	
		Year (2018)	-0.193	0.040	
	breeding + season + sex + year + (1|ind.)	Intercept	-4.543	0.565	8
		Breeding (yes)	-0.327	0.057	
		Season (livestock)	0.412	0.026	
		Sex (male)	-0.981	0.712	
		Year (2016)	0.317	0.027	
		Year (2017)	0.357	0.028	
		Year (2018)	-0.193	0.040	

SEASONAL CHANGES IN THE FORAGING AREAS OF THE GPS-TRACKED GRIFFON VULTURES

Griffon vultures tracking generated 11 805 GPS fixes in the study area and 544 429 outside it. According to the GLMM with higher performance, the proportion of inside vs. outside fixes depended on vulture breeding status, livestock season, sex, and year, as well as individual as random factor (**Table 3**). In particular, the proportion of GPS fixes inside the study area increased during the livestock season (**Fig. 3**), especially for non-breeding vultures and females, with some variation among years (**Table 4**). However according to R^2, this model had low explanatory capacity (4%), which became lower after excluding the variable "sex" (**Table 4**). During the livestock season, the proportion of GPS fixes inside vs. outside the study area increased for 19 individuals (c. 63% of the GPS-tracked individuals; **Fig. 3**A).

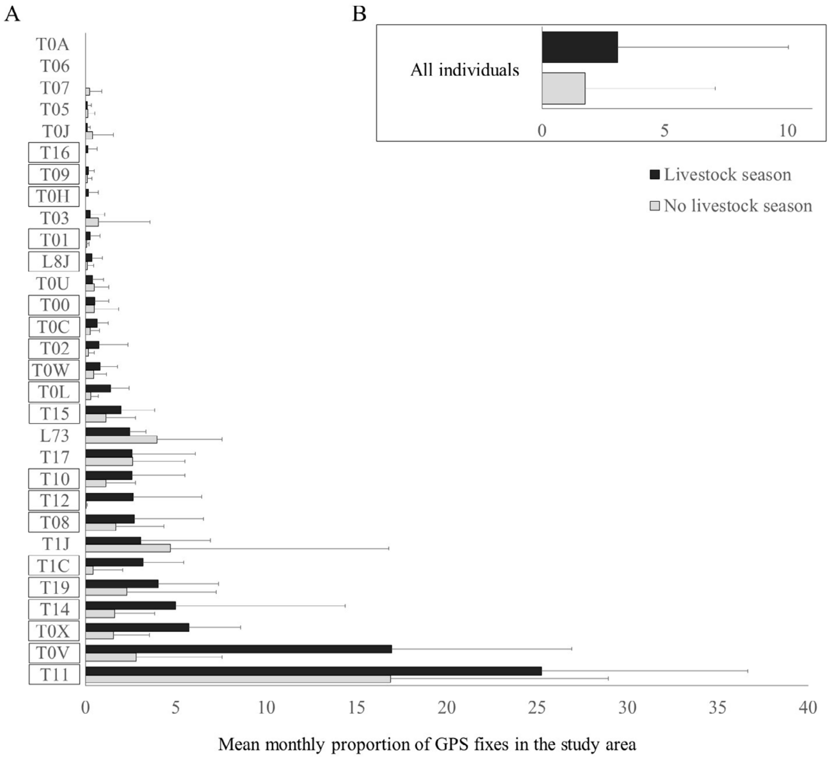

Figure 3. GPS fixes of the tracked griffon vultures in the study area during the livestock and no livestock seasons per tracked individual (A) and for all the tracked individuals together (B). Bars show the average of the monthly proportion of GPS fixes in relation to the total fixes; thin lines show the standard error. The individuals for which the proportion of fixes in the study area is higher during the livestock season than during the no livestock season are highlighted with boxes.

DISCUSSION

The results obtained from field observations and the GPS-tracked griffon vultures revealed that vulture (mostly griffons) abundance in the studied pastureland increased after transhumant herds had arrived. This agrees with previous research conducted in northern Spain, which found that the occurrence of griffon vultures increased at the roosting sites near transhumant sheep's summer pastures (Olea and Mateo-Tomás 2009). In contrast, the presence of transhumant livestock did not lead to an increase in the abundance of observed avian facultative scavengers. This was true even for species that frequently scavenge, such as the golden eagle, which is a regular carrion consumer in nearby Mediterranean mountains where griffon vultures are absent (Blázquez et al. 2009; Sánchez-Zapata et al. 2010). In the study area, however, golden eagles do not feed on livestock carcasses, likely because vultures quickly consume them (Arrondo et al. 2019). The high abundance of vultures here, especially during the livestock season, could therefore prevent other less efficient scavengers from responding to transhumant herds, as found in other areas and with other carcass types (Sebastián-González et al. 2013; Morales-Reyes et al. 2017).

These seasonal differences in carrion availability were probably perceived by griffon vultures, as c. two thirds of the GPS-tracked individuals increased their use of the study area during the livestock season (**Fig. 3**). However, our models indicated high inter-individual variability, so there must be other variables associated with the tracked individuals that influenced their movement, such as carrion availability outside the study area. In fact, this area is very small (c. 150 km^2) compared to the griffon vulture home range in southern Spain (average = c. 11 000 km^2; Arrondo et al. 2020b). Though this small area congregates more than 35 000 transhumant ungulates every summer, vultures may also find abundant food in many other areas within their home ranges (Arrondo et al. 2018; Arrondo et al. 2020b). For instance, Martin-Díaz et al. (2020) found that griffon vultures from south-eastern Spain widely forage in big game areas, feeding on wild ungulate carcasses from hunting activities. However, the main hunting season, which takes place in autumn-winter, overlaps only partially with the presence of transhumant herds in our study area. Outside the hunting season, griffon vultures greatly tend to forage in grasslands with abundant livestock (Martin-Díaz et al. 2020), as it is the case of our study area. Regardless, griffon vultures' observed individual response to transhumant livestock sufficed to trigger the above-mentioned strong seasonal variation in vulture abundance in the study area at the landscape level. An alternative, non-mutually exclusive explanation is that griffon vultures from other populations could also be attracted by transhumant herds to our study area, thus contributing to the increased vulture numbers there during the livestock season.

We also found that non-breeding and female griffon vultures were the individuals that responded the most to the presence of transhumant herds. On one hand, most of the griffon vultures observed using roosts near transhumant livestock in northern Spain were immature (Olea and Mateo-Tomás 2009). However, why breeding vultures respond less to an abundant food resource that is very close to their nesting sites is difficult to explain. On the other hand, griffon vultures have very slight sexual dimorphism (Xirouchakis and Poulakakis 2008) and share chick-rearing investment (XirouchakKis and Mylonas 2007). Thus, finding differences between sexes was an unexpected result. This contrasts to other vulture species with marked sexual dimorphism, such as Andean condors (*Vultur gryphus*), which show different resource exploitation patterns (Perrig et al. 2021). However, recent studies suggest that sex-partitioning in resource exploitation on a fine scale should not be ruled out in griffons (Arrondo et al. 2020a; Arrondo et al. 2020b). In any case, our results do not support a strong influence of the studied individual traits on griffon vulture responses to transhumant livestock.

Transhumance implies that the presence of domestic ungulates is drastically different between seasons. Although the seasonal absence of livestock could facilitate access of wild ungulates to the plateau after release from pasture competition, which occurs in other areas (Chirichella et al. 2014), our results showed that wild ungulates' seasonal abundance did not change seasonally. This might be due to the harsh climatic conditions in winter, which limits pasture availability in the plateau. In autumn-winter, some big game hunting takes place in the study area, which could make wild ungulates more cautious during this period. This generally means that when transhumant livestock leaves the plateau, carrion availability in the study area sharply declines, which leads to vultures' lower abundance and foraging activity.

Overall, our findings indicate that pasturelands with extensive livestock are important foraging areas for vultures. Although livestock farming has historically been involved in landscape transformation, extensive livestock farming might support high biodiversity values compared to intensive farming practices (Bernués et al. 2016). In particular, extensive farming modulates plant diversity in mountain pastures (Komac et al. 2014) and limits the vegetation succession in rewilding contexts (Riedel et al. 2013). Nevertheless, the global trend of increasing resources demand to supply the growing human population drives the intensification of production systems. Thus, the risk of traditional livestock practices, such as transhumance, being completely replaced with more intensive techniques in the near future is high, especially in developed countries. This may seriously compromise the sustainable development of human societies, as intensive farming demands high inputs of energy, water, and feed, which is linked to land degradation, water pollution, greenhouse gas emission, and, eventually, biodiversity loss (Ilea 2009). Thus, if the rewilding process is not properly managed, this situation could compromise not only vultures' conservation, but also the maintenance of other values associated with traditional activities, including local ecological knowledge (Oteros-Rozas et al. 2013b). In Mediterranean areas, the social stakeholders linked to extensive farming systems (e.g., shepherds) positively value scavengers' role (mostly vultures) as providers of ecosystem services (Cortés-Avizanda et al. 2018; Morales-Reyes et al. 2018). Therefore, loss of traditional practices as a result of disconnecting people from nature could imply a negative impact on the perception of the scavenger guild (Gigante et al. 2021) and a rise in harmful practices for scavengers, such as poisoning (Brink et al. 2021). Moreover, with the decline of extensive farming systems and the reduction of grassland areas in abandoned rural areas, scavenging birds will be driven to exploit resources in more anthropized landscapes, where the physiological condition and survival rates of vultures are lower (Arrondo et al. 2020b; Gangoso et al. 2021).

Until rewilding processes may lead to natural landscapes where wild ungulate carrion is made abundantly accessible to avian scavengers, it is essential for scavenger conservation to maintain extensive livestock farming against further development of intensive farming practices. This requires addressing the causes that are driving traditional farming systems towards extinction. Among them, the low profitability of the extensive livestock's product stands out as the main concern for Spanish farmers (Oteros-Rozas et al. 2013a). Hence, agro-economic policies need to be aimed at enhancing the market value of products by creating quality seals and effective publicity campaigns. In our study area, there is a system of public incentives, from both the European Union and regional administrations, that contributes to support transhumance, as well as an educational centre specialised in training young shepherds. These strategies have successfully helped to maintain a relatively important transhumant activity in this area, so they could also be implemented elsewhere. At the same time, intensive farming should be subject to stricter regulatory policies that allow minimize their multiple negative impacts on ecosystems and rural communities (Leip et al. 2015). Consequently, a more comprehensive understanding of the ecological consequences of abandoning traditional farming practices is crucial for environmental managers and policy makers to harmonize human activities and biodiversity in the current global ecological transition.

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REFERENCES

Acevedo, P., M. Á. Farfán, A. L. Márquez, M. Delibes-Mateos, R. Real, and J. M. Vargas. 2011. Past, present and future of wild ungulates in relation to changes in land use. *Landscape Ecology* 26: 19–31. doi:10.1007/s10980-010-9538-2.

Alarcón, P. A. E., and S. A. Lambertucci. 2018. A three-decade review of telemetry studies on vultures and condors. *Movement Ecology* 6. Movement Ecology: 1–13. doi:10.1186/s40462-018-0133-5.

Apollonio, M., R. Andersen, and R. Putman. 2010. *European ungulates and their management in the 21st century*. Edited by Marco Apollonio, Reidar Andersen, and Rory Putman. Cambridge University Press.

Arrondo, E., M. Moleón, A. Cortés-Avizanda, J. Jiménez, P. Beja, J. A. Sánchez-Zapata, and J. A. Donázar. 2018. Invisible barriers: Differential sanitary regulations constrain vulture movements across country borders. *Biological Conservation* 219: 46–52. doi:10.1016/j.biocon.2017.12.039.

Arrondo, E., Z. Morales-Reyes, M. Moleón, A. Cortés-Avizanda, J. A. Donázar, and J. A. Sánchez-Zapata. 2019. Rewilding traditional grazing areas affects scavenger assemblages and carcass consumption patterns. *Basic and Applied Ecology* 41: 56–66. doi:10.1016/j.baae.2019.10.006.

Arrondo, E., J. Navarro, J. M. Perez-García, R. Mateo, P. R. Camarero, R. C. R. Martin-Doimeadios, M. Jiménez-Moreno, A. Cortés-Avizanda, et al. 2020a. Dust and bullets: Stable isotopes and GPS tracking disentangle lead sources for a large avian scavenger.

Environmental Pollution 266. doi:10.1016/j.envpol.2020.115022.

Arrondo, E., A. Sanz-Aguilar, J. M. Pérez-García, A. Cortés-Avizanda, J. A. Sánchez-Zapata, and J. A. Donázar. 2020b. Landscape anthropization shapes the survival of a top avian scavenger. *Biodiversity and Conservation*. Springer Netherlands. doi:10.1007/s10531-020-01942-6.

Barton, K. 2013. MuMIn: Multi-Model Interference. R package version 1.9.13.

Bates, D., M. Martin, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1–48. doi:10.18637/jss.v067.i01.

Bernués, A., E. Tello-García, T. Rodríguez-Ortega, R. Ripoll-Bosch, and I. Casasús. 2016. Agricultural practices, ecosystem services and sustainability in High Nature Value farmland : Unraveling the perceptions of farmers and nonfarmers. *Land Use Policy* 59: 130–142. doi:10.1016/j.landusepol.2016.08.033.

Bibby, C. J., N. D. Burgess, D. M. Hillis, D. A. Hill, and S. Mustoe. 2000. *Bird census techniques*. 2nd ed. London: Elsevier.

Blanco, G., A. Cortés-Avizanda, Ó. Frías, E. Arrondo, and J. A. Donázar. 2019. Livestock farming practices modulate vulture diet-disease interactions. *Global Ecology and Conservation* 17: e00518. doi:10.1016/j.gecco.2018.e00518.

Blázquez, M., J. A. Sánchez-Zapata, F. Botella, M. Carrete, and S. Eguía. 2009. Spatio-temporal segregation of facultative avian scavengers at ungulate carcasses. *Acta Oecologica* 35: 645–650. doi:10.1016/j.actao.2009.06.002.

Brink, C. W., R. L. Thomson, A. Amar, M. Girardello, and A. Santangeli. 2021. Prevalence and drivers of poison use by South African commercial farmers and perceptions of alternative livestock protection measures. *Ambio* 50: 1211–1221. doi:10.1007/s13280-020-01461-2.

Bunce, R. G. H., M. Pérez-Soba, R. H. . Jongman, A. Gómez Sal, F. Herzog, and I. Austad. 2004. *Transhumance and Biodiversity in European Mountains, Report of the EU-FP5 project TRANSHUMOUNT (EVK2-CT-2002-80017)*. Edited by R.G.H. Bunce, M. Pérez-Soba, R.H.G Jongman, A. Gómez Sal, F. Herzog, and I. Austad. Alterra and IALE.

Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference. A practical information-theoretic approach* 2.

Chirichella, R., M. Apollonio, and R. Putman. 2014. Competition between domestic and wild and wild ungulates. In *Behaviour and Management of European Ungulates*, 110–123. Caithness: Whittles Publishing.

Corlett, R. T. 2016. The role of rewilding in landscape design for conservation. *Current Landscape Ecology Reports* 1: 127–133. doi:10.1007/s40823-016-0014-9.

Cortés-Avizanda, A., J. A. Donázar, and H. M. Pereira. 2015. Top Scavengers in a Wilder Europe. In *Rewilding European Landscapes*, ed. H. M. Pereira and L. M. Navarro, 85–106. Berlin: Springer International Publishing. doi:10.1007/978-3-319-12039-3_5.

Cortés-Avizanda, A., B. Martín-López, O. Ceballos, and H. M. Pereira. 2018. Stakeholders perceptions of the endangered Egyptian vulture: Insights for conservation. *Biological Conservation* 218. Elsevier: 173–180. doi:10.1016/j.biocon.2017.09.028.

DeVault, T. L., O. E. Rhodes, and J. A. Shivik. 2003. Scavenging by vertebrates: Behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102: 225–234. doi:10.1034/j.1600-0706.2003.12378.x.

Donázar, J. A. 1993. *Los buitres ibéricos: biología y conservación*. JM Reyero (in Spanish).

Gangoso, L., A. Cortés-Avizanda, A. Sergiel, B. Pudifoot, F. Miranda, J. Muñoz, A. Delgado-González, M. Moleón, et al. 2021. Avian scavengers living in anthropized landscapes have shorter telomeres and higher levels of glucocorticoid hormones. *Science of the Total Environment* 782: 146920. doi: 10.1016/j.

scitotenv.2021.146920.

Gigante, F. D., J. P. V. Santos, J. V. López-Bao, P. P. Olea, B. Verschuuren, and P. Mateo-Tomás. 2021. Farmers' perceptions towards scavengers are influenced by implementation deficits of EU sanitary policies. *Biological Conservation* 259: 109166. doi:10.1016/j.biocon.2021.109166.

Ilea, R. C. 2009. Intensive livestock farming: Global trends, increased environmental concerns, and ethical solutions. *Journal of Agricultural and Environmental Ethics* 22: 153–167. doi:10.1007/s10806-008-9136-3.

Komac, B., M. Domènech, and R. Fanlo. 2014. Effects of grazing on plant species diversity and pasture quality in subalpine grasslands in the eastern Pyrenees (Andorra): Implications for conservation. *Journal for Nature Conservation* 22: 247–255. doi:10.1016/j.jnc.2014.01.005.

Leip, A., G. Billen, J. Garnier, B. Grizzetti, L. Lassaletta, S. Reis, D. Simpson, M. A. Sutton, et al. 2015. Impacts of European livestock production: Nitrogen, sulphur, phosphorus and greenhouse gas emissions, land-use, water eutrophication and biodiversity. *Environmental Research Letters* 10: 115004. doi:10.1088/1748-9326/10/11/115004.

Margalida, A., J. A. Donázar, M. Carrete, and J. A. Sánchez-Zapata. 2010. Sanitary versus environmental policies: Fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology* 47: 931–935. doi:10.1111/j.1365-2664.2010.01835.x.

Margalida, A., M. À. Colomer, and D. Sanuy. 2011. Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. *PLoS ONE* 6: e20248. doi:10.1371/journal.pone.0020248.

Margalida, A., P. Oliva-Vidal, A. Llamas, and M. À. Colomer. 2018. Bioinspired models for assessing the importance of transhumance and transboundary management in the conservation of European avian scavengers. *Biological Conservation* 228: 321–330. doi:10.1016/j.biocon.2018.11.004.

MARM (Ministerio de Medio Ambiente y Medio Rural y Marino). 2011. *Libro Blanco de la transhumancia*. Edited by Ministerio de Medio Ambiente y Medio Rural y Marino. Madrid: Dirección de Desarrollo Sostenible del Medio Rural, Ministerio del Medio Ambiente, y Medio Rural y Marino (in Spanish).

Martin-Díaz, P., A. Cortés-Avizanda, D. Serrano, E. Arrondo, J. A. Sánchez-Zapata, and J. A. Donázar. 2020. Rewilding processes shape the use of Mediterranean landscapes by an avian top scavenger. *Scientific Reports* 10: 1–12. doi:10.1038/s41598-020-59591-2.

Martínez-Martínez, T. 2002. Comparison and overlap of sympatric wild ungulate diet in Cazorla, Segura y Las Villas Natural Park. *Pirineos* 157: 103–115. doi: 10.3989/pirineos.2002.v157.65.

Mateo-Tomás, P., and P. P. Olea. 2010. Diagnosing the causes of territory abandonment by the Endangered Egyptian vulture *Neophron percnopterus*: The importance of traditional pastoralism and regional conservation. *ORYX* 44: 424–433. doi:10.1017/S0030605310000189.

Mateo-Tomás, P., P. P. Olea, M. Moleón, N. Selva, and J. A. Sánchez-Zapata. 2017. Both rare and common species support ecosystem services in scavenger communities. *Global Ecology and Biogeography* 26: 1459–1470. doi:10.1111/geb.12673.

Ministerio de Agricultura Pesca y Alimentación. 2019. Efectivos y producciones ganaderas. 8.1.4.2. Efectivos ganaderos-ganado ovino:analisis provincial del número de animales según tipos, 2019 (Noviembre) (in Spanish).

Moleón, M., J. A. Sánchez-Zapata, A. Margalida, M. Carrete, N. Owen-Smith, and J. A. Donázar. 2014. Humans and scavengers:

The evolution of interactions and ecosystem services. *BioScience* 64: 394–403. doi:10.1093/biosci/biu034.

Moleón, M., N. Selva, M. M. Quaggiotto, D. M. Bailey, A. Cortés-Avizanda, and T. L. DeVault. 2019. Carrion availability in space and time. In *Carrion Ecology and Management*, ed. P. P. Olea, P. Mateo-Tomás, and J. A. Sánchez-Zapata, 23–44. doi:https://doi.org/10.1007/978-3-030-16501-7_2.

Moleón, M., A. Cortés-Avizanda, J. M. Pérez-García, J. Bautista, C. Geoghegan, M. Carrete, A. Amar, J. A. Sánchez-Zapata, et al. 2020. Distribution of avian scavengers inside and outside of protected areas: contrasting patterns between two areas of Spain and South Africa. *Biodiversity and Conservation* 29: 3349–3368. doi:10.1007/s10531-020-02027-0.

Del Moral, J. C., and B. Molina. 2018. *El buitre Leonado en España, población reproductora en 2018 y método de censo*. Madrid: SEO/BirdLife (in Spanish).

Morales-Reyes, Z., J. A. Sánchez-Zapata, E. Sebastián-González, F. Botella, M. Carrete, and M. Moleón. 2017. Scavenging efficiency and red fox abundance in Mediterranean mountains with and without vultures. *Acta Oecologica* 79: 81–88. doi:10.1016/j.actao.2016.12.012.

Morales-Reyes, Z., B. Martín-López, M. Moleón, P. Mateo-Tomás, F. Botella, A. Margalida, J. A. Donázar, G. Blanco, et al. 2018. Farmer Perceptions of the Ecosystem Services Provided by Scavengers: What, Who, and to Whom. *Conservation Letters* 11: 1–11. doi:10.1111/conl.12392.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133–142. doi:10.1111/j.2041-210x.2012.00261.x.

Navarro, L. M., and H. M. Pereira. 2015. Rewilding Abandoned Landscapes in Europe. In *Rewilding European Landscapes*, ed. H. M. Pereira and L. M. Navarro, 3–23. Berlin: Springer International Publishing. doi:10.1007/978-3-319-12039-3_1.

Ogada, D. L., F. Keesing, and M. Z. Virani. 2012. Dropping dead: causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences* 1249: 57–71. doi:10.1111/j.1749-6632.2011.06293.x.

Olea, P. P., and P. Mateo-Tomás. 2009. The role of traditional farming practices in ecosystem conservation: The case of transhumance and vultures. *Biological Conservation* 142: 1844–1853. doi:10.1016/j.biocon.2009.03.024.

Oteros-Rozas, E., B. Martín-López, C. A. López, I. Palomo, and J. A. González. 2013a. Envisioning the future of transhumant pastoralism through participatory scenario planning: a case study in Spain. *The Rangeland Journal* 35: 251–272. doi:http://dx.doi.org/10.1071/RJ12092.

Oteros-Rozas, E., R. Ontillera-Sánchez, P. Sanosa, E. Gómez-Baggethun, and V. Reyes-García. 2013b. Traditional ecological knowledge among transhumant pastoralists in Mediterranean Spain. *Ecology and Society* 18. doi:http://dx.doi.org/10.5751/ES-05597-180333.

Parra, J., and J. L. Tellería. 2004. The increase in the Spanish population of Griffon Vulture *Gyps fulvus* during 1989 – 1999: effects of food and nest site availability. *Bird Conservation International* 14: 33–41. doi:10.1017/S0959270904000048.

Pérez-García, J. M., J. A. Sánchez-Zapata, S. A. Lambertucci, F. Hiraldo, and J. A. Donázar. 2018. Low-frequency , threatened habitats drive the large-scale distribution of Andean Condors in southern Patagonia. *Ibis* 160: 647–658. doi:10.1111/ibi.12563.

Pérez, J. M., M. Sarasa, G. Moço, J. E. Granados, J. P. Crampe, E. Serrano, L. Maurino, P. G. Meneguz, et al. 2014. The effect of data analysis strategies in density estimation of mountain ungulates using distance sampling. *Italian Journal of Zoology* 82: 262–270. doi:10.1080/11250003.2014.974695.

Perrig, P. L., S. A. Lambertucci, P. A. E. Alarcón, A. D. Middleton, J. Padró, P. I. Plaza, G. Blanco, J. A. Sánchez-Zapata, et al. 2021. Limited sexual segregation in a dimorphic avian scavenger, the Andean condor. *Oecologia* 196: 77–88. Springer Berlin Heidelberg. doi:10.1007/s00442-021-04909-8.

Putman, R., M. Apollonio, and R. Andersen. 2011. *Ungulate Management in Europe: Problems and Practices*. Cambridge University Press.

R Core Team. 2019. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Riedel, J. L., A. Bernués, and I. Casasús. 2013. Livestock grazing impacts on herbage and shrub dynamics in a Mediterranean Natural Park. *Rangeland Ecology & Management* 66: 224–233. doi:10.2111/REM-D-11-00196.1.

Rivas-Martínez, S. 1987. *Mapa de las Series de Vegetación de España*. Madrid: ICONA (in Spanish).

Ruxton, G. D., and D. C. Houston. 2004. Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology* 228: 431–436. doi:10.1016/j.jtbi.2004.02.005.

Sánchez-Zapata, J. A., J. A. Donázar, A. Delgado, Forero, Manuela G., O. Ceballos, and F. Hiraldo. 2007. Desert locust outbreaks in the Sahel: resource competition, predation and ecological effects of pest control. *Journal of Applied Ecology* 44: 323–329. doi:10.1111/j.1365-2664.2007.01279.x.

Sánchez-Zapata, J. A., S. Eguía, M. Blázquez, M. Moleón, and F. Botella. 2010. Unexpected role of ungulate carcasses in the diet of Golden Eagles Aquila chrysaetos in Mediterranean mountains. *Bird Study* 57: 352–360. doi:10.1080/00063651003674946.

Sebastián-González, E., J. A. Sánchez-Zapata, J. A. Donázar, N. Selva, A. Cortés-Avizanda, F. Hiraldo, M. Blázquez, F. Botella, et al. 2013. Interactive effects of obligate scavengers and scavenger community richness on lagomorph carcass consumption patterns. *Ibis* 155: 881–885. doi:10.1111/ibi.12079.

Seré, C., A. van der Zijpp, G. Persley, and E. Rege. 2008. Dynamics of livestock production systems, drivers of change and prospects for animal genetic resources. *Animal Genetic Resources Information* 42: 3–24. doi:10.1017/s1014233900002510.

Tejedor-Rodríguez, C., M. Moreno-García, C. Tornero, A. Hoffmann, Í. García-Martínez de Lagrán, H. Arcusa-Magallón, R. Garrido-Pena, J. I. Royo-Guillén, et al. 2021. Investigating Neolithic caprine husbandry in the Central Pyrenees: Insights from a multi-proxy study at Els Trocs cave (Bisaurri, Spain). *Plos One* 16: e0244139. doi:10.1371/journal.pone.0244139.

Vergara, P. 2010. Time-of-day bias in diurnal raptor abundance and richness estimated by road surveys. *Revista Catalana d'Ornitologia* 26: 22–30.

Vincent, J.-P., J.-M. Gaillard, and E. Bideau. 1991. Kilometric index as biological indicator for monitoring forest roe deer populations. *Acta Theriologica* 36: 315–328.

Wink, M., H. Sauer-Gürth, F. Martinez, G. Doval, G. Blanco, and O. Hatzofe. 1998. The use of (GACA)4 PCR to sex old world vultures (Aves: Accipitridae). *Molecular Ecology* 7: 779–782. doi:10.1046/j.1365-294x.1998.00377.x.

Xirouchakis, S. M., and N. Poulakakis. 2008. Biometrics, sexual dimorphism and gender determination of Griffon Vultures Gyps fulvus from Crete. *Ardea* 96: 91–98. doi:10.5253/078.096.0110.

XirouchakKis, S. M., and M. Mylonas. 2007. Breeding behaviour and parental care in the griffon vulture *Gyps fulvus* on the Island of Crete (Greece). *Ethology Ecology and Evolution* 19: 1–26. doi:10.1080/08927014.2007.9522578.

Zuur, A., E. N. Leno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. New York: Springer.

CHAPTER 2.

Biases in the detection of intentionally poisoned animals: Public health and conservation implications from a field experiment

Photo by the author.
Common genet (*Genetta genetta*) detected by camera trap in the Sierras de Cazorla, Segura y las Villas, feeding on the experimental baits.

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ABSTRACT

Intentional poisoning is a global wildlife problem and an overlooked risk factor for public health. Managing poisoning requires unbiased and high-quality data through wildlife monitoring protocols, which are largely lacking. We herein evaluated the biases associated with current monitoring programmes of wildlife poisoning in Spain. We compared the national poisoning database for the 1990–2015 period with information obtained from a field experiment during which we used camera-traps to detect the species that consumed non-poisoned baits. Our findings suggest that the detection rate of poisoned animals is species-dependent: Several animal groups (e.g., domestic mammalian carnivores and vultures) tended to be over-represented in the poisoning national database, while others (e.g., corvids and small mammals) were underrepresented. As revealed by the GLMM analyses, the probability of a given species being overrepresented was higher for heaviest, aerial, and cryptic species. In conclusion, we found that monitoring poisoned fauna based on heterogeneous sources may produce important biases in detection rates; thus, such information should be used with caution by managers and policy-makers. Our findings may guide to future search efforts aimed to reach a more comprehensive understanding of the intentional wildlife poisoning problem.

Keywords: human-wildlife conflict; predator control; public health; vultures; wildlife conservation; wildlife poisoning

INTRODUCTION

Intentional poisoning is a critical global wildlife conservation problem that may affect individuals, populations, and even entire communities [1–5]. Consequently, many countries have passed strict legislation with severe penalties and invested considerable resources to reduce wildlife poisoning [1,3,6–8]. However, these measures have largely proved insufficient to date, and deliberate poisoning is still pervasive (e.g., [8,9]). Although many reasons lie behind this illegal activity, most are associated with human–wildlife conflicts related to predator control in game hunting and livestock farming areas [2,10], hence the most impacted species are mammalian carnivores and large raptors [2,6,11,12]. One dramatic example is the thousands of vultures that have been poisoned by elephant and rhino poachers and traditional medicine users in Africa in recent years [3,9,13].

Managing poisoning events requires high-quality data on the species, location and the number of individuals affected, which can be obtained through detection protocols of poisoned wildlife. However, as systematic approaches are rare, searching efforts may be biased by not only substantially underrepresenting the number of real events and affected individuals, but also overestimating the representation of certain species that may be more conspicuous or attractive to researchers and conservationists [3]. Frequently, poisoned animals are opportunistically detected by people who accidentally find them dead and inform local authorities. Thus, an accurate quantification of the potential impact of poison and its population-scale consequences requires improving the detection rate of poisoning animals and a comprehensive identification of affected species [3,14,15].

To date, several methods have been proposed to obtain a more complete approach to the wildlife poisoning problem. For instance, telemetry is a useful tool to evaluate the relative importance in the study population of different mortality causes, including poisoning [16,17]. However, telemetry is costly in both logistic and economic terms and its use is prevented on a large spatial-temporal scale. Dogs may also be efficiently trained to detect wildlife poisoning [18]. Currently, these canine patrols are successfully operating in Spain and other European countries, frequently as part of LIFE projects [19]. However, the information obtained through these procedures is probably biased towards the most likely detected species, such as the largest ones, domestic animals or endangered species, which are the object of monitoring programmes. To improve management and conservation actions, these biases should be evaluated.

Here we take Spain as a case study because it is one of the most biodiverse countries in the European Union according to the IUCN (https://www.iucn.org/regions/europe/resources/country-focus/spain), with 27.4% of the Spanish territory included in the Natura 2000 network. In this country, the use of poison has been considered a crime since 1995 (Organic Law 10/1995 of the Criminal Code), and at least 160 judgements have been made for illegal poisoning. National regulatory legislation was established in 2007 (Law 42/2007 on Natural Heritage and Biodiversity) and is applicable regionally by each Spanish Autonomous Community in different action plans. Yet despite Spain being a pioneer in the application of criminal law and administrative sanctions in Europe [20], wildlife poisoning is still a frequent illegal activity performed mainly to kill predators in game hunting areas and on pasturelands [2,18,21]. Every year, hundreds of individuals of threatened species, such as the Spanish imperial eagle (*Aquila adalberti*) [22], Egyptian vultures (*Neophron percnopterus*) [12], cinereous vultures (*Aegypius monachus*) [11], bearded vultures (*Gypaetus barbatus*) [16], and brown bears (*Ursus arctos*) [23], are poisoned. Furthermore, poisoning has been described as a major factor that contribute to the population decline of Egyptian vultures [24,25] and red kites (*Milvus milvus*) [4] on local and national scales. In addition, poisoning frequently involves domestic animals, including pets (particularly dogs and cats) and livestock [18,26], which might pose public health a risk. Given the environmental and public health consequences of intentional poisoning, research is necessary to improve the assessment of the risk associated with this activity.

Our main goal was to explore whether an experiment using non-poisoned baits could reveal the potential biases associated with the long-term Spanish poisoned fauna database. We compared this database to the information obtained from a field experiment in which we used camera-traps to detect the species that consumed non-poisoned baits. Our starting hypothesis was that the detection rate of poisoned animals would be species-dependent, which could lead to under or overestimate the representation of certain species in the poisoning database. Thus, our study could have profound implications for wildlife management, with important ramifications for domestic animals and human health.

2. MATERIALS AND METHODS

STUDY AREAS

The study was carried out in six areas of peninsular Spain (**Figure 1A**): Sierra de Cabrera (hereafter Cabrera); Sabinar de Calatañazor—Sierra de Cameros (hereafter Cameros); Pre-Pyrenees of Lleida (hereafter Pre-Pyrenees); Sierra Harana (hereafter Harana); Cazorla, Segura y Las Villas Natural Park (hereafter Cazorla); and Sierra Escalona (hereafter Escalona). These areas are located in different administrative regions (six provinces) and covering a wide gradient in environmental conditions (three Mediterranean areas and three transitional Mediterranean to Euro-Siberian areas), land uses (livestock types and densities, and intensity and type of sport game activities), presence and abundance of obligate scavengers and top predators (i.e., wolves *Canis lupus*), and degrees of protection, ranging from unprotected areas to the largest Spanish protected area (Cazorla, **Figure 1A**, **Table 1**). Thus, we obtained a wide representation of the socio-environmental variability that characterises peninsular Spain, including areas with the presence of particularly vulnerable species to poisoning (vultures) and others considered controversial that are usual targets for poisoning (wolves; [2]; see **Table 1** for details).

Table 1. Description of the six study areas.

Area	Habitat Type	Hunting Type/ Intensity	Natural Park	Livestock/ Density	Vulture Abundance	Wolf Abundance
Cabrera	Mosaic of transitional Mediterranean to Euro-Siberian scrubs, forests and meadows	Small and big game/ low	No	Cattle, sheep/ high	Low	High
Pre-Pyrenees	Mosaic of transitional Mediterranean to Euro-Siberian forests and meadows	Small and big game/ low	No	Cattle, sheep/ high	High	(Absent)
Cameros	Mosaic of transitional Mediterranean to Euro-Siberian forests and meadows	Small and big game/ medium	No	Cattle, horses, sheep/high	High	Low
Harana	Mosaic of xeric Mediterranean scrubs, forests and crops	Small and big game/ high	No	Sheep, goats/ low	Low	(Absent)
Cazorla	Mediterranean forests	Big game/ medium	Yes	Sheep, goats/ medium	High	(Absent)
Escalona	Mosaic of xeric Mediterranean scrubs, forests and crops	Small game/high	No	Sheep/very low	(Absent)	(Absent)

POISONING DATABASE

We used the "Antídoto Programme" database (https://www.venenono.org/), which compiles data from poisoning events in Spain from 1990 to 2015. A poisoning event in this database is defined as the finding of a poisoned bait and/or a group of animals (one individual or mores of one species or several) poisoned by the same poison and bait types, and in a given spatiotemporal location (within 1 km and 1 month) [2,27]. For each event, data include the affected species, date and location. In all, the "Antídoto Programme" registered 18,212 poisoned individuals of 182 species, with widespread events throughout Spain (**Figure 1A**). Data availability varied depending on the administrative region, with some regions investing lots of poisoning search efforts (e.g., Andalusia, South Spain, Catalonia, Northeastern Spain), while others barely reported any data [28]. The most frequently found species were dogs (*Canis lupus familiaris*), red foxes (*Vulpes vulpes*), domestic cats (*Felis silvestris catus*), and several scavenging bird species [18]. Information on bait type was provided in 16.2% of database records (n = 2011), with the most commonly used being pieces of meat (50.7%), followed by sausages (6.5%) and eggs (5.7%). Bait usage frequency varied among areas (**Figure 1B**).

The location of poisoning events was recorded at the municipality level (**Figure 1A**). For our study, we extracted the number of poisoned individuals per species recorded in the municipalities included in each study area. Because of the limited sample size, we were unable to analyse the effects of bait type on the number of individuals and species affected by poisoning. This limitation also led us to consider the whole period for the available data without separating it into different subperiods.

FIELD EXPERIMENT

To detect and quantify the community of animal species that can potentially feed on poisoned baits, we designed a field experiment by a non-invasive methodology based on the monitoring of non-poisoned baits. As baits, we used those identified by the "Antídoto Programme" as the most widely used bait types: small meat pieces (one fresh chicken piece, 100 g), sausages (one sausage, 50 g) and eggs (three chicken eggs, 70 g each, placed together to simulate a ground nests). At each study site, we deployed 10 baits of each type from March 2019 to September 2019, which included the period of the year with the highest poisoning incidence in Spain [18].

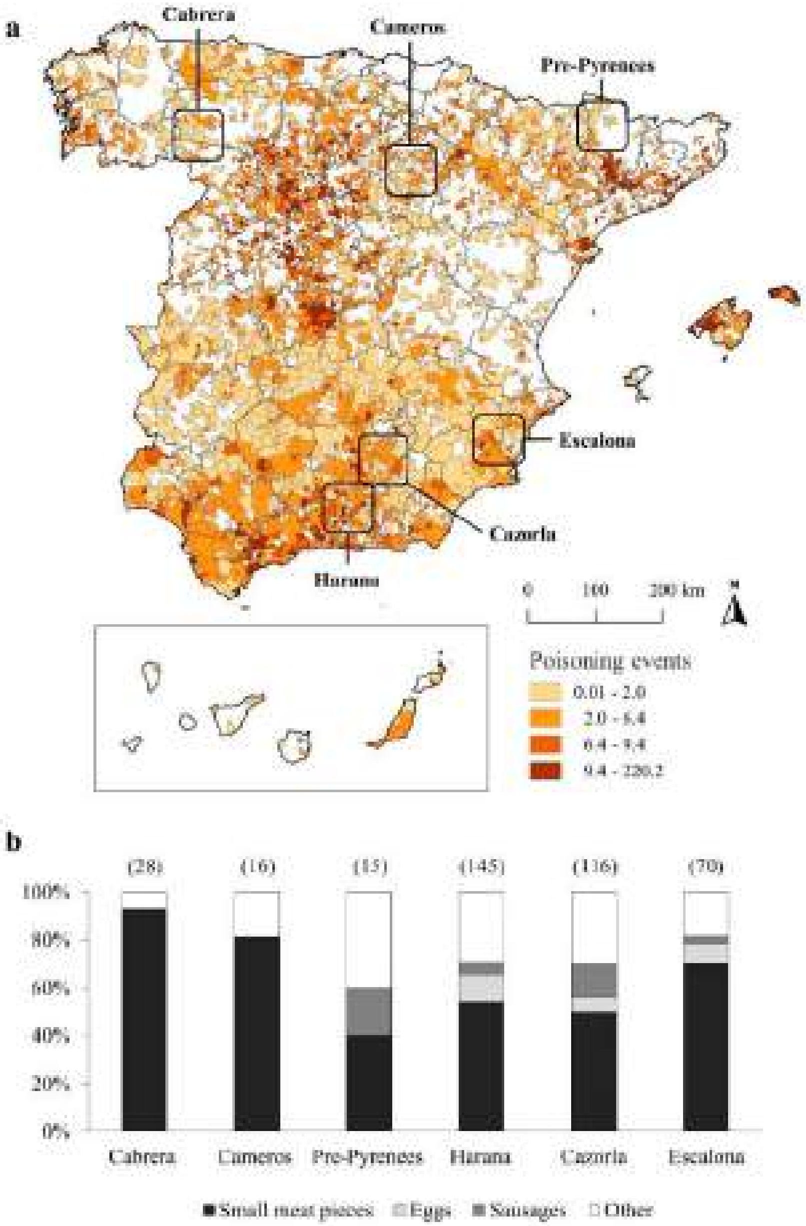

Figure 1. Poisoning events from the national database ("Antídoto Programme") for the 1990–2015 period. (**a**) Distribution of poisoning events in Spain based on municipalities (no. of poisoning events per 100 km^2 of municipality surface) and location of the six study areas. Grey lines delimit the administrative provinces. Blank areas denote lack of data, which should not be interpreted as zero poison. (**b**) Bait types used to poison the fauna in the study areas, as recorded in the national poisoning database. Number of events are in brackets.

Finally, we monitored the consumption process of 161 baits by means of passive infrared triggered cameras (Bushnell HD™ and Browning Strike Force HD™) placed 4–6 m away from baits. Cameras were programmed to take three pictures per trigger, with a 30-s delay whenever they detected movement. Meat pieces and sausages were fixed to the ground by wire or some similar material to ensure they were consumed in front of the cameras. Baits were placed on wildlife paths to simulate poisoners' *modus operandi*. The distance between cameras was generally >1 km [29], except for Escalona and Pre-Pyrenees, where they were separated <200 m to simulate gamekeepers and shepherds' reported local poisoning strategy. Experiments were reviewed weekly until bait had completely disappeared. If after 1 month bait remained untouched, we still finished the experiment. Generally, due to its small size, each bait was consumed only by one individual of each scavenger species that visited the site with bait. Thus, per individual bait, each consumer species was taken as one individual in the subsequent analyses.

ETHIC STATEMENT

We conducted the field experiment without handling or disturbing wildlife. Authorisations to photograph wildlife using bait attractants were obtained from the respective administrative offices in the study areas (EP/SO/389/2019, SF/002, 47/CV/20, SGMN/GyB/JMIF). If the study was conducted on private property, express authorisation was requested from owners.

STATISTICAL ANALYSES

First, we classified the different species into nine groups following taxonomic and behavioural criteria as follows: wild carnivores (i.e., mammalian carnivores); domestic carnivores (dogs and cats); suids (wild boar *Sus scrofa*); small mammals (rodents, shrews, hedgehogs); corvids; vultures; other raptors; other birds; and reptiles. Separately for each study area, we compared the representation of each group (frequency of occurrence) between both data sources: the "Antídoto Programme" poisoned animals database and the field experiment results. Frequency of occurrence was defined as the percentage of the total number of individuals: (a) poisoned (the "Antídoto Programme" database) and (b) recorded consuming baits (field experiment) that corresponded to a given group. Comparisons of frequencies were made by χ^2 tests on 2 × 2 contingency tables. Bonferroni's correction was applied for *P*-levels.

Second, we used Generalised Linear Mixed Models (GLMMs; [30]) to explore the factors that potentially influenced the differences between both data sources (the "Antídoto Programme" database and the field experiment) in the representation of the different species. Specifically for a given species in a certain area, our response variable was the number of poisoned individuals included in the "Antídoto Programme" database, minus the number of baits consumed by that species during the field experiment. Thus, the value could be positive or negative, depending on whether the species was over- or underrepresented, respectively, in the poisoning database in relation to the field experiment data. Study area was included as random factor, while fixed factors were: species weight (mean adult—female and male—weight in Spain in kg; log-transformed); colour (conspicuous –with the presence of black and white or shiny black patches—/cryptic otherwise); mobility (aerial—birds—/terrestrial—mammals and reptiles—); sociality (social—foraging in large or family groups—/solitary—foraging alone or in pairs—); and conservation status (endangered/non-endangered) (see Table S1 for species details). The weight data were obtained from the Virtual Encyclopaedia of Spanish Vertebrates (http://www.vertebradosibericos.org/) and [31]. First, we constructed two models with all the explanatory variables (no interactions were considered given the small sample size): one with no random term and another one with a random term. Then we selected the model with the most appropriate random structure by a restricted maximum likelihood (REML) procedure and the glmer() function of the *lme4* package of R [32]. We used Gaussian error distributions and identity link functions. Having identified the most suitable random structure (i.e., with a random term; see the Results), we selected the model with the most appropriate fixed structure using maximum likelihood (ML). For this purpose, we explored the complete set of alternative models using the dredge() function of the *MuMIn* package of R [33]. We then proceeded to model selection, according to Akaike's information criterion corrected for small sample sizes (AIC_c). By this approach, we identified the most parsimonious model (lowest AIC_c) by ranking the remaining models from the lowest to highest delta-AIC_c (the difference in AIC_c between each model and the most parsimonious model). We considered those models with delta-AIC_c <2 to have similar support [34]. Then we recalculated the selected model by REML, and the resulting model was taken as the final model. The final model's performance was assessed by calculating marginal R^2, which measures how much variability of the response variable is explained by the model's fixed term [35]. To do so, we used the r.squaredGLMM() function of the *MuMIn* package of R [33]. All the analyses were conducted with the R statistical software (https://www.r-project.org/).

RESULTS

In the six study areas, we detected 38 species actually or potentially suffering from intentional poisoning (27 species included in the poisoning database and 26 species feeding on the experimental baits) (**Tables 2 and 3**, **Figure 2)**. According to the poisoning database, the most frequent groups were wild and domestic carnivores, vultures, and other raptors, while wild carnivores, small mammals and corvids were the groups that most frequently consumed experimental baits (**Figure 3B**). The most represented species in the study areas were domestic dogs (108 individuals poisoned; three experimental baits consumed), griffon vultures (104 individuals poisoned; seven experimental baits consumed) and red foxes (62 individuals poisoned; 57 experimental baits consumed; Table S2). The pool of species detected either in the field experiment or the poisoning database well represents the Spanish community of wild carnivores, corvids and raptors, especially vultures, as the four European species were represented between the two data sources (**Table 2**). Most of the chicken pieces (95.8%) and sausages (95.1%) used in the experiment were completely consumed, while nearly half the egg groups (41.2%) remained untouched at the end of the experiment.

We found differences ($p < 0.0005$ with Bonferroni's correction) between both data sources for 15 comparisons (27.7% of 54 χ^2 comparisons), with three groups detected at higher rates than expected by random in eight comparisons (14.8%) and another three groups were underdetected in seven comparisons (12.9%; **Figure 3)**. In general, the results among the six areas were consistent: For wild carnivores and other raptors, we found no differences between data sources in five areas; for domestic carnivores, we found an over-representation in the poisoning database in five areas; for suids, other birds and reptiles, of which very few were detected, we found no differences between data sources in all the areas (**Figure 3)**. Corvids and small mammals were underrepresented in the poisoning database in three areas, and vultures were overrepresented in this database in two areas; in other areas, we found no difference in the representation of these groups between data sources (**Figure 3)**. Thus, we found no contrasting results for any group; i.e., overrepresentation in the poisoning database in one area, but underrepresentation in the poisoning database in another area, or vice versa.

Table 2. Number of species recorded as poisoned in the "Antídoto Programme" database and observed feeding on baits during the field experiment in the six study areas per species group. The total shows the number of species that occurred in both the database and the experiment. We also show the number of species of each group that are present in peninsular Spain, along with the percentage of species that represents those involved in this study.

Source	Wild Carnivores	Domestic Carnivores	Suids	Small Mammals	Corvids	Vultures	Other Raptors	Other Birds	Reptiles	N
Database	6	2	1	2	4	3	9	1	1	27
Experiment	5	2	1	3	5	3	3	4	2	26
Total	7		1	5	5	4	9	5	2	38
Spain	16 (44%)		1 (100%)	34 (15%)	9 (56%)	4 (100%)	31 (29%)	528 (1%)	57 (4%)	680 (6%)

Figure 2. Individuals of the nine species groups feeding on experimental baits. (**a**). Wild carnivores, *Vulpes vulpes*. (**b**). Domestic carnivores, *Canis lupus familiaris*. (**c**). Suids, *Sus scrofa*. (**d**). Small mammals, *Eliomys quercinus*. (**e**). Corvids, *Corvus corone*. (**f**). Vultures, *Aegypius monachus*, *Gyps fulvus* and *Neophron percnopterus*. (**g**). Other raptors, *Falco tinnunculus*. (**h**). Other birds, *Parus major*. (**i**). Reptiles, *Timon lepidus*.

As revealed by the GLMMs (**Table S3**), the factors that influenced the differences between the number of poisoned individuals included in the "Antídoto Programme" database and the number of individuals recorded consuming baits during the field experiment were the species' weight, colour and mobility. According to marginal R^2, this model explained c. 20% of the variability in the response variable. Study area (i.e., random term) was also included in the selected model (Table S3). However, this variable explained very little variability of the response variable (0.7%), which agrees with the results described in the previous paragraph. In particular, heavy, aerial and cryptic species were overrepresented in the poisoning database vs. the field experiment compared to light, terrestrial and conspicuous species (**Table 3**).

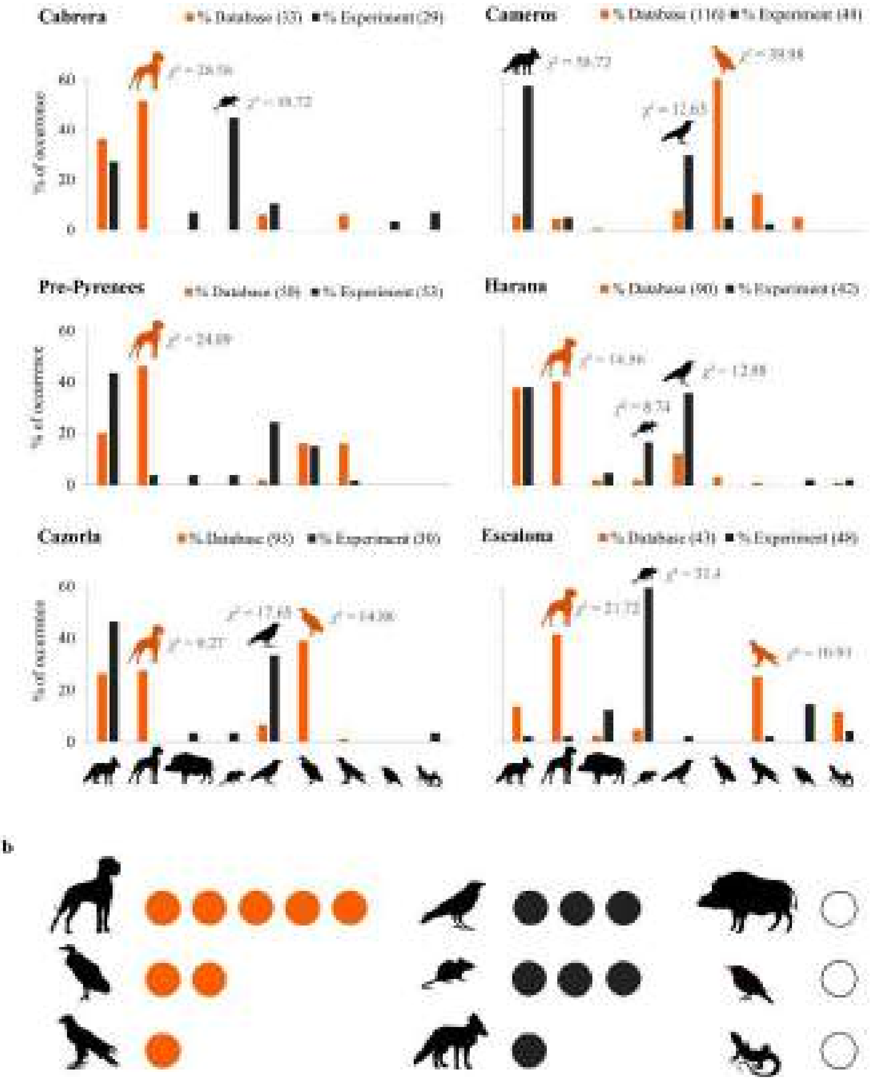

Figure 3. Comparison between the national poisoned fauna database ("Antídoto Programme") and the field experi-ment results according to the different species groups and study areas. (a) Frequency of occurrence of individuals in each group recorded in the "Antídoto Programme" (orange bars) compared to the percentage of baits consumed during the field experiment per group (from left to right: wild carnivores, domestic carnivores, suids, small mammals, corvids, vultures, other raptors, other birds, and reptiles). Brackets indicate the total number of poisoned individuals in the da-tabase and the estimated total number of different individuals that consumed baits (see the text for details). The pair-wise χ^2 tests results are shown whenever we detected significant differences between both data sources ($p < 0.05$). (b) Number of study areas in which each group was over- (orange dots) or underrepresented (black dots) in the nation-al database compared to the results of experimental baits. White dots denote the groups for which we detected no sig-nificant differences between data sources.

Table 3. Selected Linear Generalised Mixed Model (GLMM) showing the variables explaining the difference between (a) the number of poisoned individuals included in the "Antídoto Programme" database and (b) the number of individuals recorded consuming baits during the field experiment. The estimates of the parameters (including the sign) and the standard error of parameters (SE) are shown.

Parameter	Estimate	SE
(Intercept)	1.154	1.325
weight	3.612	0.950
color (conspicuous)	−5.139	1.960
mobility (aerial)	4.289	1.863

4. DISCUSSION

By a field experiment to identify the community of species that are potentially poisoned in different Spanish areas, we evaluated possible biases in the detection rates of poisoned animals resulting from current wildlife poisoning monitoring programmes to offer a pioneering approach to this key global wildlife conservation problem [36].

Our main hypothesis was supported by data as the detection rates differed among poisoned species. We identified three factors that influence the probability of a species being over- or underrepresented in the poisoning database in relation to bait-based field experiment results. First, larger species were more susceptible to be overrepresented in the poisoning database, which is likely because these species are easier to detect by searchers [37]. Second, compared to mammals and reptiles, birds were more frequently poisoned than expected according to the field experiment, which could be explained by secondary poisoning. Birds like vultures and other raptors might feed on the carcasses of animals that have been previously poisoned. Secondary poisoning may affect mainly birds because of their higher response capacity due to great searching and movement abilities compared to terrestrial animals [38,39]. Our experiment was unable to capture these cascading effects, which could be relevant to fully assess the impact of poisoning along the food web, as previously described for rodenticides [40]. Third, conspicuous species like those herein defined (see Materials and Methods) were more susceptible to be underrepresented in the poisoning database. This is probably because most conspicuous species were either rare (e.g., bearded and Egyptian vultures), with a limited contribution to the global pattern, or, especially, corvids. Corvids comprise a relatively conspicuous group of medium-sized birds with non-cryptic colours that are relatively abundant in the study areas. Thus, their underrepresentation in poisoning records could be related to a lesser local effort in monitoring them as they are not target species of conservation programmes. The fact that they are common could imply that they are ignored when considering species affected by poisoning events. However, this should not be the case of regions in which efficient canine patrols operate, specifically if they look for poisoned baits and dead animals. Moreover, we assigned only one individual to each species that was observed feeding on a given bait. This could lead to an underrepresentation of small gregarious species (e.g., several corvid species) as larger species like carnivores normally ate all the bait. Therefore, alternative explanations for low corvid detection rates by poisoned fauna searchers are required, but difficult to establish.

Besides corvids, poisoned small mammals and wild carnivores were underrepresented in poisoning records. This was expected for small mammals because this group includes several small-sized burrowing species, which are difficult to detect after poisoning events [41], especially in closed habitats. In addition, small carcasses could also degrade faster [42] and may disappear before being detected. Also, several small mammal species are considered "pests", which may lead searchers to ignore them. To solve this problem, it is necessary to develop specific monitoring programmes for those scenarios with endangered small-sized species. Despite being the subject of several scientific and conservation monitoring programmes in Spain, the representation of mammalian carnivores in the poisoning database was no higher than that expected based on the field experiment results. Indeed, poisoned wild carnivores were underrepresented in one study area (Cameros), a result that could be partially related to local monitoring procedures, which apparently focus more on locating poisoned vultures and partially disregard other poisoned species (**Figure 3**). In any case, other factors like species-specific behavioural responses might influence these results. Carnivores, like corvids, are major facultative scavengers worldwide [43,44] and may display flexible behaviours and outstanding learning capacity [45,46]. These abilities can help them to avoid consuming poisoned baits and other risky carrion sources [29]. Thus, with fierce poisoning pressure, carnivores and corvids might refuse to eat potentially risky baits. For example, our experiment found that wolves detected at least two (non-poisoned) baits in the only study areas where they were present, but did not consume them.

Poisoned pets like dogs and cats, were recorded in the national poisoning database more often than when they were observed in the field experiment in most of the study areas. This was an expected result because these pets are easier to detect than smaller species. In addition, a higher presence of pets would be expected near inhabited areas [47], whereas field experiments were run in natural areas, usually far from these areas. Moreover, dogs and cats are probably more familiar with the bait types commonly used for poisoning than wild species are [48], which could increase the risk of the former being poisoned due to reduced aversion or neophobia to baits [49]. Also, pet owners might often report the occurrence of poison to authorities because they look for their missing pets or contact their veterinarians whenever they suspect a poisoning event [26]. Pets might pose a high public health risk because of their proximity to humans. Similarly, poisoned wild boars could also be taken into account because of their potential consumption by humans.

We found some geographical variations in the detection bias of poisoned fauna. Geography-based variations were affected by administrative divisions, which determined: 1) the local poison sources and preferred way to poison (**Figure 1B**); and 2) the different poisoning monitoring approaches followed by environmental authorities [18]. For example, the specialised canine patrols that detect poisoned animals or baits in some Spanish Autonomous Communities (e.g., Andalusia, where two of the study areas were located: Harana and Cazorla) are well-known for increasing the efficiency of searches [18]. In addition, the presence and management of hunting areas may affect poisoning type and intensity [11,12]. Unfortunately, the "Antídoto Programme" database does not allow a more detailed analysis of the different geographical scenarios because it does not record the methodological approaches used to detect poisoning. In any case, the fact that the study area was relatively unimportant in the GLMMs indicated that geographical differences must be related mainly to the detection rate of poisoned animals (i.e., with some areas invest more search efforts than others) rather than to differences in the probability of over- or underrepresenting poisoned species. This suggests that the people involved in poisoning detection from different administration may share similar search criteria. However, whether these criteria for searching poisoned fauna have changed with time is an open question.

CONCLUSIONS AND CONSERVATION IMPLICATIONS

Intentional poisoning is a global conservation concern for scavenger species, especially vultures [3,13,24,50,51], but also other endangered species [4]. Poisoning big game species, such as wild boars, and pet species, such as dogs and cats, may pose a risk for humans. Thus, deliberate poisoning is not only a wildlife problem, but an environmental and human health matter.

We found potentially important biases in the detection of different animal groups that are vulnerable to deliberate poisoning, even within administrative divisions with exceptional global poisoning monitoring programmes. We particularly highlight that the detection rate of poisoned fauna from current monitoring schemes based on heterogeneous sources is strongly species-dependent. So, these data must be interpreted with caution. Having identified the several species traits influencing the detection rate of poisoned animals, our findings may guide future search efforts to more comprehensively understand the extent of the intentional poisoning problem. This could mean that, from a practitioner viewpoint, the personnel responsible for wildlife vigilance (e.g., guards, rangers, gamekeepers) can conform to an appropriate tool to detect poisoning events that affect vultures and other raptors, especially if they are supported by local people previously trained by education and engagement programmes [18]. Given the biases revealed by this field experiment, more attention should be paid to consider small mammals and corvids found dead as susceptible to poisoning. Few administrative regions currently operate with specialised canine units, which are essential to improve the detection of poisoned fauna [37]. Therefore, implementing canine units in all regions would be a priority in the fight against wildlife poisoning [52]. All these measures could benefit from the establishment of a national body that coordinates anti-poisoning strategies [52]. Only by developing unbiased monitoring programmes for deliberate poisoning can we achieve healthy ecosystems for wildlife, domestic animals and humans.

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Chapter 3.
Role of scavengers in providing non-material contributions to people

Photo by Carlos Javier Durá Alemañ.
Grey Wolf (*Canis lupus signatus*) detected by camera trap in the Sierra de la Cabrera (León).

This chapter corresponds to the article:

Aguilera-Alcalá, N., Morales-Reyes, Z., Martín-López B., Moleón, M., Sánchez-Zapata, J.A., 2020. Role of scavengers in providing non-material contributions to people. *Ecol. Indic.* 117, 106643. https://doi.org/10.1016/j.ecolind.2020.106643

ABSTRACT

In today's societies, scavengers play an important role as providers of nature's contribution to people (NCP), such as disease control and carcass removal. Yet very little is known about the non-material NCP (i.e. nature's effects on subjective and psychological aspects of people's well-being) that scavengers provide societies with. The first aim of this study is to determine which species of obligate and facultative scavengers provide different non-material NCP in Spain, including recreational and aesthetic experiences, learning and inspiration, and supporting identities. The second aim is to identify which ecological variables determine their capacity to provide the aforementioned non-material NCP. To assess non-material NCP nationwide, data were collected from different sources, including the Internet (websites of nature photography and wildlife watching tours, Global Biodiversity Information Facility, and Google Trends), outreach magazines and scientific articles. A top predator, *Canis lupus,* followed by another top scavenger, *Gyps fulvus,* were among the most prominent species to provide multiple non-material NCP. Aesthetic experiences were provided mainly by common species, such as *Genetta genetta*, *Milvus migrans* and corvids. The NCP of recreation and learning by civil society were provided by threatened and charismatic species, such as *C. lupus*, *Ursus arctos* and *Aquila adalberti*. Knowledge acquired by scientists was provided mainly by meso-carnivores. Finally, the NCP of supporting identities was related with species capable of providing beneficial and detrimental contributions, such as *C. lupus* and *Sus scrofa*. Integrating data mined from different sources has allowed it to reveal the interweaving among non-material categories. Recognising that all species of scavengers are essential for providing non-material NCP can raise society's awareness about their important cultural role and may, hence, contribute to their conservation.

Keywords: cultural ecosystem services; functional traits; people's quality of life; physical and psychological experiences; social media; vultures.

INTRODUCTION

In the last 20 years, a new stream of studies has emerged to disentangle the link between nature and humans (Costanza et al., 2017) to highlight the dependence of human well-being on the maintenance of ecosystem functioning. This dependence on nature was first named "nature's services" by Westman (1977), but it was from Daily (1997) and Costanza et al. (1997)'s publications when this topic began to receive wider scientific attention. The term "ecosystem services" was formalised in the Millennium Ecosystem Assessment (2005) to define the direct or indirect benefits that people obtain from ecosystem functioning. Recently, and drawing on the ecosystem service concept, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) has coined the concept of "nature's contributions to people" (NCP), which comprises both positive and negative effects of living nature to people's quality of life (Díaz et al., 2018). The generalising perspective of NCP, which seeks to compare multiple NCP, recognises three broad categories: regulating, material and non-material. Regulating NCP refers to the functional and structural aspects of ecosystems and biodiversity that contribute to societies' well-being by modifying environmental conditions and regulating the provision of material and non-material NCP. Material NCP are elements collected from ecosystems and biodiversity that directly contribute to people's physical existence through supplies; e.g. food, energy or raw materials. Non-material NCP are nature's effects on the subjective and psychological aspects of people's well-being, including recreational and aesthetic experiences, learning and inspiration, and supporting identities (which in this research refers to people's satisfaction derived from knowing that a particular species exists) (Díaz et al., 2018).

Most previous research into ecosystem services and NCP has focussed to date on material and regulating contributions (Luederitz et al., 2015; Fagerholm et al., 2016; Hevia et al., 2017) and has left non-material NCP underrepresented (Daniel et al., 2012; Milcu et al., 2013). Different reasons have been argued for this underrepresentation of non-material NCP, such as the epistemological challenge of engaging with multiple disciplinary and methodological perspectives (Milcu et al., 2013), and the challenge of unpacking the interlinkages between biodiversity and non-material NCP (UK NEA, 2011; Balvanera et al., 2016). In addition, little research has focused on understanding which functional traits of biodiversity are important for the provision of non-material NCP (Hevia et al., 2017), despite linking functional traits with non-material NCP provision can offer a way to understand people's appreciation of biodiversity (Echeverri et al., 2019).

Furthermore, some taxonomic groups and functional guilds in ecosystem services and NCP research have received little attention, such as vertebrates (Cardinale et al., 2012; Hevia et al., 2017) and the scavenger guild (Moleón et al., 2014; DeVault et al., 2016). However, scavengers (i.e. animals that rely totally -obligate scavengers- or partially -facultative scavengers- on carrion as a food resource) have always benefited humans by helping to find food, providing feathers and other animal tissues as ornamental resources (i.e. material NCP), controlling diseases and pests by eliminating carcasses, and recycling nutrients (i.e. regulating NCP; Moleón et al., 2014). Scavengers have contributed to the well-being of ancient societies by providing non-material NCP too. For example, vultures were involved in many sacred rituals and celebrations held by Egyptians and Native Americans (Gordillo, 2002; Morelli et al., 2015). In addition, human-scavenger relations also lead to conflicts because of the predatory behaviour of some species. For example, top predators in Europe and North America, such as the grey wolf (*Canis lupus*) and the brown bear (*Ursus arctos*), have been historically persecuted and hunted for years because their attacks to livestock and game species (Chapron et al., 2014). In Africa, hyaenas (*Crocuta crocuta*, *Hyaena* sp.), lions (*Panthera leo*) and leopards (*P. pardus*) have been killed in retaliation for livestock predation (e.g. Kissui et al., 2008; Yirga et al., 2014; Koziarski et al., 2016), and in Asia, tigers (*P. tigris*), snow leopards (*Uncia uncia*) and leopards may cause livestock losses (e.g. Sangay and Vernes, 2008, Battharai and Fischer, 2014; Carter et al., 2014; Johansson et al., 2015). Moreover, farmers may also perceive that vultures attack their livestock. For example, in South America, farmers associate the Andean condor (*Vultur gryphus*) with predation of sheep and cattle (Manzano-García et al., 2017; Restrepo-Cardona et al., 2019). Likewise, in Southern Europe farmers have complaint reports about griffon vultures (*Gyps fulvus*) attacking livestock (Margalida et al., 2011, 2014; Duriez et al., 2019).

In today's societies, scavengers also play a relevant role in providing NCP, particularly regulating. For instance, Old World vultures contribute widely to regulate zoonotic diseases (O'Bryan et al., 2018), to remove human corpses in the Zoroastrian culture (Markandya et al., 2008), to remove organic material (Grilli et al., 2019) and to remove waste in urban areas (Gangoso et al., 2013). Some scavenging mammals, such as spotted hyenas (*Crocuta crocuta*) and golden jackals (*Canis aureus*), contribute to the removal of livestock carcass and waste in rural environments (Yirga et al., 2015; Ćirović et al., 2016). In Spain, scavengers contribute to reduce greenhouse gas emissions through the natural elimination of livestock carcasses that should otherwise be transported in trucks to incineration and processing plants (Morales-Reyes et al., 2015). Although there is evidence for the importance of scavengers to provide regulating NCP, their role in the provision of non-material NCP remains understudied. Only a few studies have explored the role of particular scavengers on providing wildlife-based tourism and recreation in protected areas. For example, large carnivores have been identified in Africa as potential providers of non-material NCP, such as wildlife-based tourism and aesthetic experiences (Willemen et al., 2015; Ament et al., 2017). Moreover, it has been estimated that the economic annual value of viewing the Eurasian griffon vulture (*Gyps fulvus*) in Israel to be more than 1.1 million USD (Becker et al., 2005).

Despite the importance of scavengers providing NCP, many are globally endangered species, particularly vultures and large carnivores (Estes et al., 2011; Ogada et al., 2012; Ripple et al., 2014). On the one hand, 12 of the 23 vulture species are globally threatened (nine of them are Critically Endangered; IUCN, 2018). Poisoning, climate change, sanitary policies on leaving domestic carcasses in the field, and collision with wind turbines and power lines are some of the main causes that lead to declining vulture populations (DeVault et al., 2016). On the other hand, top-predators are globally threatened as a result of a wide array of human-related impacts (Estes et al., 2011). In addition to these pressures, the skewed viewpoints provided by magazines and media as to damage caused by scavengers, i.e. attacks on livestock by vultures (Margalida et al., 2011) or wolves (Dressel et al., 2015), foster negative social perceptions that challenge the conservation of scavengers (O'Bryan et al., 2018). However, social perceptions of scavengers vary according to the functional guild. For example, whereas obligate scavengers (i.e. vultures) are usually perceived positively by farmers as providers of NCP, some facultative scavengers are negatively perceived due to their role as predators (e.g. foxes, wolves and bears) (Morales-Reyes et al., 2018). Moreover, conflicts and detrimental NCP have been more widely studied in the scientific literature than the beneficial NCP provided by carnivores (Expósito-Granados et al., 2019; Lozano et al., 2019), which can also influence social perceptions of scavengers and social support for their conservation (Martín-López et al., 2009). Evidencing the beneficial NCP provided by scavengers may not only contribute to improve scientific knowledge but might also promote positive social perceptions and support conservation policies.

The main goal of this study is to assess the beneficial role played by vertebrate scavengers in people's well-being by uncovering the provision of non-material NCP. In particular, it firstly aims to determine which scavenger species are able to provide: (1) physical and psychological experiences related to recreational and aesthetic enjoyment; (2) learn and inspire in association with knowledge acquisition; (3) supporting identities (i.e. people's satisfaction derived from knowing that a particular scavenger exists). Secondly, it aims to identify which ecological variables (i.e. conservation status, taxonomy and functional traits) determine scavengers' capacity to provide non-material NCP. We considered both obligate (vultures) and facultative scavengers (other raptors, corvids and mammals). We conducted this study in Spain, which hosts more than 90% of European vultures (Margalida et al., 2010) and important populations of large facultative scavengers, such as the brown bear and the grey wolf (Chapron et al., 2014).

METHODS

DATA COLLECTION

To determine the role of scavengers as providers of non-material NCP, we collected 12 indicators of: *physical and psychological experiences*, particularly aesthetic enjoyment and recreation; *learning and inspiration,* derived from knowledge acquisition; *supporting identities,* based on people's satisfaction derived from knowing that a particular scavenger species exists (see **Table 1**). We considered 22 obligate and facultative scavenger species that inhabit in Spain (see the complete list in **Table D.1** in **Appendix D**).

To assess the aesthetic enjoyment provided by scavengers, we used three different indicators to represent the aesthetic relevance of these species through photography. The photographs posted on social media platforms, such as Panoramio, Instagram and Flickr, have been used to evaluate people's aesthetic appreciation of species (Willemen et al., 2015; Martínez Pastur et al., 2016), with Spain being one of the countries with more users of social media in relation to Important Bird and Biodiversity Areas (Hausmann et al., 2019). In this research, we used the images posted on Fotonatura (www.fotonatura.org), which represents the Spanish-speaking nature photographers' community. The Fotonatura platform has already been used to assess cultural ecosystem services associated with trees in the Iberian Peninsula (Vaz et al., 2018). We derived three quantitative indicators to represent the aesthetic enjoyment

Table 1. Indices and indicators used to assess non-material nature's contributions to people (NCP) provided by scavengers in Spain based on six sources of information: photography, wildlife-based tourism, outreach magazines, the Global Biodiversity Information Facility (GBIF), scientific articles and Google Trends. Associations between indices and non-material NCP were established based on the literature.

Index	Indicators	Non-material NCP	References
Photography	1. Percentage of photos posted relative to the total number of scavenger's photos 2. Average number of received views 3. Average number of received votes	*Physical and psychological experiences*, particularly aesthetic enjoyment. They can also represent recreational experiences, and *supporting identities* (people's satisfaction of knowing that a species exists).	Willemen et al., 2015; Martínez Pastur et al., 2016
Wildlife-based tourism	1. Percentage of websites offering wildlife-based tours related to each species relative to the total of records 2. Average number of times that each species name appears on the websites	*Physical and psychological experiences*, particularly recreational experiences based on wildlife-based tourism. They can also represent aesthetic enjoyment, and *supporting identities* (people's satisfaction of knowing that a species exists).	Nahuelhual et al., 2013
Outreach magazines	1. Percentage of covers in which each species appears relative to the total of issues 2. Percentage of issues in which each species appears on their headlines relative to the total of issues 3. Percentage of articles in which each species appears in the summary relative to the total of the summaries	*Learning and inspiration*, particularly citizens acquiring knowledge. They can also represent *Physical and psychological experiences*, particularly recreational experiences, and *supporting identities* (people's satisfaction of knowing that a species exists).	Herrera, 1989; Sastre et al., 2004
The GBIF	1. Percentage of recorded human observations relative to the total of records 2. Percentage of recorded human observations relative to the total of records, excluded the records of the official census of the Spanish Ministry of the Environment	*Learning and inspiration*, particularly scientists acquiring knowledge.	UN Environment World Conservation Monitoring Centre, 2017
Scientific articles	1. Percentage of publications of each species in the biodiversity conservation literature relative to the total number of reviewed articles	*Learning and inspiration*, particularly scientists acquiring knowledge.	Fazey et al., 2005; Velasco et al., 2015
Google Trends	1. Average search score	*Supporting identities,* based on human satisfaction of knowing that a particular scavenger exists.	Nghiem et al., 2016; Soriano-Redondo et al., 2017

of scavengers of each species: (1) the percentage of photos posted for each species relative to the total number of scavenger's photos; (2) the average number of received views in the photos by the Fotonatura audience; (3) the average number of obtained votes. Of the 38,454 photos posted between 2000 and 2016 on Fotonatura in Spain, we selected those that represented any of the 22 species considered herein; i.e. 1,174 images (3.05% of all the photos posted on Fotonatura). All the analysed images were stored in the Fotonatura gallery "geotagged" to check geographical locations, and were assigned to the dominant species on the photograph or whose species name appeared in its title. We considered images representing both wild and captive animals.

To assess the recreational experiences provided by scavengers, we collected information on wildlife-based tourism in Spain. We used two different indicators: (1) the percentage of websites that advertise wildlife watching tours and include any of the 22 species regards to the total web reviewed; (2) the average number of times that each species name appears on each website. To identify those websites offering nature-based tours related to the 22 scavenger species, in 2017 we searched on the World Wide Web using Google's Search Engine. We used a search string for each species, which included either its popular English name or scientific name, recreational activity, i.e. "wildlife watching", and location, i.e. "Spain" (see details in **Appendix A**). We analysed those websites provided by the first five Google search pages, by excluding personal comments and blogs, reports about wildlife-based tours and governmental information webs. We also excluded those websites that presented captive animals, such as zoos. We obtained 150 records on 40 different websites.

We evaluated *learning and inspiration* by considering the knowledge acquired by citizens and scientists. To assess the knowledge acquired by citizens, we examined the Spanish outreach magazine *Quercus*, which is the oldest and most prestigious publication related to the study, observation and defence of nature (Martínez-Abraín et al., 2013). Both authors and the readership include researchers from universities and other scientific institutions, environmental managers, NGOs' stuff and other agents concerned with national and international wildlife. *Quercus* sales 12 000 copies per month and has more than 40 000 followers in social networks (https://revistaquercus.es/). We used three indicators: (1) the percentage of covers in which each species appears, relative to the total issues; (2) the percentage of issues in which each species appears on their headlines, relative to the total issues; (3) the percentage of articles in which each species appears in the summary, relative to the total articles in the summaries. We explored all the 204 issues with a total number of 3254 articles in the summaries published from 2000 to 2016.

To assess the knowledge acquired by scientists, we collected information from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/) and from English peer-reviewed scientific articles. The GBIF is the largest initiative worldwide to provide information about the occurrence of organisms over time and across space (Yesson et al., 2007; Otegui et al., 2013). In fact, the GBIF has been suggested as a useful tool to monitor the status and trends of biodiversity knowledge (CBD, 2016). In 2017 we searched the occurrence of the 22 scavenger species in the Spanish node of the GBIF (http://datos.gbif.es) between 2000 and 2016, which is considered the most representative sample of the biodiversity data available in the country (Otegui et al., 2013). Our search was conducted using the scientific name between quotation marks for each species, using two indicators: (1) the percentage of recorded human observations of each species, relative to the total of records for the 22 scavenger species; (2) the percentage of recorded human observations for each species, relative to the total of records for the 22 scavenger species, after excluding the official census records of the Spanish Ministry of the Environment in 2007 (MAPAMA, 2013). In addition, to assess the knowledge acquired by scientists, we also conducted a systematic review of scientific articles in English peer-reviewed scientific articles about the 22 scavenger species in Spain using the Web of Science engine. The search string comprised three main elements: (1) the functional group of scavengers (i.e. scavenger, scavenging and vulture); (2) species' scientific names; (3) their geographic location, i.e. 'Spain' (see **Appendix A** for the search string details). Searching was conducted in the research area of 'biodiversity conservation'. To avoid double counting in the review, we searched for original articles, but not reviews and conferences. The search was applied to the Abstract, Title and Keywords of articles published between 2000 and 2016. The search returned 460 articles and (see list of references in **Appendix B**). We calculated as indicator the percentage of publications of each species relative to the total number of reviewed articles.

To evaluate *supporting identities*, we explored the search volume on the Internet of each species by using Google Trends Search Engine (https://trends.google.es/trends/). Google Trends has been suggested to be one of the best proxies to assess public curiosity, attention and issue salience (Burivalova et al., 2018), also as indicator of the public interest in biodiversity and conservation topics (Ladle et al., 2016; Nghiem et al., 2016) and the public's perception of conservation (Soriano-Redondo et al., 2017).

Therefore, we used Google Trends as a proxy for acquiring information that supports identity development. Despite using Google Trends to assess the NCP of supporting identities, we are aware that other sources of information, such as photography, wildlife-based tourism and outreach magazines, can also represent this NCP (**Table 1**). In this study, we extracted information from public searches made on the Internet by searching through each species' scientific name in quotations, filtered through the *bird* and *animal* categories and geographical locations in Spain. The use of scientific names and a category filter ensured that the data extracted from Google Trends were associated only with species to avoid any source of bias due to homonyms. For example, the term 'buitre' (i.e. vulture in Spanish) often refers to 'vulture funds', which actually presents information about political corruption. The search was done for the period between January 2004 (the beginning of the available data) and December 2016. In Google Trends, a search request can be conducted only to compare up to five species. The extracted data return a monthly score, which represents the frequency of any search query in Google between 0 to 100, with 100 being the peak of a relative search volume for each keyword of the search query during the requested period. To compare the search volume on the Internet of the 22 scavengers on the same scale, we first detected that the wolf was the species with the highest monthly scores before including it as reference in all the search queries of five species. Using the extracted data, we calculated the average score for each species.

To study the relationship between non-material NCP and species, we considered different functional traits of the species: body mass, foraging activity, home range, fecundity and diel activity. In addition, we included the conservation status (i.e. threatened or non-threatened species) and the taxonomic group (i.e. vultures, raptors -excluding vultures-, corvids and mammals) of scavenger species. We selected these functional traits because they are suitable to study the functional diversity of scavengers in Spain and they have been used to associate functional diversity with scavenging NCP (Morales-Reyes et al., 2018). **Appendix D** presents data details per species (**Table D.1**) and description of considered traits (**Table D.2**).

DATA ANALYSES

We created six indices of scavenger contribution to represent the non-material NCP according to the information sources (**Table 1**): photography, wildlife-based tourism, outreach magazines, the GBIF, scientific articles and Google Trends. Before creating the six indices and allowing their comparability, we scaled the values of the 12 indicators from 0 to 1 by considering the maximum value to be 1 and weighting the rest. To create the indices that were comprised by more than one indicator (i.e. photography, wildlife-based tourism, outreach magazines and the GBIF; **Table 1**), we summed up the scaled indicators and then we scaled the indices between 0 and 1 (see **Appendix C** and **Figure C.1** for calculation details of indices).

To explore whether the taxonomic group can determine scavengers' capacity to provide non-material NCP to society, we performed median and mean comparison tests (i.e. analysis of variance (ANOVA) for photography and wildlife-based tourism, and the Kruskal-Wallis test for outreach magazines, Google Trends, the GBIF and scientific articles; $\alpha = 0.05$). Before the comparison analysis, we tested normality by the Shapiro-Wilk test ($\alpha = 0.05$).

To determine which ecological variables underpinned scavengers' capacity to provide non-material NCP, we performed a canonical correspondence analysis (CCA). We used the six indices as the dependent variables in the CCA. We included conservation status, taxonomic group and functional traits (body mass, foraging activity, home range, fecundity and diel activity) as explanatory variables (see **Table D.1** in **Appendix D** for details). To avoid heteroscedasticity, we log-transformed the continuous variables; i.e. body mass and fecundity. We employed the Monte Carlo permutation test (500 iterations) to test the significance of the CCA.

We used the XLSTAT software (version 2016.04, Addinsoft) to conduct all the statistical analyses.

RESULTS

The species that contributed to provide non-material NCP varied across the six indices (**Figure 1A**), although the grey wolf emerged among the three most relevant species in four indices: photography, wildlife-based tourism, outreach magazines and Google Trends. Besides the wolf, the most relevant species in the index associated with photography were the common genet (*Genetta genetta*) and the griffon vulture.

However, the saliency of these species varied according to the particular indicator used. Whereas griffon vultures were the most photographed, wolves obtained the most received views and common genets received the most votes (**Figure 1B**). Regarding wildlife-based tourism, the wolf had the highest score, followed by the Spanish imperial eagle (*Aquila adalberti*) and the brown bear (**Figure 1A**). In this case, the wolf was the most prominent species in the two indicators used: the number of websites advertising wildlife-based tourism (together with the Spanish imperial eagle) and the number of times each species was named in each website (**Figure 1B**). In the index of outreach magazines, apart from bearded vultures (*Gypaetus barbatus*), two facultative scavengers, wolves and bears, were the most prominent species (**Figure 1A**). Wolf was the most important species in the three indicators used to assess the knowledge acquired by citizens: number of covers, number of issues with headlines, number of articles (**Figure 1B**). Regarding the knowledge acquired by researchers, we found differences for most of the relevant species between both indices (i.e. the GBIF and scientific articles). Whereas griffon vultures, black kites (*Milvus migrans*) and carrion crows (*Corvus corone*) obtained the most observations in the GBIF, two mammalian scavengers, the wild boar (*Sus scrofa*) and the red fox (*Vulpes vulpes*), were found in more scientific articles (**Figure 1A**). Differences were also found in the source of the GBIF observations: whereas the black kite was the most observed when official censuses were considered, the griffon vulture had the highest record when official censuses were excluded (**Figure 1B**). Finally, Google Trends revealed that mammals were the focus of web search interest, especially the wolf and the wild boar (**Figure 1A**). Although different species of vultures, raptors, corvids and mammals were the most relevant in the different indices used to assess non-material NCP (**Figure 1A**), we did not find any significant differences among taxonomic groups for each index (**Figure 2**).

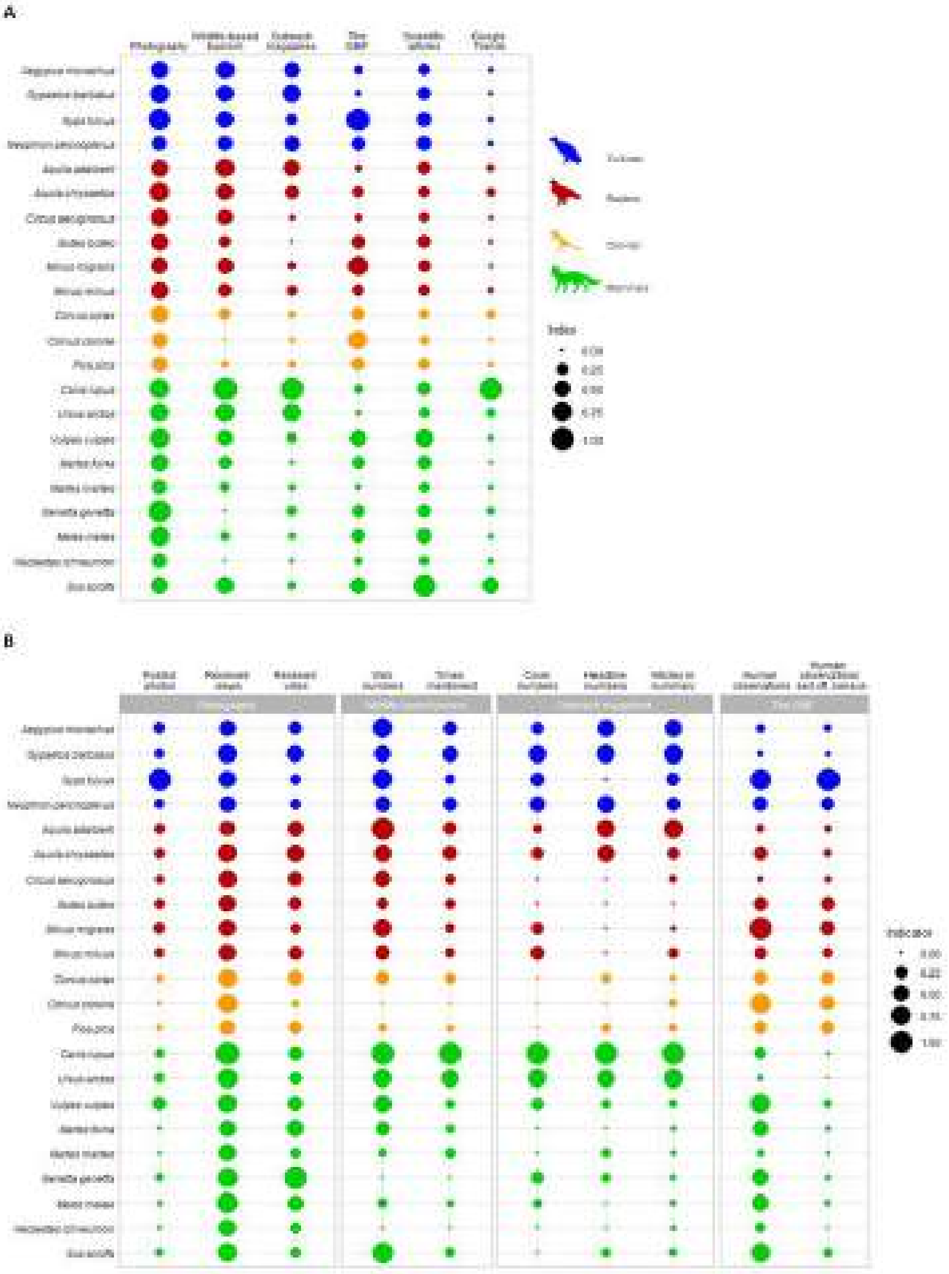

Figure 1. Scavengers contribution index by species in Spain. A. Indices showing non-material nature's contributions to people (NCP) provided by species. B. Indicators showing non-material NCP provided by species used to construct the indices that were comprised by more than one indicator (i.e. photography, wildlife-based tourism, outreach magazines and the GBIF). The different colours display the taxonomic groups -i.e., vultures (in blue), raptors (red), corvids (orange) and mammals (green)-. Calculation details of indices are in methods, **Appendix C** and **Figure C.1**. The comparison among taxonomic groups is shown in **Figure 2**.

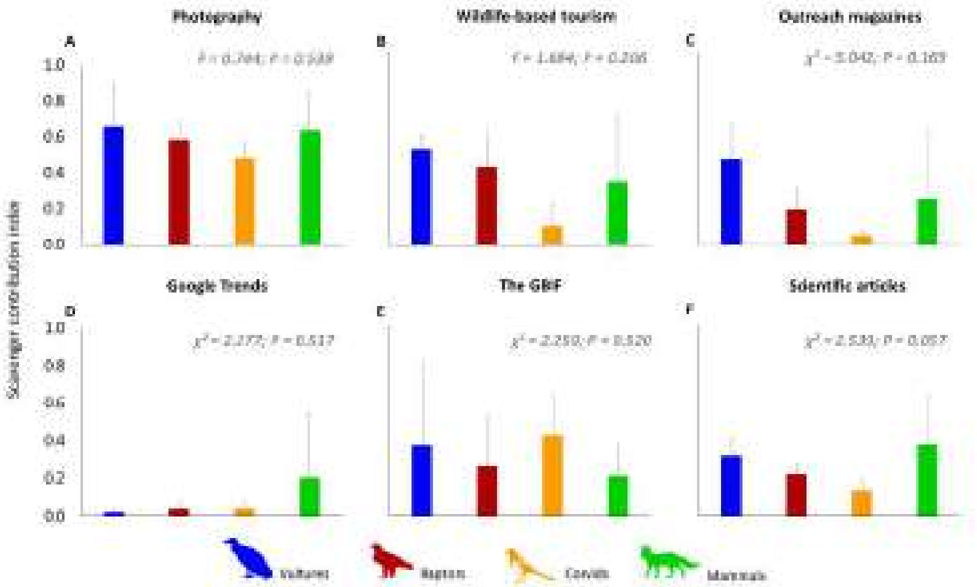

Figure 2. Scavenger contribution index by taxonomic groups in Spain. Bars and whiskers indicate the mean value of indices showing non-material nature's contributions to people (NCP) provided by taxonomic groups ± SD. Differences among taxonomic groups in photography and wildlife-based tourism were estimated by an ANOVA test (α = 0.05) and in outreach magazines, Google Trends, the GBIF and scientific articles by a Kruskal–Wallis test (α = 0.05). Calculation details of indices are in methods, **Appendix C** and **Figure C.1**. Results per species are shown in **Figure 1**.

The CCA showed statistically significant associations between the ecological variables and indices representing non-material NCP. Three axes explained 93.74% of total variance (**Table 2**). The first axis (56.17% of variance) revealed a gradient between the information sources of photography and the GBIF (in positive scores) and outreach magazines and wildlife tourism (in negative scores). Whereas photography and the GBIF of scavengers were associated with the taxonomic group of corvids and with non-threatened species with small body mass and small home range, the indices of outreach magazines and wildlife-based tourism were associated with threatened species, with large body mass and large home range (**Table 2**). Griffon vultures, carrion crows, magpies (*Pica pica*), ravens (*Corvus corax*), black kites, common buzzards (*Buteo buteo*), western marsh harriers (*Circus aeruginosus*), common genets and red foxes were the species associated with the positive scores of the first axis, i.e. photography and the GBIF. In contrast, the Spanish imperial eagle, the wolf and the brown bear appeared in the negative scores, i.e. wildlife-based tourism and outreach magazines (**Figure 3A**; **Table D.3** in **Appendix D**). The second axis (25.62%) represented Google Trends in its positive scores in relation to non-threatened species belonging to social mammals with high fecundity and nocturnal diel activity, i.e. wild boars (**Table 2**, **Figure 3A**; **Table D.3**). The third axis (11.95%) represented the index of scientific articles in its negative scores. This index was related with non-social mammals (**Table 2**), particularly with the Egyptian mongoose (*Herpestes ichneumon*), the Eurasian badger (*Meles meles*), the pine marten (*Martes martes*) and the stone marten (*M. foina*) (**Figure 3B**; **Table D.3**).

Table 2. Summary statistics and results of the CCA showing the associations between the indices representing non-material nature's contributions to people (NCP) provided by scavengers and the ecological variables (i.e. conservation status, taxonomic group and functional traits).

	Axis 1	Axis 2	Axis 3
Indices of non-material NCP			
Outreach magazines	**-0.635**	-0.383	0.067
Photography	**0.230**	-0.052	-0.150
Wildlife-based tourism	**-0.320**	-0.150	0.111
Google Trends	-0.817	**0.998**	0.125
The GBIF	0.617	0.072	0.341
Scientific articles	0.090	0.173	**-0.254**
Conservation status			
Threatened	**-0.205**	**-0.214**	-0.019
Taxonomic group			
Vultures	-0.027	**-0.140**	0.041
Raptors	0.037	-0.079	0.017
Corvids	**0.177**	0.034	0.074
Mammals	-0.111	**0.167**	**-0.092**
Functional traits			
Body mass	**-0.299**	0.085	0.000
Foraging act-social	-0.007	**0.144**	**0.144**
Home range	**-0.230**	-0.092	0.039
Fecundity	0.011	**0.212**	-0.027
Diel act-both	-0.048	-0.060	-0.019
Diel act-diurnal	0.125	**-0.161**	0.076
Diel act-nocturnal	-0.101	**0.212**	-0.069
CCA statistics			
Explained variation (%)	56.167	25.624	11.952
Cumulative explained variation (%)	56.167	81.791	93.743

Factor score of response (i.e. indices of non-material NCP), explanatory variables (i.e. conservation status, taxonomic group and functional traits) are shown in the first three axes. Bold font indicates the highest squared cosines (>0.4) for the response variables and the significant regression coefficients for the explanatory variables. The eigenvalues for the first three CCA axes were significant (Monte Carlo permutation test with 500 iterations; $P < 0.0001$). Additional information of response and explanatory variables are shown in Table 1 and Table D.1 in Appendix D. See Figure 3 and Table D.3 in Appendix D for species details).

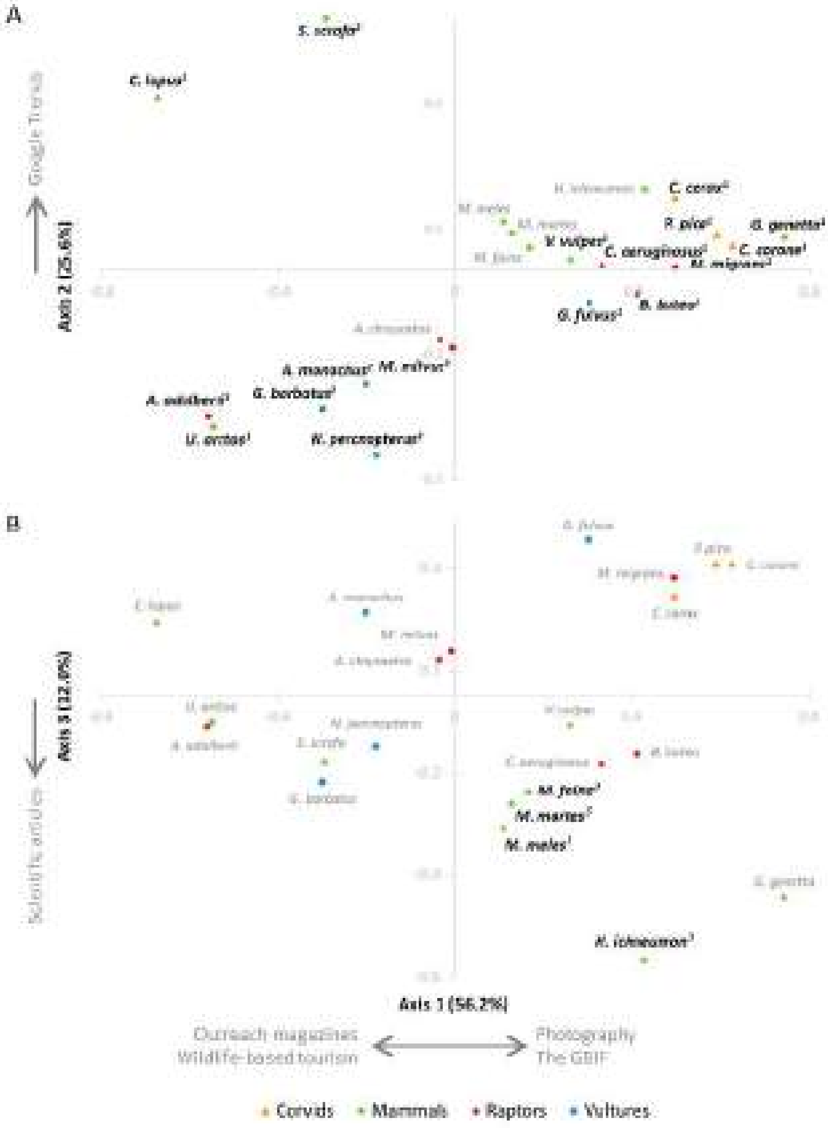

Figure 3. Results of the CCA showing the associations between the indices representing non-material nature's contributions to people (NCP) and the scavenger species. A. The axis 1 (i.e., photography and the GBIF in positive scores and outreach magazines and wildlife-based tourism in negative scores) and the axis 2 (Google Trends in positive scores). B. The axis 1 and the axis 3 (scientific articles in negative scores). Superscript numbers indicate the correspondent axis. Bold font indicates the highest squared cosines (>0.4) for the response variables and the significant regression coefficients for the explanatory variables. Eigenvalues for the first three CCA axes were significant (Monte Carlo permutation test with 500 iterations; P < 0.0001). Additional information of indices is shown in **Table 1**. See **Table D.3** in **Appendix D** for factor score details.

DISCUSSION

SCAVENGERS AS PROVIDERS OF NON-MATERIAL NCP

Our findings show, for the first time, that different species in the scavenger guild are key for providing a large set of non-material NCP in Spain. The wolf, a top predator and facultative scavenger, reached the highest values in three of the six evaluated non-material indices, followed by the griffon vulture, an obligate scavenger that stood out with high values for two indices (**Figure 1**). Previous studies have found that other NCP, such as the regulation of ecological processes by means of carcass consumption, were provided by both rare and common species, particularly vultures and top predators (Mateo-Tomás et al., 2017). Thus, top predators and vultures can be considered both ecological and cultural keystone species (Paine, 1969; Garibaldi and Turner, 2004), as they might play a major role in the functioning of social-ecological systems (Naidoo et al., 2011). Besides, both are functional groups in the scavenger guild that deserve particular attention because their populations are globally declining (Estes et al., 2011; Ogada et al., 2012; Ripple et al., 2014).

Our results showed that the indicator used to represent people's supporting identities (i.e. Google Trends) might actually represent other aspects of human-scavenger relations. The grey wolf and the wild boar were the species most searched for by people in Google (**Figure 1**). This can be explained by the fact that people may search information on these particular species not only because they show a positive interest in them, but also because people are interested in knowing about the damage that these species can cause. We also identified that the wolf is the most relevant scavenger for providing multiple non-material NCP, including photography, wildlife-based tourism and outreach magazines. However, for rural people, livestock breeders and shepherds in Spain, the wolf is considered a dangerous predator that can cause livestock losses (Dressel et al., 2015; Morales-Reyes et al., 2018) and the wild boar is associated with damage to crops, animals and vegetation (Pascual-Rico et al., 2020). All over the world, farmers and shepherds developed negative perceptions towards wolves and wild boars because of the damages caused to livestock and crops, respectively (e.g. Linkie et al., 2007; Ogra, 2008; Suryawanshi et al., 2013; Li et al., 2015). The dual role of wolves and wild boars as providers of beneficial and detrimental contributions to people's well-being supports the use of the paradigm of "nature's contributions to people" (NCP) since this concept is defined as "all the contributions, both positive and negative, of living nature (diversity of organisms, ecosystems, and their associated ecological and evolutionary processes) to people's quality of life" (Díaz et al., 2018).

TRAITS AND NCP IN THE SCAVENGER GUILD

Biological and functional traits have been previously used for ecosystem service assessments (Díaz et al., 2007; Luck et al., 2009), but very little research has been conducted to date as to how to evaluate relations between traits and NCP, particularly for those interlinkages between non-material NCP and vertebrates (Hevia et al., 2017; Echeverri et al., 2019). Our results revealed that there are some interlinkages between non-material NCP and the selected functional traits, and that these interlinkages are mediated by the taxonomic groups of scavengers (**Table 2**). For example, higher body mass and larger home range together with the endangered status of species were associated with the indices of wildlife-based tourism and outreach magazines, which represent the NCP of physical and psychological experiences and learning and inspiration, respectively (**Table 2**). This might be interpreted because those threatened species with large body sizes tend to have large home range (Tucker et al., 2014) and they are often charismatic species (e.g. the wolf, the Spanish imperial eagle, the brown bear and the bearded vulture) that attract the attention of customers. In fact, Clucas et al. (2008) revealed that the covers of US magazines focused on large charismatic species to attract new subscribers and to maintain membership. However, we also found that some species with high body mass, such as the wild boar, were not associated with the above-mentioned indices, but with Google Trends (**Figure 3**; **Table D.3**).

In addition, we found that although photography has been considered a representative indicator of aesthetic enjoyment provided by wildlife (e.g. Martínez Pastur et al., 2016), our results demonstrated that the index created with the three photography indicators is closely related to the GBIF index (**Table 2**). This result means that those species able to be photographed are also those able to be observed and recorded in the GBIF. Indeed, this association can be explained by the probability of people sighting scavengers, which is higher for the common species widely distributed in Spain (e.g. griffon vultures, ravens and red foxes) than for other scavengers.

Finally, we found that the learning and inspiration acquired through scientific articles focused mainly on mesocarnivores, such as Egyptian mongooses, Eurasian badgers, pine martens and stone martens (**Figure 3**; **Table D.3**). By contrast, a recent global review indicated that mesocarnivores received less scientific attention than large carnivores in human-carnivore relations research (Lozano et al., 2019). This could be explained because mesocarnivores in Spain are much more widely distributed and abundant than large mammalian scavengers, and thus can be investigated by comparatively more research groups. In addition, our results contrast with former research in Spain that has shown how the information provided by outreach magazines on different animal taxa goes hand in hand with scientific publications (Martín-López et al., 2009). However, when focussing on scavengers, we found that whereas the non-material NCP of the learning acquired through the outreach magazine *Quercus* relies mainly on charismatic and threatened species, the learning associated with scientific journals relies mostly on mesocarnivores.

The necessity to identify the traits of organism that intervene in the provision of NCP has been identified as an important knowledge gap in ecosystem service research (Luck et al., 2009; Bennett et al., 2015). This knowledge gap is particularly remarkable in the case of non-material NCP and vertebrates (Hevia et al., 2017). To our best knowledge, Echeverri et al. (2019) was the only study connecting functional traits with the provision of non-material NCP by birds. Similar to our findings, Echeverri et al. (2019) found that several functional traits, including plumage pattern, diet and having a crest, can contribute to explain the variation on non-material NCP provided by different bird species in Costa Rica. However, findings by Echeverri et al. (2019) also contradict our results since they found that scavengers are less likely to provide non-material NCP than other bird species because they are considered ugly and stinky. Future research is therefore needed to explore the connections between functional traits and detrimental NCP provided by scavengers.

METHODOLOGICAL CONSIDERATIONS: INSIGHTS FOR FUTURE RESEARCH

This study follows recent calls to advance conservation science by considering the data mined from social media platforms and the Internet. The so-called digital conservation is emerging as an innovative field in biological conservation to monitor biodiversity (Van der Wal and Arts, 2015; Ladle et al., 2016) and to explore patterns of wildlife-based tourism (Willemen et al., 2015; Hausmann et al., 2017; Di Minin et al., 2018). In addition, the use of social media data has been recently highlighted in ecosystem service research to assess cultural ecosystem services (Guerrero et al., 2016; Oteros-Rozas et al., 2018; Vaz et al., 2018, 2019). Although very few studies on NCP and ecosystem services have considered diverse sources of information to date (e.g. Vaz et al., 2018), to the best of our knowledge, this study is the first to comprehensively assess different non-material NCP by integrating multiple indicators derived from social media platforms and the Internet. Nevertheless, the use of data mined from social media platforms and the Internet requires some reflection as to their limitations.

Firstly, the data mined from these sources could represent only a particular sector of society. The Internet user profile seems closer to urban than to rural people (Oteros-Rozas et al., 2018) and, therefore, the results of this study may not represent the social actors who directly relate with scavengers, such as traditional livestock farmers and shepherds which perceive scavengers as beneficial and detrimental at the same time (Manzano-García et al., 2017; Morales-Reyes et al., 2018). However, in relation to livestock attacks by large carnivores, the media can widely echo the farmer perceptions, influencing the general public perception and management decisions (Fernández-Gil et al., 2016). Thus, the opinion of farmers and shepherds could partially be reflected in online resources, though probably biased towards conflicts (Fernández-Gil et al., 2016). The non-material NCP associated with farmers and shepherds deserve further scientific attention, which should be extended to hunters also.

The outreach magazine we selected to represent the NCP of inspiration and learning has a wide potential audience, including researchers, managers and the general public interested in nature. In Spain, 47.6% of people declare to be interested in ecology and the environment (CIS, 2016). However, the magazine's monthly circulation only reaches the sector of society that is *a priori* most interested in environmental issues. Thus, *Quercus* does not capture the general motivation of the Spanish society. Interestingly, however, this magazine is very much used by environmental managers in Spain as the primary source of information on wildlife monitoring and conservation strategies, as well as to be informed on environmental offences. This indicates that this magazine may have important practical implications that may pervade other society sectors.

Secondly, regarding the NCP of supporting identities, we selected a proxy (i.e. Google Trends) that can represent people interest, in our case for scavengers. However, this indicator cannot represent the other dimensions embedded in this NCP, such as sense of place and belonging, connectedness with nature and the employment of nature for narratives, rituals and celebrations (Díaz et al., 2018). To reveal the contributions of scavengers to these other dimensions, further interdisciplinary research is needed that includes additional proxies, such as local species names, place names, stories, ceremonies and folklore (see e.g. Stara et al., 2016).

Thirdly, information sources, such as photographs uploaded in social media and the GBIF observations, can only represent those species that are not elusive, nocturnal and geographically limited or with small population sizes. For example, the fact that nocturnal mammals were less represented in the posted photographs and the GBIF observations than diurnal scavengers (Figure 1A) does not necessarily mean that the former are not relevant for providing non-material NCP. This is the case of the common genet, which is very elusive and difficult to sight and photograph, but once it is portrayed, social media users experience aesthetic enjoyment as it obtains the most votes per photograph (**Figure 1B**). These are not necessarily methodological pitfalls, but should be taken into account when interpreting the results of such studies.

Finally, this study demonstrates the importance of scavengers for providing non-material NCP, but was unable to determine to what extent this guild is more relevant than other guilds. Scavengers occupied 22% of magazine covers in *Quercus* and appeared in 3% of the photographs posted on Fotonatura. Nonetheless, these data do not provide information about the importance of this guild for providing non-material NCP relative to others. Future research could determine to what extent non-material NCP are provided by different ecological guilds and which functional traits can lead to higher levels of their provision. For example, Willemen et al. (2015) found that in African protected areas, the African elephant (*Loxodonta africana*) and large predators, such as lions and leopards, were essential for providing wildlife-based tourism. Davies et al. (2018) also found that popular interest, measured by web searching, was greater in globally threatened mammals and birds than in those not threatened. Future research that applies data mining to social media platforms and the Internet should offer a high potential to unveil which species and which functional guilds and traits are essential for providing non-material NCP. In addition, the reason for people's attraction to some of scavengers remain unexplored. Although previous research has revealed that scavenger species can be dually perceived as beneficial or harmful depending on their consideration as primarily scavengers or predators (Manzano-García et al., 2017; Morales-Reyes et al., 2018), further research is needed.

CONCLUSIONS

This study contributes to advance knowledge of NCP by assessing the role of scavengers in providing non-material contributions for two main reasons. First, it sheds light on the dual role of NCP as we found that the same species (e.g. the wolf and the wild boar) can positively and negatively contribute to people's well-being. Second, we found that non-material NCP are interweaved and, therefore, the way people benefit from scavengers in non-material terms does not squarely fit only one category. These two findings fall in line with the arguments of Díaz et al. (2018), who claimed a more inclusive and flexible system than ecosystem services to assess the diverse ways by which people relate with nature. This enables the recognition that different social sectors, such as here evaluated (i.e. photographers, tourists, magazine readers, scientists, and civil society) and maybe others (e.g. farmers, shepherds, hunters), may consider scavengers as providers of both beneficial and detrimental NCP and different NCP according to their relationship with wildlife.

The knowledge of non-material NCP provided by threatened species, such as brown bear and bearded vulture in Spain, could be underestimated if the assessment relies only on one source of information. For example, both species have few photographs posted on internet and few human observations in the GBIF because of their low population size and restricted distribution. However, their photographs have high scores of views, an important demand in wildlife-based tourism, and considerable occurrence in outreach magazines (**Figure 1**). This shows the need of multiple indicators to comprehensible assess the capacity of threatened species to provide NCP. We hypothesize that the extinction of these threatened populations and species would drive the vanishing of the NCP they provide.

The present study also contributes to recent calls to better integrate scavenger conservation in the IPBES (Mateo-Tomás and Olea, 2018) by unravelling the non-material NCP provided by this guild. By assessing the non-material NCP provided by scavengers, our study supports current claims for conserving vultures and top predators because their current declining populations compromise not only the regulating NCP of scavenging, as demonstrated by the IPBES Regional Assessment of Europe and Central Asia (Martín-López et al., 2018), but also them providing multiple non-material NCP. Scavengers provide multiple beneficial non-material NCP by enhancing human-wildlife connections through recreation activities in nature, aesthetic enjoyment and learning. Identifying the ecological variables and functional traits that underpin each NCP might help to predict which NCP can be potentially provided by different species in a guild. For example, our result showed that widely distributed species (e.g. corvids and griffon vultures) acted as providers of aesthetic enjoyment, whereas scarce scavengers and species with higher body mass (e.g. bearded vultures and wolves) were associated with recreational experiences.

Detailed assessment of human-wildlife relations should be emphasized in conservation policies. Informing on both the species and the human actors involved in detriments and benefits provided by focal species groups to people may help to prioritize wildlife management strategies. Overall, this study, in combination with previous research showing the role of scavengers for regulating NCP (e.g. Morales-Reyes et al., 2015; Ćirović et al., 2016), provides with powerful arguments to raise awareness about the importance of these species for our societies.

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REFERENCES

Ament, J.M., Moore, C.A., Herbst, M., Cumming, G.S., 2017. Cultural Ecosystem Services in Protected Areas: Understanding Bundles, Trade-Offs, and Synergies. Conserv. Lett. 10, 439–449. https://doi.org/10.1111/conl.12283

Balvanera, P., Quijas, S., Martín-López, B., Barrios, E., Dee, L., Isbell, F., Durance, I., White, P., Blanchard, R., de Groot, R.S., 2016. The links between biodiversity and ecosystem services, in: Potschin, M., Haines-Young, R., Fish, R., Turner, R.K. (Ed.), Routledge Handbook of Ecosystem Services. Routledge Taylor & Francis Group, London. pp. 45–61.

Becker, N., Inbar, M., Bahat, O., Choresh, Y., Ben-Noon, G., Yaffe, O., 2005. Estimating the economic value of viewing griffon vultures *Gyps fulvus*: A Travel Cost Model study at Gamla Nature Reserve, Israel. Oryx 39, 429–434. https://doi.org/10.1109/SENSOR.2007.4300616

Bennett, E.M., Cramer, W., Begossi, A., Cundill, G., Díaz, S., Egoh, B., Geijzendorffer, I.R., Krug, C.B., Lavorel, S., Lazos, E., Lebel, L., Martín-López, B., Meyfroidt, P., Mooney, H.A., Nel, J.L., Pascual, U., Payet, K., Pérez Harguindeguy, N., Peterson, G., Prieur-Richard, A-H., Reyers, B., Roebeling, P., Seppelt, R., Solan, M., Tschakert, P., Tscharntke, T., Turner II, B.L., Verburg, P.H., Viglizzo, E.F., White, P.C.L., Woodward, G., 2015. Linking biodiversity, ecosystem services and human well-being: Three challenges for designing research for sustainability. Curr. Opin. Environ. Sustain. 14, 76–85. https://doi.org/10.1016/j.cosust.2015.03.007

Bhattarai, B.R., Fischer, K., 2014. Human–tiger *Panthera tigris* conflict and its perception in Bardia National Park, Nepal. Oryx 48, 522–528. https://doi.org/10.1017/S0030605313000483

Burivalova, Z., Butler, R.A., Wilcove, D.S., 2018. Analyzing Google search data to debunk myths about the public's interest in conservation. Front. Ecol. Environ. 16, 509–514. https://doi.org/10.1002/fee.1962

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., MacE, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148

Carter, N.H., Riley, S.J., Shortridge, A., Shrestha, B.K., Liu, J., 2014. Spatial assessment of attitudes toward tigers in Nepal. Ambio 43, 125–137. https://doi.org/10.1007/s13280-013-0421-7

CIS, Centro de Investigaciones Sociológicas. 2016. Barómetro de noviembre 2016 (Estudio nº3159). Available on: http://www.cis.es/cis/export/sites/default/-Archivos/Marginales/3140_3159/3159/Es3159mar.pdf

Convention on Biological Diversity, 2016. Decision adopted by the conference of the parties to the convention on biological diversity. Cancun, México. pp. 22.

Chapron, G., Kaczensky, P., Linnell, J.D.C., Von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balečiauskas, L., Balys, V., Bedõ, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 1517–1519. https://doi.org/10.1126/science.1257553

Ćirović, D., Penezić, A., Krofel, M., 2016. Jackals as cleaners: Ecosystem services provided by a mesocarnivore in human-dominated landscapes. Biol. Conserv. 199, 51–55. https://doi.org/10.1016/j.biocon.2016.04.027

Clucas, B., McHugh, K., Caro, T., 2008. Flagship species on covers of US conservation and nature magazines. Biodivers. Conserv. 17, 1517–1528. https://doi.org/10.1007/s10531-008-9361-0

Costanza, R., D'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260. https://doi.org/10.1038/387253a0

Costanza, R., de Groot, R., Braat, L., Kubiszewski, I., Fioramonti, L., Sutton, P., Farber, S., Grasso, M., 2017. Twenty years of ecosystem services: How far have we come and how far do we still need to go? Ecosyst. Serv. 28, 1–16. https://doi.org/10.1016/j.ecoser.2017.09.008

Daily, G.C., 1997. Nature's Services: Societal Dependence on Natural Ecosystems. Island Press, Washington D.C.

Daniel, T.C., Muhar, A., Arnberger, A., Aznar, O., Boyd, J.W., Chan, K.M.A., Costanza, R., Elmqvist, T., Flint, C.G., Gobster, P.H., Gret-Regamey, A., Lave, R., Muhar, S., Penker, M., Ribe, R.G., Schauppenlehner, T., Sikor, T., Soloviy, I., Spierenburg, M., Taczanowska, K., Tam, J., von der Dunk, A., 2012. Contributions of cultural services to the ecosystem services agenda. Proc. Natl. Acad. Sci. USA 109, 8812–8819. https://doi.org/10.1073/pnas.1114773109

Davies, T., Cowley, A., Bennie, J., Leyshon, C., Inger, R., Carter, H., Robinson, B., Duffy, J., Casalegno, S., Lambert, G., 2018. Popular interest in vertebrates does not reflect extinction risk and is associated with bias in conservation investment. PLoS One 13, e0203694. https://doi.org/10.1371/journal.pone.0203694

DeVault, T.L., Beasley, J.C., Olson, Z.H., Moleón, M., Carrete, M., Margalida, A., Sánchez-Zapata, J.A., 2016. Ecosystem Services Provided by Avian Scavengers, in: Şekercioğlu, C.H., Wenny, D.G., Whelan, C.J. (Eds.), Why Birds Matter: Avian Ecological Function and Ecosystem Services. University of Chicago Press, Chicago, pp. 235–270.

Di Minin, E., Fink, C., Tenkanen, H., Hiippala, T., 2018. Machine learning for tracking illegal wildlife trade on social media. Nat. Ecol. Evol. 2, 406–407. https://doi.org/10.1038/s41559-018-0466-x

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, T.M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proc. Natl. Acad. Sci. USA 104, 20684–20689. https://doi.org/10.1073/pnas.0704716104

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Brauman, K.A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P.W., van Oudenhoven, A.P.E., van der Plaat, F., Schröter, M., Lavorel, S., Aumeeruddy-Thomas, Y., Bukvareva, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C.A., Hewitt, C.L., Keune, H., Lindley, S., Shirayama, Y., 2018. Assessing nature's contributions to people. Science 359, 270–272. https://doi.org/10.1126/science.aap8826

Dressel, S., Sandstrom, C., Ericsson, G., 2015. A meta-analysis of studies on attitudes toward bears and wolves across Europe 1976-2012. Conserv. Biol. 29, 565–574. https://doi.org/10.1111/cobi.12420

Duriez, O., Descaves, S., Gallais, R., Neouze, R., Fluhr, J., Decante, F., 2019. Vultures attacking livestock: A problem of vulture behavioural change or farmers' perception? Bird Conserv. Int. 29, 437–453. https://doi.org/10.1017/S0959270918000345

Echeverri, A., Karp, D.S., Naidoo, R., Tobias, J.A., Zhao, J., Chan, K.M.A., 2019. Can avian functional traits predict cultural ecosystem services? People Nat. 00, 1–14. https://doi.org/10.1002/pan3.10058

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic Downgrading of Planet Earth. Science 333, 301–307. https://doi.org/10.1126/science.1205106

Expósito-Granados, M., Castro, A.J., Lozano, J., Aznar-Sanchez, J.A., Carter, N.H., Requena-Mullor, J., Malo, A.F., Olszańska, A., Morales-Reyes, Z., Moleón, M., Sánchez-Zapata, J.A., Cortés-Avizanda, A., Fischer, J., Martín-López, B., 2019. Human-carnivore relations:conflictos, tolerance and coexistence in the American West. Environ. Res. Lett. 14, 123005. https://doi.org/10.1088/1748-9326/ab5485

Fagerholm, N., Torralba, M., Burgess, P.J., Plieninger, T., 2016. A systematic map of ecosystem services assessments around European agroforestry. Ecol. Indic. 62, 47–65. https://doi.org/10.1016/j.ecolind.2015.11.016

Fazey, I., Fischer, J., Lindenmayer, D.B., 2005. What do conservation biologists publish? Biol. Conserv. 124, 63–73. https://doi.org/10.1016/j.biocon.2005.01.013

Fernández-Gil, A., Naves, J., Ordiz, A., Quevedo, M., Revilla, E., Delibes, M., 2016. Conflict misleads large carnivore management and conservation: brown bears and wolves in Spain. PLoS One 11, e0151541. https://doi.org/10.1371/journal.pone.0151541

Gangoso, L., Agudo, R., Anadón, J.D., De la Riva, M., Suleyman, A.S., Porter, R., Donázar, J.A., 2013. Reinventing mutualism between humans and wild fauna: Insights from vultures as ecosystem services providers. Conserv. Lett. 6, 172–179. https://doi.org/10.1111/j.1755-263X.2012.00289.x

Garibaldi, A., Turner, N., 2004. Cultural keystone species: implications for ecological conservation and restoration. Ecol. Soc. 9, 1. https://doi.org/10.5751/es-00669-090301

Gordillo, S., 2002. El cóndor andino como patrimonio cultural y natural de Sudamérica, in: Primer Congreso Internacional de Patrimonio Cultural. Universidad Nacional de Córdoba, pp. 327–342.

Grilli, M.G., Bildstein, K.L., Lambertucci, S.A., 2019. Nature's clean-up crew: Quantifying ecosystem services offered by a migratory avian scavenger on a continental scale. Ecosyst. Serv. 39, 100990. https://doi.org/10.1016/j.ecoser.2019.100990

Guerrero, P., Møller, M.S., Olafsson, A.S., Snizek, B., 2016. Revealing Cultural Ecosystem Services through Instagram Images: The Potential of Social Media Volunteered Geographic Information for Urban Green Infrastructure Planning and Governance. Urban Plan. 1, 1–17. https://doi.org/10.17645/up.v1i2.609

Hausmann, A., Toivonen, T., Fink, C., Heikinheimo, V., Tenkanen, H., Butchart, S.H.M., Brooks, T.M., Di Minin, E., 2019. Assessing global popularity and threats to Important Bird and Biodiversity Areas using social media data. Sci. Total Environ. 683, 617–623. https://doi.org/10.1016/j.scitotenv.2019.05.268

Hausmann, A., Toivonen, T., Heikinheimo, V., Tenkanen, H., Slotow, R., Di Minin, E., 2017. Social media reveal that charismatic species are not the main attractor of ecotourists to sub-Saharan protected areas. Sci. Rep. 7, 1–9. https://doi.org/10.1038/s41598-017-00858-6

Herrera, C.M., 1989. Las portadas de Quercus. Quercus 39, 35–39.

Hevia, V., Martín-López, B., Palomo, S., García-Llorente, M., de Bello, F., González, J.A., 2017. Trait-based approaches to analyze links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges. Ecol. Evol. 7, 831–844. https://doi.org/10.1002/ece3.2692

IUCN, 2018. The IUCN Red List of Threatened Species. Version 2018-1. www.iucnredlist.org (accessed 14 September 2018).

Johansson, Ö., McCarthy, T., Samelius, G., Andrén, H., Tumursukh, L., Mishra, C., 2015. Snow leopard predation in a livestock dominated landscape in Mongolia. Biol. Conserv. 184, 251–258. https://doi.org/10.1016/j.biocon.2015.02.003

Kissui, B. M., 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Anim. Conserv. 11, 422–432. https://doi.org/10.1111/j.1469-1795.2008.00199.x

Koziarski, A., Kissui, B., Kiffner, C., 2016. Patterns and correlates of perceived conflict between humans and large carnivores in Northern Tanzania. Biol. Conserv. 199, 41–50. https://doi.org/10.1016/j.biocon.2016.04.029

Ladle, R.J., Correia, R.A., Do, Y., Joo, G.J., Malhado, A.C.M., Proulx, R., Roberge, J.M., Jepson, P., 2016. Conservation culturomics. Front. Ecol. Environ. 14, 269–275. https://doi.org/10.1002/fee.1260

Li, C., Jiang, Z., Li, C., Tang, S., Li, F., Luo, Z., Ping, X., Liu., Z., Chen., J., Fang, H., 2015. Livestock depredations and attitudes of local pastoralists toward carnivores in the Qinghai Lake Region, China. Wildlife Biol. 21, 204–212. https://doi.org/10.2981/wlb.00083

Linkie, M., Dinata, Y., Nofrianto, A., Leader-Williams, N., 2007. Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra. Anim. Conserv. 10, 127–135. https://doi.org/10.1111/j.1469-1795.2006.00083.x

Lozano, J., Olszańska, A., Morales-Reyes, Z., Castro, A.A., Malo, A.F., Moleón, M., Sánchez-Zapata, J.A., Cortés-Avizanda, A., von Wehrden, H., Dorresteijn, I., Kansky, R., Fisher, J., Martín-López, B. 2019. Human-carnivore relations: A systematic review. Biol. Conserv. 237, 480–492. https://doi.org/10.1016/j.biocon.2019.07.002

Luck, G.W., Harrington, R., Harrison, P.A., Kremen, C., Berry, P.M., Bugter, R., Dawson, T.P., De Bello, F., Díaz, S., Feld, C.K., Haslett, J.R., Hering, D., Kontogianni, A., Lavorel, S., Rounsevell, M., Samways, M.J., Sandin, L., Settele, J., Sykes, M.T., Van Den Hove, S., Vandewalle, M., Zobel, M., 2009. Quantifying the contribution of organisms to the provision of ecosystem services. Bioscience 59, 223–235. https://doi.org/10.1025/bio.2009.59.3.7

Luederitz, C., Brink, E., Gralla, F., Hermelingmeier, V., Meyer, M., Niven, L., Panzer, L., Partelow, S., Rau, A.L., Sasaki, R., Abson, D.J., Lang, D.J., Wamsler, C., von Wehrden, H., 2015. A review of urban ecosystem services: Six key challenges for future research. Ecosyst. Serv. 14, 98–112. https://doi.org/10.1016/j.ecoser.2015.05.001

Manzano-García, J., Jiménez-Escobar, N.D., Lobo-Allende, R., Cailly-Arnulphi, V.B., 2017. El cóndor andino (*Vultur gryphus*): ¿predador o carroñero? pluralidad de percepciones entre los saberes locales y el discurso académico en las sierras centrales de Argentina. Hornero 23, 29–37. http://hdl.handle.net/20.500.12110/hornero_v032_n01_p029

MAPAMA, 2013. Inventario Español de Especies Terrestres. Available at: https://www.miteco.gob.es/es/biodiversidad/temas/inventarios-nacionales/inventario-especies-terrestres/inventario-nacional-de-biodiversidad/bdn-ieet-default.aspx

Margalida, A., Campión, D., Donázar, J.A., 2011. Scavenger turned predator: European vultures' altered behaviour. Nature 480, 457. https://doi.org/10.1038/480457b

Margalida, A., Campión, D., Donázar, J.A., 2014. Vultures vs livestock: conservation relationships in an emerging conflict between humans and wildlife. Oryx 48, 172–176. https://doi.org/10.1017/S0030605312000889

Margalida, A., Donázar, J.A., Carrete, M., Sánchez-Zapata, J.A., 2010. Sanitary versus environmental policies: Fitting together two pieces of the puzzle of European vulture conservation. J. Appl. Ecol. 47, 931–935. https://doi.org/10.1111/j.1365-2664.2010.01835.x

Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline-An appraisal of the human health and other benefits of vultures in India. Ecol. Econ. 67, 194–204. https://doi.org/10.1016/j.ecolecon.2008.04.020

Martín-López, B., Church, A., Başak Dessane, E., Berry, P., Chenu, C., Christie, M., Gerino, M., Keune, H., Osipova, E., Oteros-Rozas, E., Paillard, S., Rossberg, A.G., Schröter, M., van Oudenhoven, A.P.E., 2018. Chapter 2: Nature's contribution to people and quality of life, in: Rounsevell, M., Fisher, M., Torre-Marin Rando, A., Mader, A. (Eds.), The IPBES Regional Assessment Report on Biodiversity and Ecosystem Services for Europe and Central Asia. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem services, Bonn, pp. 57–185.

Martín-López, B., Montes, C., Ramírez, L., Benayas, J., 2009. What drives policy decision-making related to species conservation? Biol. Conserv. 142, 1370–1380. https://doi.org/10.1016/j.biocon.2009.01.030

Martínez-Abraín, A., Crespo, J., Berdugo, M., Gutiérrez, L., Lafuente, A., Mañas, A., de Miguel, J.M., 2013. Causes of human impact to protected vertebrate wildlife parallel long-term socio-economical changes in Spain. Anim. Conserv. 16, 286–294. https://doi.org/10.1111/j.1469-1795.2012.00599.x

Martínez Pastur, G., Peri, P.L., Lencinas, M. V., García-Llorente, M., Martín-López, B., 2016. Spatial patterns of cultural ecosystem services provision in Southern Patagonia. Landsc. Ecol. 31, 383–399. https://doi.org/10.1007/s10980-015-0254-9

Mateo-Tomás, P., Olea, P.P., 2018. Scavengers need help from IPBES. Nature 558, 519. https://doi.org/10.1038/d41586-018-05554-7

Mateo-Tomás, P., Olea, P.P., Moleón, M., Selva, N., Sánchez-Zapata, J.A., 2017. Both rare and common species support ecosystem services in scavenger communities. Glob. Ecol. Biogeogr. 26, 1459–1470. https://doi.org/10.1111/geb.12673

Milcu, A.I., Hanspach, J., Abson, D., Fischer, J., 2013. Cultural Ecosystem Services: A Literature Review and Prospects for Future Research. Ecol. Soc. 18. https://doi.org/10.5751/ES-05790-180344

Millennium Ecosystem Assessment (MEA), 2005. Ecosystems and Human Well-being: Synthesis. Island Press, Washington. https://doi.org/10.1196/annals.1439.003

Moleón, M., Sánchez-Zapata, J.A., Margalida, A., Carrete, M., Owen-Smith, N., Donázar, J.A., 2014. Humans and scavengers: The evolution of interactions and ecosystem services. Bioscience 64, 394–403. https://doi.org/10.1093/biosci/biu034

Morales-Reyes, Z., Martín-López, B., Moleón, M., Mateo-Tomás, P., Botella, F., Margalida, A., Donázar, J.A., Blanco, G., Pérez, I., Sánchez-Zapata, J.A., 2018. Farmer Perceptions of the Ecosystem Services Provided by Scavengers: What, Who, and to Whom. Conserv. Lett. 11, e12392. https://doi.org/10.1111/conl.12392

Morales-Reyes, Z., Pérez-García, J.M., Moleón, M., Botella, F., Carrete, M., Lazcano, C., Moreno-Opo, R., Margalida, A., Donázar, J.A., Sánchez-Zapata, J.A., 2015. Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. Sci. Rep. 5, 7811. https://doi.org/10.1038/srep07811

Morelli, F., Kubicka, A.M., Tryjanowski, P., Nelson, E., 2015. The vulture in the sky and the hominin on the land: Three million years of human–vulture interaction. Anthrozoos 28, 449–468. https://doi.org/10.1080/08927936.2015.1052279

Nahuelhual, L., Carmona, A., Lozada, P., Jaramillo, A., Aguayo, M., 2013. Mapping recreation and ecotourism as a cultural ecosystem service : An application at the local level in Southern Chile. Appl. Geogr. 40, 71–82. https://doi.org/10.1016/j.apgeog.2012.12.004

Naidoo, R., Weaver, L.C., Stuart-hill, G., Tagg, J., 2011. Effect of biodiversity on economic benefits from communal lands in Namibia. J. Appl. Ecol. 48, 310–316. https://doi.org/10.1111/j.1365-2664.2010.01955.x

Nghiem, L.T.P., Papworth, S.K., Lim, F.K.S., Carrasco, L.R., 2016. Analysis of the capacity of google trends to measure interest in conservation topics and the role of online news. PLoS One 11. https://doi.org/10.1371/journal.pone.0152802

O'Bryan, C.J., Braczkowski, A.R., Beyer, H.L., Carter, N.H., Watson, J.E.M., McDonald-Madden, E., 2018. The contribution of predators and scavengers to human well-being. Nat. Ecol. Evol. 2, 229–236. https://doi.org/10.1038/s41559-017-0421-2

Ogada, D.L., Keesing, F., Virani, M.Z., 2012. Dropping dead: causes and consequences of vulture population declines worldwide. Ann. N. Y. Acad. Sci. 1249, 57–71. https://doi.org/10.1111/j.1749-6632.2011.06293.x

Ogra, M.V., 2008. Human–wildlife conflict and gender in protected area borderlands: a case study of costs, perceptions, and vulnerabilities from Uttarakhand (Uttaranchal), India. Geoforum, 39, 1408–1422. https://doi.org/10.1016/j.geoforum.2007.12.004

Otegui, J., Ariño, A.H., Encinas, M.A., Pando, F., 2013. Assessing the Primary Data Hosted by the Spanish Node of the Global Biodiversity Information Facility (GBIF). PLoS One 8, e55144. https://doi.org/10.1371/journal.pone.0055144

Oteros-Rozas, E., Martín-López, B., Fagerholm, N., Bieling, C., Plieninger, T., 2018. Using social media photos to explore the relation between cultural ecosystem services and landscape features across five European sites. Ecol. Indic. 94, 74–86. https://doi.org/10.1016/j.ecolind.2017.02.009

Paine, R.T., 1969. A note on trophic complexity and community stability. Am. Nat. 103, 91–93. https://doi.org/10.1086/282586

Pascual-Rico, R., Martín-López, B., Sánchez-Zapata, J. A., Morales-Reyes, Z., 2020. Scientific priorities and shepherds' perceptions of ungulate's contributions to people in rewilding landscapes. Sci. Total Environ., 705, 135876. https://doi.org/10.1016/j.scitotenv.2019.135876

Restrepo-Cardona, J.S., Sáenz-Jiménez, F., Lieberman, A.A., 2019. Traditional knowledge and perceptions towards the andean condor (*Vultur gryphus* Linnaeus, 1758) in the central andes of Colombia. Ethnoscientia 4. http://dx.doi.org/10.22276/ethnoscientia.v4i1.211

Ripple, W.J., Estes, J. a, Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484. https://doi.org/10.1126/science.1241484

Sastre, B., Vázquez, M., Sánchez, D., Tena, D., Úbeda, E., Sánchez, J.L., de Miguel, J.M., 2004. Análisis de contenidos de la revista Quercus. Quercus 226, 56–60.

Sangay, T., Vernes, K., 2008. Human–wildlife conflict in the Kingdom of Bhutan: patterns of livestock predation by large mammalian carnivores. Biol. Conserv. 141, 1272–1282. https://doi.org/10.1016/j.biocon.2008.02.027

Soriano-Redondo, A., Bearhop, S., Lock, L., Votier, S.C., Hilton, G.M., 2017. Internet-based monitoring of public perception of conservation. Biol. Conserv. 206, 304–309. https://doi.org/10.1016/j.biocon.2016.11.031

Stara, K., Sidiropoulos, L., Tsiakiris, R., 2016. Bound Eagles, Evil Vultures and Cuckoo Horses. Preserving the bio-cultural diversity of carrion eating birds. Hum. Ecol. 44, 751–764. https://doi.org/10.1007/s10745-016-9864-3

Suryawanshi, K.R., Bhatnagar, Y.V., Redpath, S., Mishra, C., 2013. People, predators and perceptions: patterns of livestock depredation by snow leopards and wolves. J. Appl. Ecol. 50, 550–560. https://doi.org/10.1111/1365-2664.12061

UK, National Ecosystem Assessment, 2011. The UK National Ecosystem Assesment: Synthesis of the Key Findings. UNEP-WCMC. Cambridge.

UN Environment World Conservation Monitoring Centre, 2017. Biodiversity Indicators Partnership.

Tucker, M.A., Ord, T.J., Rogers, T.L., 2014. Evolutionary predictors of mammalian home range size: body mass, diet and the environment. Global Ecol. Biogeogr. 23, 1105-1114. https://doi.org/10.1111/geb.12194

Van der Wal, R., Arts, K., 2015. Digital conservation: An introduction. Ambio 44, S517–S521. https://doi.org/10.1007/s13280-015-0701-5

Vaz, A.S., Castro-Díez, P., Godoy, O., Alonso, Á., Vilà, M., Saldaña, A., Marchante, H., Bayón, Á., Silva, J.S., Vicente, J.R., Honrado, J.P., 2018. An indicator-based approach to analyse the effects of non-native tree species on multiple cultural ecosystem services. Ecol. Indic. 85, 48–56. https://doi.org/10.1016/j.ecolind.2017.10.009

Vaz, A.S., Moreno-Llorca, R.A., Gonçalves, J.F., Vicente, J.R., Méndez, P.F., Revilla, E., Santamaria, L., Bonet-García, F.J., Honrado, J.P., Alcaraz-Segura, D., 2019. Digital conservation in biosphere reserves: Earth observations, social media, and nature's cultural contributions to people. Conserv. Lett. e12704. https://doi.org/10.1111/conl.12704

Velasco, D., García-Llorente, M., Alonso, B., Dolera, A., Palomo, I., Iniesta-Arandia, I., Martín-López, B., 2015. Biodiversity conservation research challenges in the 21st century: A review of publishing trends in 2000 and 2011. Environ. Sci. Policy 54, 90–96. https://doi.org/10.1016/j.envsci.2015.06.008

Westman, W.E., 1977. How much are Nature's Services worth? Science 197, 960–964. https://doi.org/10.1126/science.197.4307.960

Willemen, L., Cottam, A.J., Drakou, E.G., Burgess, N.D., 2015. Using social media to measure the contribution of red list species to the nature-based tourism potential of african protected areas. PLoS One 10, e0129785. https://doi.org/10.1371/journal.pone.0129785

Yesson, C., Brewer, P.W., Sutton, T., Caithness, N., Pahwa, J.S., Burgess, M., Gray, W.A., White, R.J., Jones, A.C., Bisby, F.A., Culham, A., 2007. How global is the global biodiversity information facility? PLoS One 2, e1124. https://doi.org/10.1371/journal.pone.0001124

Yirga, G., Imam, E., De Iongh, H.H., Leirs, H., Kiros, S., Yohannes, T.G., Teferi, M., Bauer, H., 2014. Local spotted hyena abundance and community tolerance of depredation in human-dominated landscapes in Northern Ethiopia. Mamm. Biol. 79, 325–330. https://doi.org/10.1016/j.mambio.2014.05.002

Yirga, G., Leirs, H., De Iongh, H.H., Asmelash, T., Gebrehiwot, K., Deckers, J., Bauer, H., 2015. Spotted hyena (*Crocuta crocuta*) concentrate around urban waste dumps across Tigray, northern Ethiopia. Wildl. Res. 42, 563–569. https://doi.org/10.1071/WR14228


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Chapter 4. Mapping the large-scale non-material contributions of scavengers reveals the importance of protected areas

Photo by the author.
Field equipment. Griffon (*Gyps fulvus*) and Black vultures (*Aegypius monachus*) in Monfragüe National Park.

ABSTRACT

Scavengers play an important role in both the regulation of ecosystems and the provision of non-material Nature's Contributions to People (NCP). Non-material NCP, such as aesthetic enjoyment and recreational activities, are closely linked with human well-being. Understanding where non-material NCP are spatially distributed could allow us to comprehend how humans interact with nature. For this purpose, we mapped the non-material NCP that vertebrate scavengers provide people within continental Spain using 10x10 km grids. We explored indicators about nature photography, wildlife-based tourism, and records of scavenger observations recorded at the Global Biodiversity Information Facility, and we calculated hotspots of contributions. We also explored the environmental factors that could influence their provision: presence of protected areas, human footprint, and scavenger species richness. Our findings revealed the importance of protected areas for scavengers' non-material NCP, particularly of National Parks. Tourism was linked to more pristine areas whereas aesthetic enjoyment and the contribution to knowledge categories could be performed in areas with some index of anthropisation. These findings help to recognise the importance of scavenging species for people's quality of life, supporting their conservation policies.

Keywords: cultural ecosystem services; ecotourism; learning and inspiration; physical and psychological experiences; supporting identities; vultures.

INTRODUCTION

The Natures' Contributions to People (NCP) framework provides a conceptualisation of human-nature interactions (Díaz et al., 2018). Of all the NCP categories, material and regulating contributions have been most frequently assessed (Fagerholm et al., 2016; Hevia et al., 2017; Luederitz et al., 2015) for being directly related to the consumptive goods that support the development of human societies. Contrarily, the intangible aspect of non-material contributions (i.e., effects of nature on the subjective or psychological aspects that affect human quality of life (Díaz et al., 2018)) and the indirect benefits that enhance people's quality of life are underrepresented in the scientific literature (Daniel et al., 2012; Milcu et al., 2013). Notwithstanding, some aspects of non-material contributions, such as recreational experiences, are being shown increasing interest (Hernández-Morcillo et al., 2013; Milcu et al., 2013).

In the non-material contributions context, vertebrates in general (Cardinale et al., 2012; Hevia et al., 2017), and scavengers in particular (DeVault et al., 2016; Moleón and Sánchez-Zapata, 2015), have been paid less scientific attention than other taxonomic and functional groups like mammals and reptiles (Methorst et al., 2020). Recent studies have highlighted that scavengers provide numerous NCP , mainly related with carrion consumption supporting key ecological functions in ecosystems (DeVault et al., 2016; Markandya et al., 2008; Moleón et al., 2014; Morales-Reyes et al., 2015). Recreational activities likes ecotourism have been studied in relation to scavengers on the local scale to reveal their importance for non-material NCP, particularly supporting identities (García-Jiménez et al., 2022) and their positive economic impact (Becker et al., 2005; García-Jiménez et al., 2021). To our knowledge, only one national-scale research work based on several indicators has revealed that scavengers provide many non-material contributions based on species traits: common species are prone to provide aesthetic enjoyment, charismatic species lead recreational experiences, and the species that play the dual role of being beneficial and detrimental provide supporting identities (Aguilera-Alcalá et al., 2020). Some scavenging species have been historically misperceived as harmful by some social groups, such as livestock farmers (Lambertucci et al., 2021; Margalida et al., 2014). As the scavenger guild includes highly endangered species (e.g., vultures and apex predators; Buechley and Şekercioğlu, 2016; Wolf and Ripple, 2018), adequately highlighting their socio-cultural benefits could be an efficient strategy to improve scavengers' conservation policies and to alleviate human-scavenger conflicts.

The spatial mapping of NCP can be a powerful tool to understand where and how humans relate to nature, and can help to guide better environmental conservation and management (Hernández-Morcillo et al., 2013; Martínez-Harms and Balvanera, 2012). Mapping research is general conducted on local scales (Fagerholm et al., 2016; Plieninger et al., 2013; Wu et al., 2013), usually in protected areas (PA) (i.e., Ament et al. (2017); Vaz et al. (2020)). PA are currently designed to protect nature from degradation and human impact (Chape et al., 2005), although the establishment of the first national parks in the USA, and in other world regions, at the beginning of the 20th century was to mainly conserve landscape for aesthetic enjoyment, among other purposes (e.g., declaration of the Yellowstone National Park, National Park Service Organic Act of 1916, 16 U.S.C. 1). So it is not surprising that most NCP research has focused on these areas. However, exploring the provision of NCP on larger spatial scales is essential because different resolutions can help to improve to make management decisions according to different administrative levels (Ceaușu et al., 2021). Moreover, large-scale mapping exercises can help to identify which factors lie behind the distribution of NCP (Ceaușu et al., 2021; Maes et al., 2012). Regarding highly mobile species like scavengers, large-scale mapping of regulating contributions has been carried out (Ceaușu et al., 2021; Morales-Reyes et al., 2015), but, surprisingly, no study has to date mapped the large-scale arrangement of their non-material contributions. This prevents relevant applied conclusions being reached; for instance, it remains unclear if PA are also efficient in preserving non-material NCP.

Here we assess the spatial distribution of the non-material NCP provided by the functional guild of scavengers on a national scale by taking the scavenger community of continental Spain a study focus (Aguilera-Alcalá et al., 2020). We focus on the physical and psychological experiences (aesthetic enjoyment and recreational experiences) and learning and inspiration (particularly, contribution to scientific knowledge). We firstly identify hotspots of provision of non-material NCP and explore the relations among the different non-material NCP categories. We secondly explore the landscape features that may condition the provision of NCP, namely the presence of protected areas, the degree of landscape alteration (i.e., human footprint index, HF), and the avian and mammal scavengers' local richness. As PA are designed to protect species and their environment (Chape et al., 2005), we expect to find higher values for non-material NCP in this areas. We also expect non-material NCP to be linked with the distribution of scavenger species richness. In contrast, we expect those areas with high human footprint values to be related to little NCP provision.

METHODS

DATA COLLECTION

This study focused on continental Spain (494,011 km^2). We considered 22 scavenger species, including specialists or obligate scavengers (vultures), and opportunistic or facultative scavengers (other raptors, corvids and mammals) (see the Species List in Table S1). We compiled the NCP indicators and the environmental factors described below into geographical units of 10x10 km UTM grids.

Non-material NCP's indicators

We firstly identify the areas where scavenger species provide the physical and psychological experiences of aesthetic enjoyment, exploring the photographs posted by people on the website of Spanish-speaking nature photographers *Fotonatura* (www.fotonatura.org). This website allows all the published nature photographs to be freely browsed. We explored the "geotagged" gallery, which contains only georeferenced photographs. Then we collected the coordinates of the location of the photographs showing scavengers. Of the 38,454 photos posted between 2000 and 2016 in Spain, we explored those that featured any of the 22 herein considered species, i.e., 1,031 images (2.68% of all the photos posted on *Fotonatura*). We selected the number of photographs posted per 10x10 km grid as an indicator of aesthetic enjoyment (**Table 1**).

Then we explored the recreational experiences associated with scavengers. We carried out a search of the wildlife watching tourism in Spain. For this purpose, in September 2017 we explored a search string on Google by including, for each scavenger species, the English and scientific names, the focal recreational activity (i.e., "wildlife watching") and country name (i.e., "Spain"; see Table S2 in the Supplementary Material for further details). We performed the search in English to focus on the main companies that cover both national and international tourism because Spain is the target of substantial foreign tourism, mostly from the European Union (INE, 2022). We looked at the links found on the first five pages of the Google search (the first 50 links) by looking for the companies offering wildlife watching tourism. Then we recorded the municipality or, if not provided, the region where wildlife watching was offered, and excluded those companies not based in continental Spain, as well as tour reports, personal comments, personal blogs, and governmental information webs because they cannot be attributed to specific tourism offers. This gave us 40 company websites. Then we calculated the number of companies (different webs) operating per location. As each municipality or region was an irregular polygon, and to standardise spatial information, we transformed the number of companies from polygons to the 10x10 km grid by performing a spatial join in QGIS (version 3.10.0) calculating the average number of companies per grid as an indicator of recreational experiences (**Table 1**). In those cases in which the municipality and region polygons spatially overlapped, we separately calculated the average number of companies per grid according to each polygon origin, and then selected the maximum per grid from both values to prevent redundancies.

Table 1. Indicators of the non-material NCP categories assessed.

Non-material NCP	Proxy	Spatial resolution	Indicator per 10x10 km grid	References
Physical and psychological experiences, particularly *aesthetic enjoyment*. They also represent recreational experiences, and people's satisfaction of knowing that a species exists (*supporting identities*).	Photography	x, y coordinates	Number of georeferenced photos posted	(Martínez-Pastur et al., 2016; Willemen et al., 2015)
Physical and psychological experiences, particularly *recreational experiences* based on wildlife-based tourism. They also represent aesthetic enjoyment, and people's satisfaction of knowing that a species exists (*supporting identities*).	Wildlife-based tourism	Polygon of municipality or protected area	Mean number of companies advertising wildlife watching	(Nahuelhual et al., 2013)
Learning and inspiration, particularly scientists acquiring knowledge.	The GBIF	x, y coordinates	Number of observations recorded	UN Environment World Conservation Monitoring Centre (2017) (Horns et al., 2018)

We thirdly extracted the location of people's observations of scavengers from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/), which provides information about occurrence of organisms (Otegui et al., 2013; Yesson et al., 2007) from various databases, including those of citizen science. This allowed us to spatially assess the areas in which humans can obtain knowledge about scavengers (i.e., the learning and inspiration category; Díaz et al., 2018). Moreover, as people reports of biodiversity observation contribute to improve scientific knowledge (Horns et al., 2018), we searched the GBIF's Spanish node (https://datos.gbif.es/) for any data recorded between 2000 and 2016 in continental Spain by employing the scientific name of each scavenger species in quotation marks (to avoid searching for other species with a shared scientific nomenclature). Then we extracted the location, and excluded any data corresponding to observations made from official Spanish Ministry of the Environment censuses (MAPAMA, 2013), and those from scientific bird ringing surveys, because they do not represent citizen records. Our search gave 11,477 records. We selected the number of observations reported per 10x10 km grid as an indicator of contribution to knowledge (**Table 1**).

Environmental factors

We firstly identified the 10x10 km grids that contained a PA on more than 10% of their surface. We considered the main PA categories in Spain (including National Parks and Natural Parks, among other less frequent categories; MITECO, 2020), plus the PA included in the EU's Natura 2000 Network (European Environment Agency, 2019).

Then we downloaded the human footprint (HF) dataset for 2009 (available at https://wcshumanfootprint.org/ in 1x1 km resolution) and calculated the mean HF for each 10x10 km grid. HF is a measure of the cumulative human impact on the environment (Venter et al., 2016), which is available in a data layer with an index scaled from 0 (minimum impact) to 50 (maximum impact). HF includes the extent of built environments, population density, night light, crop and pasture lands, roads, railways and navigable waterways (Venter et al., 2016).

We thirdly collected the geographic distribution of the avian and mammalian scavenger species from the atlas dataset of the 2007 National Biodiversity Inventory (available at https://www.miteco.gob.es/), with a grid resolution of 10x10 km. Bird species data represent their distribution during the breeding period, while mammals' distribution is permanent. Then we calculated the number of species ("richness") present per grid (see Table S1 for species list).

STATISTICAL ANALYSES

The spatial pattern of NCP

We explored the spatial pattern of the three non-material NCP categories: aesthetic enjoyment ("photography"); recreational activities ("tourism"); contribution to knowledge (GBIF records of "observation"). We identified the hotspots (i.e., contiguous spatial units with high values of NCP) for the three categories using the Getis-Ord Gi* spatial statistic in QGIS (version 3.10.0). Gi* returns Z-scores that measure cluster intensity based on queen's continuity criterion, and gives statistical significance. In this way, hotspots were defined from Z-scores ≥ 1.65 and p-values ≤ 0.10 (90% confidence) onwards (see **Figure 1** caption). We also evaluated the hotspots for a "non-material NCP index", which resulted from joining the three above-mentioned NCP non-material categories. To obtain this integrative NCP index, we standardised values between 0 and 1, based on the minimum and maximum values for each category (Maes et al., 2012). Then we summed up the three NCP values of each grid, and once again standardised from 0 to 1. The resulting index represents the capacity of each grid cell to provide multiple non-material NCP.

We also checked the correlation among the non-material categories with the Spearman correlation test ($\alpha = 0.05$) to detect synergies in the performance of NCP categories.

Environmental factors that influence NCP provision

We checked the influence of PA presence, HF and scavenger species richness (i.e., explanatory variables) on the provision of aesthetic enjoyment, recreational activities and contribution to knowledge. To do so, we fitted Generalised Linear Models (GLMs) using the value of the NCP indicators: "photography", "tourism" and "observations", as well as the presence (yes/no) of their respective hotspots and the "non-material NCP hotspots", as response variables. We used negative binomial distributions with log link functions for the NCP raw data, and binomial distributions and logit link functions for hotspots' presence/absence data. Firstly for each response variable, we constructed the full model, i.e., with the three explanatory variables. We secondly explored all the possible alternative models (including the "null" model, i.e., without explanatory variables) with the dredge() function of the *MuMIn* package in R (Barton, 2013). Models were ranked by Akaike's Information Criterion (AIC) for small sample sizes (AIC_c), with those with delta-$AIC_c < 2$ in relation to the model with the lowest AIC_c being considered to provide similar support (Burnham and Anderson, 2002). Then we explored the proportion of explained deviance (D2) for the selected models according to formula D2 = (null deviance – residual deviance) / null deviance * 100 (Burnham and Anderson, 2002). Finally, we focused on the most explanatory model. Statistical analyses were performed using the R software (version 3.6.1) (http://www.r-project.org/R).

RESULTS

The distribution of the non-material NCP provided by scavengers throughout continental Spain was highly heterogeneous, and we identified different hotspots for each non-material NCP category (**Figure 1**). We found a weak correlation between the distribution of the different non-material categories (all $r_s < 0.25$). However, the non-material NCP index identified 18 hotspots as important areas for the provision of scavengers' non-material NCP. In particular, these hotspots were associated with PA, and notably, overlapped with seven of the 10 National Parks of continental Spain (**Figure 1**, **Table 2**).

The provision of the different non-material NCP categories by scavengers was associated with not only PA, but also with scavenger species richness and HF (**Table 3**). In particular, the provision of the non-material NCP was positively related to scavenger richness and the presence of protected areas (**Figure 2**, **Table S3**). In contrast, the relation between HF and the provision of the non-material NCP depended on specific NCP: HF was related positively to the provision of aesthetic enjoyment (i.e., "photography" and "photography hotspot") and contribution to knowledge (i.e., scavengers' "observation" and "observation hotspot"), but negatively to recreational activities (i.e., "tourism" and "tourism hotspot") and the "non-material NCP hotspot" (**Figure 2**, **Table S3**).

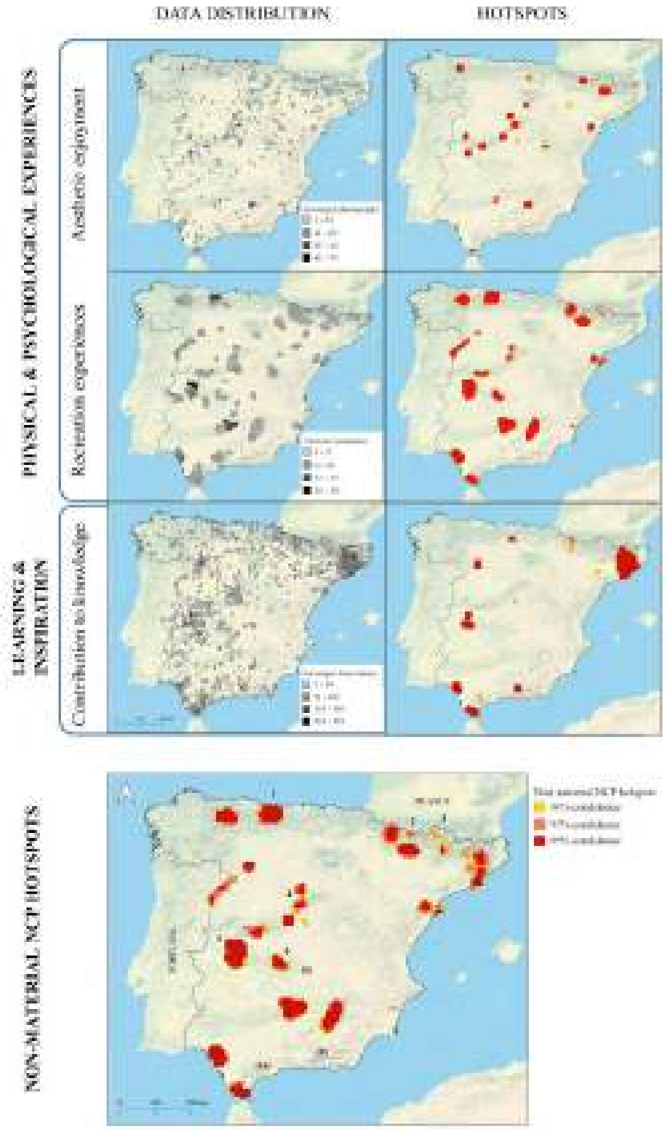


Figure 1. Spatial distribution of non-material NCP provided by scavengers in continental Spain. We show raw data and hotspots (i.e., set of contiguous spatial units characterised by high values, identified with Local Getis-Ord Gi* in QGIS (version 3.10.0)) for physical and psychological experiences: aesthetic enjoyment (photography), and recreational activities (tourism companies); learning and inspiration: contribution to knowledge (scavengers' observations). We also show the non-material NCP hotspot. Numbers indicate the associated National Parks: 1, Picos de Europa; 2, Ordesa y Monte Perdido; 3, Aigüestortes i Estany de Sant Maurici; 4, Sierra de Guadarrama; 5, Monfragüe; 6, Cabañeros; 7, Doñana. Numbers in brackets indicate National Parks without non-material NCP hotspots associated: (8) Tablas de Daimiel; (9) Sierra Nevada; (10) Sierra de las Nieves. 90% confidence: Z-score ≥ 1.65 and < 1.96, and p-value ≤ 0.1 and > 0.05; 95% confidence: Z-score ≥ 1.96 and < 2.58, and p-value ≤ 0.05 and > 0.01; 99% confidence: Z-score ≥ 2.58, and p-value ≤ 0.01.

Table 2. Protected areas located on the non-material NCP hotspots. The protection category (National Park, highest protection category; Natural Park and Regional Park, high protection; Natural Reserve, medium protection), and the leading species in each indicator (aesthetic enjoyment: photography; recreational activities: wildlife-based tourism companies; contribution to knowledge: scavenger's observations) are shown. In cases where two species were equally represented in a NCP category, both are shown.

		Leading species		
Hotspot name	**Protection category**	**Aesthetic enjoyment**	**Recreational activities**	**Contribution to knowledge**
Picos de Europa	National Park	*Canis lupus*	*Canis lupus*	*Gyps fulvus*
Ordesa y Monte Perdido	National Park	*Gypaetus barbatus*	*G. barbatus*	*G. barbatus* & *G. fulvus*
Aigüestortes i Estany de Sant Maurici	National Park	*G. barbatus* & *G. fulvus*	*G. barbatus*	*G. fulvus*
Sierra de Guadarrama; Hoces del Río Duratón	National Park; Natural Park	*Aquila adalberti*	*N. percnopterus* & *Aquila chrysaetos*	*G. fulvus*
Cabañeros	National Park	*G. fulvus*	*A. chrysaetos*	*G. fulvus*
Doñana	National Park	*Milvus migrans*	*A. adalberti*	*M. migrans*
Monfragüe; Llanos de Cáceres	National Park, Natural Park	*G. fulvus*	*A. adalberti* & *A. monachus*	*G. fulvus*
Somiedo; Fuentes del Narcea, Degaña e Ibias	Natural Park	*Ursus arctos*	*U. arctos*	*Corvus corone*
Arribes del Duero	Natural Park	*G. fulvus*	*A. chrysaetos*	*G. fulvus*
Valles Occidentales	Natural Park	*G. fulvus* & *N. percnopterus*	*G. barbatus*	*G. fulvus*
Sierra y los Cañones de Guara	Natural Park	*G. fulvus*	*G. barbatus*	*G. fulvus*
Estrecho, Alcornocales	Natural Park	*G. fulvus*	*M. migrans*	*G. fulvus*
Sierra de Cardeña y Montoro, Andújar	Natural Park	*G. fulvus* & *A. chrysaetos*	*Sus scrofa*	*G. fulvus*
Sierra de Cazorla, Seguras y Las Villas	Natural Park	*Vulpes vulpes*	*G. barbatus*	*G. fulvus*
El Hondo	Natural Park	NA	*C. corax*	*A. chrysaetos* & *Pica pica*
Lagunas de Villafáfila	Natural Reserve	*M. migrans*	*C. lupus* & *Circus aeruginosus*	*C. corone*
Sierra de Gredos	Regional Park	*A. monachus*	*A. adalberti* & *A. chrysaetos*	*G. fulvus*
Els Ports; Delta de l'Ebre	Natural Park	*G. fulvus*	*G. fulvus*	*G. fulvus* & *P. pica*

Table 3. Generalized linear models (GLMs) obtained from the AIC-based model selection to assess the effects of protected areas (PA), human footprint (HF) and scavenger species richness (Richness) on aesthetic enjoyment (photography, photography hotspot), recreational activities (tourism, tourism hotspot), contribution to knowledge (observation, observation hotspot) and non-material NCP hotspots. Number of estimated parameters (k), AIC_c values, AIC_c differences (ΔAIC_c) with the highest ranked model (that with the lowest AIC_c) and the variability of the models explained by the predictors (D2) are shown. Selected models are indicated in bold.

Response variable	Model	k	AIC_c	Δ-AIC_c	D2
Photography	**PA + HF + Richness**	**3**	**3756.9**	**0.00**	**22.04%**
	HF + Richness	2	3798.7	41.87	
	PA + Richness	2	3806.0	49.18	
	Richness	1	3838.0	81.16	
	PA + HF	2	3949.9	192.99	
	PA	1	3961.6	204.71	
	HF	1	4019.7	262.84	
	null	0	4020.0	263.13	
Photography hotspot	PA + Richness	2	1447.1	0.00	10.31%
	PA + HF + Richness	**3**	**1448.2**	**1.10**	**10.36%**
	Richness	1	1461.8	14.70	
	HF + Richness	2	1463.4	16.30	
	PA + HF	2	1561.5	114.43	
	PA	1	1562.5	115.36	
	HF	1	1604.9	157.82	
	null	0	1608.7	161.59	
Observation	**PA + HF + Richness**	**3**	**11146.7**	**0.00**	**18.50%**
	PA + HF	2	11309.1	162.45	
	HF + Richness	2	11341.3	194.65	
	PA + Richness	2	11364.0	217.31	
	PA	1	11434.4	287.74	
	Richness	1	11492.0	345.28	
	HF	1	11560.0	413.36	
	null	0	11603.6	456.95	
Observation hotspot	**PA + HF + Richness**	**3**	**1734.8**	**0.00**	**11.76%**
	PA + HF	2	1766.7	31.94	
	PA + Richness	2	1801.0	66.20	
	PA	1	1810.9	76.14	
	HF + Richness	2	1861.4	126.60	
	Richness	1	1921.7	186.95	
	HF	1	1927.7	192.94	
	null	0	1958.9	224.13	

Table 3. (Cont.)

Response variable	Model	k	AIC_c	Δ-AIC_c	D2
Tourism	**PA + HF + Richness**	**3**	**5782.8**	**0.00**	**25.83%**
	PA + Richness	2	5787.7	4.90	
	PA + HF	2	5899.4	116.61	
	PA	1	5945.9	163.03	
	HF + Richness	2	6020.3	237.43	
	Richness	1	6025.9	243.08	
	HF	1	6219.7	436.92	
	null	0	6300.5	517.71	
Tourism hotspot	**PA + HF + Richness**	**3**	**2557.5**	**0.00**	**16.44%**
	PA + Richness	2	2581.7	24.16	
	PA + HF	2	2685.8	128.28	
	PA	1	2745.9	188.37	
	HF + Richness	2	2746.3	188.80	
	Richness	1	2783.1	225.56	
	HF	1	2960.3	402.74	
	null	0	3053.4	495.86	
Non-material NCP hotspot	**PA + Richness**	**2**	**2852.8**	**0.00**	**14.879%**
	PA + HF + Richness	**3**	**2854.6**	**1.84**	**14.884%**
	PA + HF	2	3027.2	174.36	
	PA	1	3039.5	186.72	
	Richness	2	3049.8	196.98	
	HF + Richness	1	3049.9	197.12	
	HF	1	3318.1	465.30	
	null	0	3346.4	493.60	

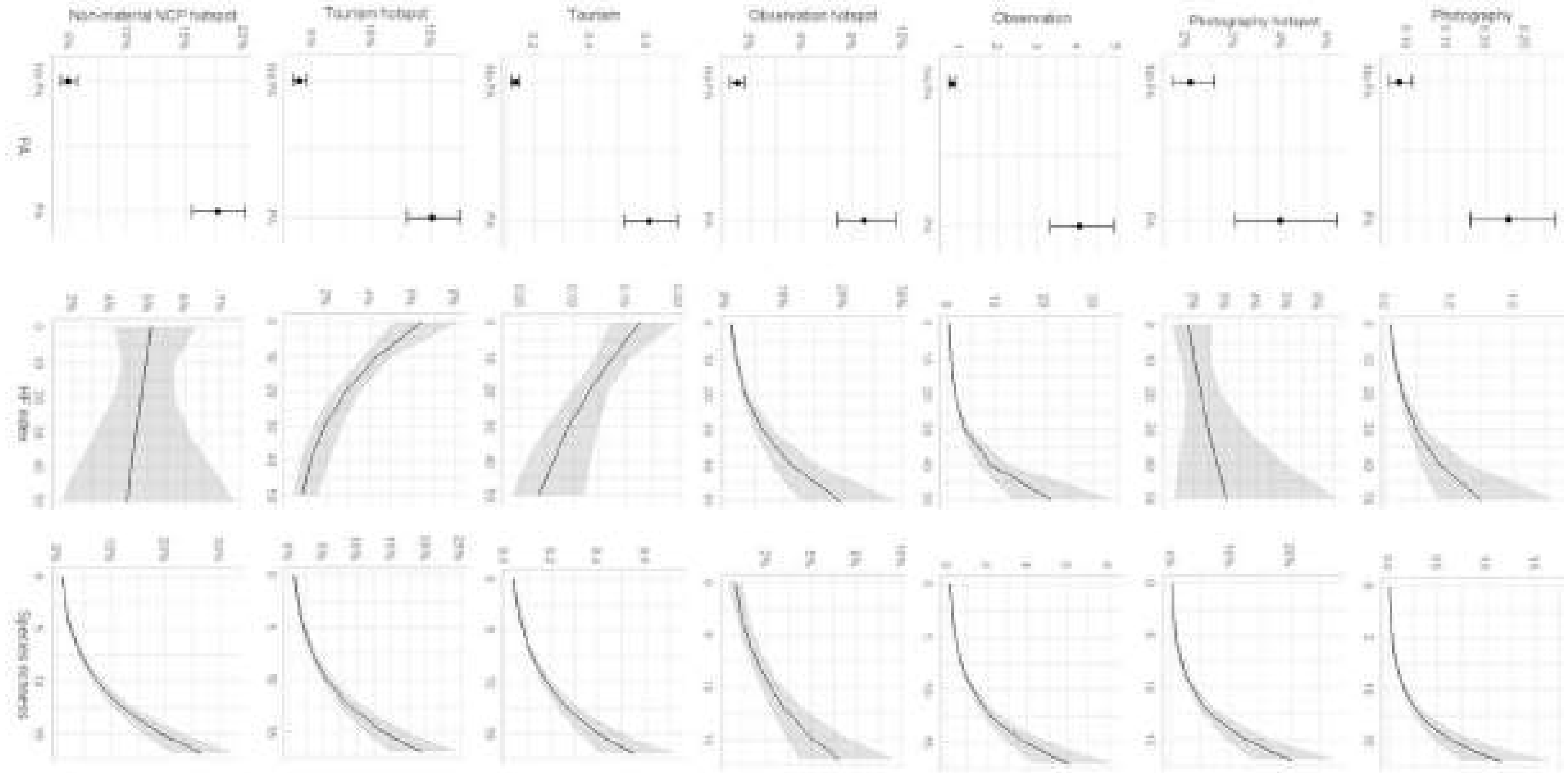


Figure 2. Predicted values of the effects of PA, HF, and scavenger species richness on non-material NCP categories (aesthetic enjoyment - photography, photography hotspot -, recreational activities - tourism, tourism hotspot -, contribution to knowledge - observation, observation hotspot - and non-material NCP hotspot) derived from GLM estimates, see Table S3.

DISCUSSION

Mapping non-material nature's contribution to people allows researchers and managers to understand where and how humans relate to nature. Non-material contributions, as opposed to regulation or material ones, tend to aggregate in certain areas in relation to human accessibility to people (Queiroz et al., 2015). Our work highlights that protected natural areas play an important role for the human-scavengers relation. In line with our expectation, the three explored non-material NCP categories (i.e., aesthetic enjoyment, recreational experiences, contribution to knowledge) were positively related to the presence of PA. In particular, the index that assembled the three categories (i.e., non-material NCP index) showed their hotspots covering seven of the 10 national parks of continental Spain (**Figure 1**). National parks have a long-standing history of protection, publicity and appreciation. In 1918, the first two Spanish National Parks were established (*Picos de Europa* and *Ordesa y Monte Perdido*) for the purpose of recognising their aesthetic and scenic importance. The interest in conserving valuable ecosystems progressively led to the designation of several new protected areas at different protection levels, with the last Spanish national park being declared in 2021 (*Sierra de las Nieves*). Our results support the notion that the recreational role of PA is still fundamental as they are scenarios that connect both "people with nature" and also "people with people" (Roux et al., 2020). To maintain and enhance this role, PA require well-designed use and management plans to be established, with economic investment for safeguarding, and developing infrastructures to promote visitors. Otherwise, uncontrolled crowding could have a negative impact on natural areas, which could bring about the loss of both positive affect and non-material contributions (Taff et al., 2019). These assets, together with the societal appreciation of ecosystems that entails setting up PA in a given territory (Hernández-Morcillo et al., 2013), could evoke a call effect on people (Adamowicz et al., 2011). These facilities for visiting PA would contribute to the humans-nature relation and, thus, to the provision of non-material contributions.

We found that the provision of non-material scavenger contributions was also positively related to scavengers' species richness. However, the scavengers guild was distributed beyond where hotspots were located, which could have been interpreted as habitat suitability with the potential to provide NCP (Burkhard and Maes, 2017). So, the provision of non-material contributions could be preferentially linked with the spaces in which humans and scavengers co-occur, rather than with the distribution of the species responsible for providing them. This would reinforce the idea that people come to areas where there is infrastructure and information that facilitate enjoyment. PA are habitats of charismatic species that attract visitors (Arbieu et al., 2018). In fact charismatic species like brown bears and bearded vultures are related to touristic activities in Spain (Aguilera-Alcalá et al., 2020).

The NCP categories benefited by HF were aesthetic enjoyment and contribution to knowledge (i.e., photography and observations recorded on the GBIF). Nevertheless, studies at a higher scale of resolution also showed that the use of social media inside African protected areas is not directly related to the richness of charismatic mammals, which would be expected, but to areas with fewer access restrictions (Hausmann et al., 2017). The GBIF records reflect the occurrence of biodiversity in Spain (Otegui et al., 2013); that is, common scavenger species are more represented. Common scavengers, such as griffon vultures or black kites (Aguilera-Alcalá et al., 2020), are easy to observe outside PA, and to also photograph. This means that the HF variable does not negatively condition the provision of these non-material NCP. Nevertheless, HF has negative impacts on both global biodiversity hotspots (Weinzettel et al., 2018) and global scavenger richness (Sebastián-González et al., 2019). Therefore, low HF levels may suggest that humans access nature, while high HF levels could exclude the species responsible for providing NCP by inhabiting these territories.

METHODOLOGICAL CONSIDERATIONS BY EVALUATING NON-MATERIAL CONTRIBUTIONS

As non-material NCP are intrinsically related to human activities, perceptions and the cultural valuation of nature, their distributions are anthropocentrically biased. Our assessment was developed by employing data about the involved stakeholders; that is, preferences of photographers, areas with tourist activities and places where scavenger species have been sighted. Therefore, non-material NCP assessments capture human behaviour in nature. Contrarily, assessments of regulating contributions reflect the ecological process that species perform in ecosystems, and covers the full species distribution range. For example, avian scavengers have a vast home range (Alarcón and Lambertucci, 2018) and perform regulating contributions to carrion depletion in their distribution area (Morales-Reyes et al., 2017), regardless of people being present.

Consequently, non-material mapping allows us to understand how people relate to nature, but should not be used to identify areas on which conservation programmes should focus.

Data mining from Internet sources offers the advantage of obtaining larger data volumes, and on a broader scale than conventional surveys performed by researchers in the field, such as interviews. However, data from Internet sources entail limitations that should be considered. For example, urban and young adults are more prone to use technology and social media (Oteros-Rozas et al., 2018; Schwartz et al., 2013; Toivonen et al., 2019). Photo posting, recreational offers and observation reports, used herein as indicators of non-material NCP, have an inherent bias related to people who access technology and Internet users' ability, and may not represent all the social groups in a given country (Burkhard and Maes, 2017; Oteros-Rozas et al., 2018). In addition, regional biases could exist; for example, a regional citizen science platform that operates in northeast Spain (Catalonia) (www.ortnitho.cat) could increase biodiversity observations compared to the rest of the country. However, at the same time, this would demonstrate a particular interest in sharing biodiversity information in a region.

In this paper, we separately explore the non-material NCP categories by using different indicators, and each one is affected by HF in a different sense. Aggregating many contributions is useful for detecting general patterns, but more detailed studies that relate distinct indicators allow us to uncover not only intertwining NCP categories (Aguilera-Alcalá et al., 2020), but also the underlying processes in the humans-nature relation.

CONCLUSIONS

Our results might contribute to understand the context for non-material NCP development. These findings could be included in decision-making processes to improve people´s accessibility to wildlife enjoyment as a positive societal valuation of biodiversity can positively impact and support future conservation programmes (Bennett, 2016; Lenda et al., 2020; Martín-López et al., 2009). As protected areas play an important role in this regard, proper management is essential to prevent crowding from being counterproductive for wildlife conservation. Future studies which aim to monitor the impact of the people who visit nature are key to properly manage these activities. Additionally, as non-material NCP tend to be context-dependent and strongly influenced by local culture, new issues arise to assess whether these provision patterns are analogous to other regions and in other wildlife groups.

REFERENCES

Adamowicz, W.L., Naidoo, R., Nelson, E., Polasky, S., Zhang, J., 2011. Nature-based tourism and recreation, in: Kareiva, P., Tallis, H., Ricketts, T.H., Daily, G.C., Polasky, S. (Eds.), Natural Capital: Theory and Practice of Mapping Ecosystem Services. Oxford. https://doi.org/10.1093/acprof:oso/9780199588992.001.0001

Aguilera-Alcalá, N., Morales-Reyes, Z., Martín-López, B., Moleón, M., Sánchez-Zapata, J.A., 2020. Role of scavengers in providing non-material contributions to people. Ecol. Indic. 117, 106643. https://doi.org/10.1016/j.ecolind.2020.106643

Alarcón, P.A.E., Lambertucci, S.A., 2018. A three-decade review of telemetry studies on vultures and condors. Mov. Ecol. 6, 1–13. https://doi.org/10.1186/s40462-018-0133-5

Ament, J.M., Moore, C.A., Herbst, M., Cumming, G.S., 2017. Cultural Ecosystem Services in Protected Areas: Understanding Bundles, Trade-Offs, and Synergies. Conserv. Lett. 10, 439–449. https://doi.org/10.1111/conl.12283

Arbieu, U., Grünewald, C., Martín-López, B., Schleuning, M., Böhning-Gaese, K., 2018. Large mammal diversity matters for wildlife tourism in Southern African Protected Areas : Insights for management. Ecosyst. Serv. 31, 481–490. https://doi.org/10.1016/j.ecoser.2017.11.006

Barton, K., 2013. MuMIn: Multi-Model Interference. R package version 1.9.13.

Becker, N., Inbar, M., Bahat, O., Choresh, Y., Ben-Noon, G., Yaffe, O., 2005. Estimating the economic value of viewing griffon vultures *Gyps fulvus*: A Travel Cost Model study at Gamla Nature Reserve, Israel. Oryx 39, 429–434. https://doi.org/10.1109/SENSOR.2007.4300616

Bennett, N.J., 2016. Using perceptions as evidence to improve conservation and environmental management. Conserv. Biol. 30, 582–592. https://doi.org/10.1111/cobi.12681

Buechley, E.R., Şekercioğlu, Ç.H., 2016. The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions. Biol. Conserv. 198, 220–228. https://doi.org/10.1016/j.biocon.2016.04.001

Burkhard, B., Maes, J., 2017. Mapping Ecosystem Services. Pensoft, Sofia.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference. A practical information-theoretic approach. Springer-Verlag, New York.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., MacE, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67. https://doi.org/10.1038/nature11148

Ceaușu, S., Apaza-Quevedo, A., Schmid, M., Martín-López, B., Cortés-Avizanda, A., Maes, J., Brotons, L., Queiroz, C., Pereira, H.M., 2021. Ecosystem service mapping needs to capture more effectively the biodiversity important for service supply. Ecosyst. Serv. 48, 101259. https://doi.org/10.1016/j.ecoser.2021.101259

Chape, S., Harrison, J., Spalding, M., Lysenko, I., 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philos. Trans. R. Soc. B 360, 443–455. https://doi.org/10.1098/rstb.2004.1592

Daniel, T.C., Muhar, A., Arnberger, A., Aznar, O., Boyd, J.W., Chan, K.M.A., Costanza, R., Elmqvist, T., Flint, C.G., Gobster, P.H., Gret-Regamey, A., Lave, R., Muhar, S., Penker, M., Ribe, R.G., Schauppenlehner, T., Sikor, T., Soloviy, I., Spierenburg, M., Taczanowska, K., Tam, J., von der Dunk, A., 2012. Contributions of cultural services to the ecosystem services agenda. Proc. Natl. Acad. Sci. USA 109, 8812–8819. https://doi.org/10.1073/pnas.1114773109

DeVault, T.L., Beasley, J.C., Olson, Z.H., Moleón, M., Carrete, M., Margalida, A., Sánchez-Zapata, J.A., 2016. Ecosystem Services Provided by Avian Scavengers, in: C.H., Ş., D.G., W., C.J., W. (Eds.), Why Birds Matter: Avian Ecological Function and Ecosystem Services. University of Chicago Press, Chicago, pp. 235–270.

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., Hill, R., Chan, K.M.A., Baste, I.A., Brauman, K.A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P.W., van Oudenhoven, A.P.E., van der Plaat, F., Schröter, M., Lavorel, S., Aumeeruddy-Thomas, Y., Bukvareva, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C.A., Hewitt, C.L., Keune, H., Lindley, S., Shirayama, Y., 2018. Assessing nature's contributions to people. Science (80- .). 359, 270–272. https://doi.org/10.1126/science.aap8826

European Environment Agency, 2019. Natura 2000 Network [WWW Document]. URL https://cmshare.eea.europa.eu/s/n5L8Lrs9aYD775S/download (accessed 3.24.21).

Fagerholm, N., Torralba, M., Burgess, P.J., Plieninger, T., 2016. A systematic map of ecosystem services assessments around European agroforestry. Ecol. Indic. 62, 47–65. https://doi.org/10.1016/j.ecolind.2015.11.016

García-Jiménez, R., Morales-Reyes, Z., Pérez-García, J.M., Margalida, A., 2021. Economic valuation of non-material contributions to people provided by avian scavengers: Harmonizing conservation and wildlife-based tourism. Ecol. Econ. 187, 107088. https://doi.org/10.1016/j.ecolecon.2021.107088

García-Jiménez, R., Pérez-García, J.M., Margalida, A., Morales-Reyes, Z., 2022. Avian scavengers' contributions to people: The cultural dimension of wildlife-based tourism. Sci. Total Environ. 806, 150419. https://doi.org/10.1016/j.scitotenv.2021.150419

Hausmann, A., Toivonen, T., Heikinheimo, V., Tenkanen, H., Slotow, R., Di Minin, E., 2017. Social media reveal that charismatic species are not the main attractor of ecotourists to sub-Saharan protected areas. Sci. Rep. 7, 1–9. https://doi.org/10.1038/s41598-017-00858-6

Hernández-Morcillo, M., Plieninger, T., Bieling, C., 2013. An empirical review of cultural ecosystem service indicators. Ecol. Indic. 29, 434–444. https://doi.org/10.1016/j.ecolind.2013.01.013

Hevia, V., Martín-López, B., Palomo, S., García-Llorente, M., de Bello, F., González, J.A., 2017. Trait-based approaches to analyze links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges. Ecol. Evol. 7, 831–844. https://doi.org/10.1002/ece3.2692

Horns, J.J., Adler, F.R., Şekercioğlu, Ç.H., 2018. Using opportunistic citizen science data to estimate avian population trends. Biol. Conserv. 221, 151–159. https://doi.org/10.1016/j.biocon.2018.02.027

INE, 2022. INE. Instituto Nacional de Estadística. Frontur [WWW Document]. URL https://www.ine.es/uc/ttSi6UA7

Lambertucci, S.A., Margalida, A., Speziale, K.L., Amar, A., Ballejo, F., Bildstein, K.L., Blanco, G., Botha, A.J., Bowden, C.G.R., Cortés-Avizanda, A., Duriez, O., Green, R.E., Hiraldo, F., Ogada, D., Plaza, P., Sánchez-Zapata, J.A., Santangeli, A., Selva, N., Spiegel, O., Donázar, J.A., 2021. Presumed killers? Vultures, stakeholders, misperceptions, and fake news. Conserv. Sci. Pract. 3, e415. https://doi.org/10.1111/csp2.415

Lenda, M., Skórka, P., Mazur, B., Sutherland, W., Tryjanowski, P., Moroń, D., Meijaard, E., Possingham, H.P., Wilson, K.A., 2020. Effects of amusing memes on concern for unappealing species. Conserv. Biol. 34, 1200–1209. https://doi.org/10.1111/cobi.13523

Luederitz, C., Brink, E., Gralla, F., Hermelingmeier, V., Meyer, M., Niven, L., Panzer, L., Partelow, S., Rau, A.L., Sasaki, R., Abson, D.J., Lang, D.J., Wamsler, C., von Wehrden, H., 2015. A review of urban ecosystem services: Six key challenges for future research. Ecosyst. Serv. 14, 98–112. https://doi.org/10.1016/j.ecoser.2015.05.001

Maes, J., Paracchini, M.L., Zulian, G., Dunbar, M.B., Alkemade, R., 2012. Synergies and trade-offs between ecosystem service supply, biodiversity, and habitat conservation status in Europe. Biol. Conserv. 155, 1–12. https://doi.org/10.1016/j.biocon.2012.06.016

Margalida, A., Campión, D., Donázar, J.A., 2014. Vultures vs livestock: Conservation relationships in an emerging conflict between humans and wildlife. ORYX 48, 172–176. https://doi.org/10.1017/S0030605312000889

Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline-An appraisal of the human health and other benefits of vultures in India. Ecol. Econ. 67, 194–204. https://doi.org/10.1016/j.ecolecon.2008.04.020

Martín-López, B., Montes, C., Ramírez, L., Benayas, J., 2009. What drives policy decision-making related to species conservation? Biol. Conserv. 142, 1370–1380. https://doi.org/10.1016/j.biocon.2009.01.030

Martínez-Harms, M.J., Balvanera, P., 2012. Methods for mapping ecosystem service supply: A review. Int. J. Biodivers. Sci. Ecosyst. Serv. Manag. 8, 17–25. https://doi.org/10.1080/21513732.2012.663792

Martínez-Pastur, G., Peri, P.L., Lencinas, M. V., García-Llorente, M., Martín-López, B., 2016. Spatial patterns of cultural ecosystem services provision in Southern Patagonia. Landsc. Ecol. 31, 383–399. https://doi.org/10.1007/s10980-015-0254-9

Methorst, J., Arbieu, U., Bonn, A., Böhning-Gaese, K., Müller, T., 2020. Non-material contributions of wildlife to human well-being: A systematic review. Environ. Res. Lett. 15, 093005. https://doi.org/10.1088/1748-9326/ab9927

Milcu, A.I., Hanspach, J., Abson, D., Fischer, J., 2013. Cultural Ecosystem Services: A Literature Review and Prospects for Future Research. Ecol. Soc. 18. https://doi.org/10.5751/ES-05790-180344

MITECO, 2020. Natural Protected Areas [WWW Document]. URL https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-naturaleza/informacion-disponible/ENP_Descargas.aspx (accessed 3.24.21).

Moleón, M., Sánchez-Zapata, J.A., 2015. The Living Dead: Time to Integrate Scavenging into Ecological Teaching. Bioscience 65, 1003–1010. https://doi.org/10.1093/biosci/biv101

Moleón, M., Sánchez-Zapata, J.A., Margalida, A., Carrete, M., Owen-Smith, N., Donázar, J.A., 2014. Humans and scavengers: The evolution of interactions and ecosystem services. Bioscience 64, 394–403. https://doi.org/10.1093/biosci/biu034

Morales-Reyes, Z., Pérez-García, J.M., Moleón, M., Botella, F., Carrete, M., Donázar, J.A., Cortés-Avizanda, A., Arrondo, E., Moreno-Opo, R., Jiménez, J., Margalida, A., Sánchez-Zapata, J.A., 2017. Evaluation of the network of protection areas for the feeding of scavengers in Spain: from biodiversity conservation to greenhouse gas emission savings. J. Appl. Ecol. 54, 1120–1129. https://doi.org/10.1111/1365-2664.12833

Morales-Reyes, Z., Pérez-García, J.M., Moleón, M., Botella, F., Carrete, M., Lazcano, C., Moreno-Opo, R., Margalida, A., Donázar, J.A., Sánchez-Zapata, J.A., 2015. Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. Sci. Rep. 5, 7811. https://doi.org/10.1038/srep07811

Nahuelhual, L., Carmona, A., Lozada, P., Jaramillo, A., Aguayo, M., 2013. Mapping recreation and ecotourism as a cultural ecosystem service : An application at the local level in Southern Chile. Appl. Geogr. 40, 71–82. https://doi.org/10.1016/j.apgeog.2012.12.004

Otegui, J., Ariño, A.H., Encinas, M.A., Pando, F., 2013. Assessing the Primary Data Hosted by the Spanish Node of the Global Biodiversity Information Facility (GBIF). PLoS One 8, e55144. https://doi.org/10.1371/journal.pone.0055144

Oteros-Rozas, E., Martín-López, B., Fagerholm, N., Bieling, C., Plieninger, T., 2018. Using social media photos to explore the relation between cultural ecosystem services and landscape features across five European sites. Ecol. Indic. 94, 74–86. https://doi.org/10.1016/j.ecolind.2017.02.009

Plieninger, T., Dijks, S., Oteros-Rozas, E., Bieling, C., 2013. Assessing, mapping, and quantifying cultural ecosystem services at community level. Land use policy 33, 118–129. https://doi.org/10.1016/j.landusepol.2012.12.013

Queiroz, C., Meacham, M., Richter, K., Norström, A. V., Andersson, E., Norberg, J., Peterson, G., 2015. Mapping bundles of ecosystem services reveals distinct types of multifunctionality within a Swedish landscape. Ambio 44, 89–101. https://doi.org/10.1007/s13280-014-0601-0

Roux, D.J., Smith, M.K.S., Smit, I.P.J., Freitag, S., Slabbert, L., Mokhatla, M.M., Hayes, J., Mpapane, N.P., 2020. Cultural ecosystem services as complex outcomes of people–nature interactions in protected areas. Ecosyst. Serv. 43, 101111. https://doi.org/10.1016/j.ecoser.2020.101111

Schwartz, H.A., Eichstaedt, J.C., Kern, M.L., Dziurzynski, L., Ramones, S.M., Agrawal, M., Shah, A., Kosinski, M., Stillwell, D., Seligman, M.E.P., Ungar, L.H., 2013. Personality, Gender, and Age in the Language of Social Media: The Open-Vocabulary Approach. PLoS One 8, e73791. https://doi.org/10.1371/journal.pone.0073791

Sebastián-González, E., Barbosa, J.M., Pérez-García, J.M., Morales-Reyes, Z., Botella, F., Olea, P.P., Mateo-Tomás, P., Moleón, M., Hiraldo, F., Arrondo, E., Donázar, J.A., Cortés-Avizanda, A., Selva, N., Lambertucci, S.A., Bhattacharjee, A., Brewer, A., Anadón, J.D., Abernethy, E., Rhodes, O.E., Turner, K., Beasley, J.C., DeVault, T.L., Ordiz, A., Wikenros, C., Zimmermann, B., Wabakken, P., Wilmers, C.C., Smith, J.A., Kendall, C.J., Ogada, D., Buechley, E.R., Frehner, E., Allen, M.L., Wittmer, H.U., Butler, J.R.A., du Toit, J.T., Read, J., Wilson, D., Jerina, K., Krofel, M., Kostecke, R., Inger, R., Samson, A., Naves-Alegre, L., Sánchez-Zapata, J.A., 2019. Scavenging in the Anthropocene: Human impact drives vertebrate scavenger species richness at a global scale. Glob. Chang. Biol. 25, 3005–3017. https://doi.org/10.1111/gcb.14708

Taff, B.D., Benfield, J., Miller, Z.D., D'antonio, A., Schwartz, F., 2019. The role of tourism impacts on cultural ecosystem services. Environments 6, 1–12. https://doi.org/10.3390/environments6040043

Toivonen, T., Heikinheimo, V., Fink, C., Hausmann, A., Hiippala, T., Järv, O., Tenkanen, H., Di Minin, E., 2019. Social media data for conservation science: A methodological overview. Biol. Conserv. 233, 298–315. https://doi.org/10.1016/j.biocon.2019.01.023

Vaz, A.S., Moreno-Llorca, R.A., Gonçalves, J.F., Vicente, J.R., Méndez, P.F., Revilla, E., Santamaria, L., Bonet-García, F.J., Honrado, J.P., Alcaraz-Segura, D., 2020. Digital conservation in biosphere reserves : Earth observations, social media, and nature' s cultural contributions to people. Conserv. Lett. 1–9. https://doi.org/10.1111/conl.12704

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Global terrestrial Human Footprint maps for 1993 and 2009. Sci. Data 3, 1–10. https://doi.org/10.1038/sdata.2016.67

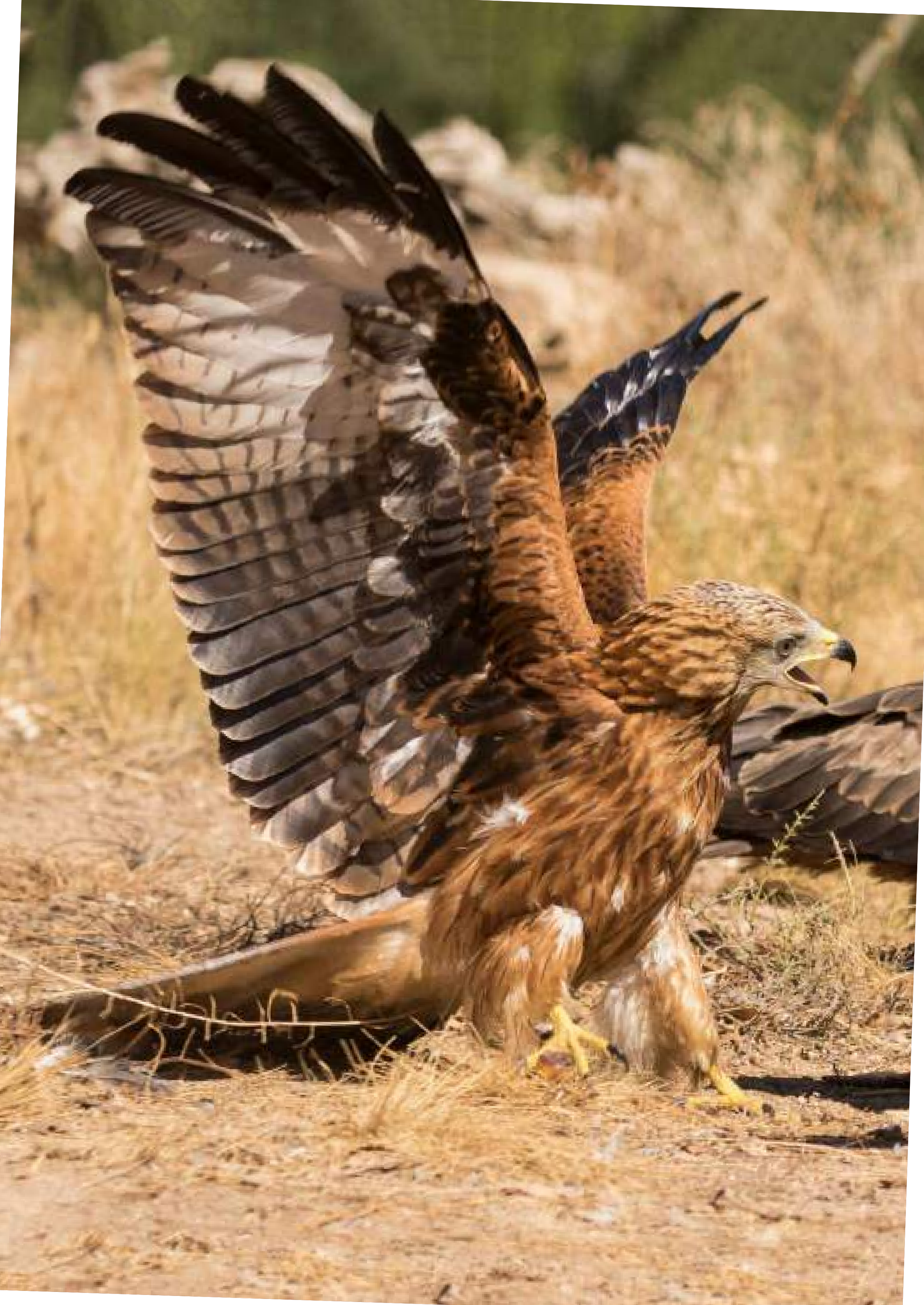
Weinzettel, J., Vačkář, D., Medková, H., 2018. Human footprint in biodiversity hotspots. Front. Ecol. Environ. 16, 447–452. https://doi.org/10.1002/fee.1825

Willemen, L., Cottam, A.J., Drakou, E.G., Burgess, N.D., 2015. Using social media to measure the contribution of red list species to the nature-based tourism potential of african protected areas. PLoS One 10, e0129785. https://doi.org/10.1371/journal.pone.0129785

Wolf, C., Ripple, W.J., 2018. Rewilding the world' s large carnivores. R. Soc. Open Sci. 5, 172235. https://doi.org/http://dx.doi.org/10.1098/rsos.172235

Wu, J., Feng, Z., Gao, Y., Peng, J., 2013. Hotspot and relationship identification in multiple landscape services: A case study on an area with intensive human activities. Ecol. Indic. 29, 529–537. https://doi.org/10.1016/j.ecolind.2013.01.037

Yesson, C., Brewer, P.W., Sutton, T., Caithness, N., Pahwa, J.S., Burgess, M., Gray, W.A., White, R.J., Jones, A.C., Bisby, F.A., Culham, A., 2007. How global is the global biodiversity information facility? PLoS One 2, e1124. https://doi.org/10.1371/journal.pone.0001124



General Discussion

Photo by Pilar Oliva Vidal.
Red kite (*Milvus milvus*) and black kite (*Milvus migrans*)
discussing in Pre-Pyrenees of Lleida.

In the context of the current global environmental change, understanding human-wildlife relations is, more than ever, an urgent task. This includes investigating the impact of human activities on ecosystems, while acknowledging the multiple contributions that nature provides to people. By using different methodological approaches, the findings presented in this thesis may contribute to a better understanding of the wide array of pathways in which humans and scavengers interact, which has strong conservation ramifications. In doing so, it also pretends to stimulate further research on both old and new questions related to this promising topic. The way we address the present challenges for scavenger conservation will contribute to determine how humans will relate with scavengers in the future.

The conservation of scavenger species is closely related to several human activities, such as livestock farming and sport hunting, which eventually are chief drivers of the use of poison (Santangeli et al. 2016). Importantly, these activities appear to be declining in developed countries (Oteros-Rozas et al. 2013; Massei et al. 2015; De la Bodega et al. 2020). This thesis has contributed to understand these issues. Livestock management has a direct impact on the conservation of scavenger species, especially for obligate scavengers, whose populations widely benefit from the carrion provided by extensive and intensive livestock (Margalida and Colomer 2012; Morales-Reyes et al. 2017). Also, the availability of livestock carrion in the field strongly shapes the use of foraging areas by highly mobile avian scavengers (Arrondo et al. 2018; González-Delgado et al. 2022). The findings from this dissertation support that the extensive livestock practices of transhumance affect the spatial foraging patterns of avian scavengers, even in those areas where pasturelands are small in size relative to vultures' home range (Alarcón and Lambertucci 2018) (Aguilera-Alcalá et al. 2021). Therefore, the current transition towards intensive livestock husbandry (Ilea 2009), abandoning the extensive one, may directly affect to the species whose populations depends on it if rewilding process are not properly managed. The recovery of wild ungulates in many European areas has been noticeable (Apollonio et al. 2010; Acevedo et al. 2011; Carpio et al. 2021). However, if this increase does not compensate for the decline of extensive livestock farming in terms of carrion biomass availability and spatiotemporal arrangement, the scavenger populations may be affected.

Although poisoning has decreased in Spain in the last decades (De la Bodega et al. 2020), it still poses a worrying mortality risk for scavengers. To date, no experimental approaches have been carried out to contrast the diversity of species that are recorded as victims of poisoning with those that could potentially die from this illegal activity.

The findings presented in Chapter 2 of this thesis (Gil-Sánchez et al. 2021) shed light on this issue. The records in the official poisoning database have underestimated several facultative scavenger species as victims. These findings can be very useful to improve detection protocols for poisoned wildlife. Even more, considering that Spanish protocols are reference models for other European countries in the fight against poisoning (Silva et al. 2018), the improvements implemented here can be easily transferred to other areas.

The decline of these traditional activities goes together with changes in societal lifestyles, such as the abandonment of rural areas in favour of urban life (Llorent-Bedmar et al. 2021). This entails a polarisation in the perception of nature and its contributions to people. For example, rural people are more prone to recognise a higher diversity of nature contributions than urban people, probably because their own well-being is closely connected with nature (Martín-López et al. 2012). Urban people tends to be cognitively disconnected from the human dependence of environment, recognising preferentially non-material contributions of ecosystems (Martín-López et al. 2012). Therefore, the importance of non-material contributions to people, such as those described in this thesis for the scavengers' guild (Aguilera-Alcalá et al. 2020), will become increasingly recognised and valued.

Recreational experiences are among the most assessed non-material contributions (Kosanic and Petzold 2020), likely because nature-based tourism, such as birdwatching, is flourishing worldwide (Ma et al. 2013; Steven et al. 2014). Wildlife tourism arises as an opportunity to develop political and financial support for conservation programs of endangered species, not only scavengers (Becker et al. 2005; García-Jiménez et al. 2021), but also other species, such as mountain gorillas (Nielsen and Spenceley 2010), whales and turtles (Wilson and Tisdell 2003), and others (Buckley et al. 2012). However, other categories of non-material contributions that are also linked to people's well-being, have received less research attention (Kosanic and Petzold 2020). Taking scavengers as example, recreation experiences are linked to charismatic species, often endangered, but other (non-threatened) species also play an important role in providing wider non-material contributions, which are very highlighted in aesthetic enjoyment experiences (Aguilera-Alcalá et al. 2020).

The non-material scavengers' contributions addressed in this thesis, have been measured by different indicators that assess the perceiving human-nature experiences (Russell et al. 2013). These perceiving contributions are not necessarily mediated by living within nature (e.g., shepherds who directly benefit from the regulating contributions of livestock carcass removal). Rather, non-material contributions can be perceived even by people from other places, such as tourists that travel or citizens that read dissemination magazines, being decoupled from the place in which originate. This means that the benefits to people's well-being are extended far beyond their origin areas. The areas in which non-material contributions take place are mostly linked to natural environments, especially to protected areas (Chapter 4).

Therefore, the modern human-nature relations and the perceived contributions opens up a new paradigm that may condition future conservation challenges. For example, an excess of visitors in protected areas may cause disturbance to wildlife (Donázar et al. 2018; Perona et al. 2019), which would be disadvantageous to the provision of their contributions. Pristine areas, such as the Tibet, are currently threatened by increasing human pressures (Li et al. 2018), and the unregulated crowding of natural areas can diminish their positive perception (Taff et al. 2019). In short, future conservation concerns will have to harmonise the provision of non-material contributions and the conservation of ecosystems in order to achieve a sustainable coexistence between humans and natural elements.

CONSIDERATIONS AND FUTURE PERSPECTIVES

During the development of this thesis, some limitations have been identified that should be considered for future research. The effect of transhumant livestock presence on scavengers has been addressed on summering areas of southern Spain. However, the foraging behaviour of scavengers in the livestock's wintering areas remains unexplored. The wintering areas of the transhumant herds considered in Chapter 1 are scattered along Sierra Morena mountains, making the assessment of the scavenger response unclear. Therefore, it would be desirable to extend this work to larger areas in order to explore how transhumance affects scavenger foraging behaviour in the two different areas according to seasons. In addition, if the decline of extensive livestock farming continues, rewilding processes will need to be monitored to ensure that these transitions do not jeopardise the population dynamics of scavengers.

The database of poisoned wildlife has the limitation that data collection comes from heterogeneous sources, and, also, the detection efforts of poisoning episodes are variable among administrative regions. However, this heterogeneity could be adjusted by developing spatial modelling to describe the risk of poisoning in future research. Yet, the available information has great potential that deserves to be explored in depth.

For example, spatially explicit information about poisoning episodes would allow the creation of mortality risk maps on a national scale, which can be matched with the movement patterns of the griffon vultures tracked in Chapter 1 (Aguilera-Alcalá et al. 2021), and then, to detect priority areas for anti-poisoning surveillance. Furthermore, the mortality risk mapping could be assessed in comparison with the non-material contribution mapping developed in Chapter 4 to identify areas with potential loss of contributions to people. Furthermore, the development of non-material contribution mapping, addressed in Chapter 4, opens up the opportunities to explore synergies and trade-offs with regard to previous research on the regulating contributions provided by scavengers (e.g. Morales-Reyes et al. 2015; Morales-Reyes et al. 2017).

Data mined from social media arise as an important source of information to study human-nature interactions (Di Minin et al. 2015), although it has certain limitations that need to be considered in the interpretation of the results found. Internet users' profile is biased to young people (Schwartz et al. 2013), to urban profiles (Oteros-Rozas et al. 2018), and even to certain administrative regions, as we noticed in the observations of scavengers assessed in Chapter 4. Therefore, according to the research question under consideration, it would be desirable to contemplate complementary methods to help unravel the perception about nature contributions by different stakeholders (Martín-López et al. 2012). Thus, new approaches are needed to assess the non-material scavengers' contributions to those stakeholders not captured by data mining from the internet (employed on Chapter 3 & 4). For example, recently, some approaches that assess non-material scavengers' contribution by interviews to wildlife watching tourist have emerged (García-Jiménez et al. 2022), and further studies could cover the contributions perceived by other stakeholders, especially of those who have an impact on scavengers' conservation derived from their activities, such as hunters, farmers or wildlife managers.

Evaluations of social perception about wildlife have shown that news about human-scavenger conflicts in the media and social networks boosts the negative perception of the species, even when it is not promoted by empirical conflicts (Fernández-Gil et al. 2016; Lambertucci et al. 2021). Therefore, highlighting the benefits provided by scavengers, such as those described in this thesis (Aguilera-Alcalá et al. 2020; Chapter 4), could provide new arguments to improve the social perception about these species. Thus, it would be desirable to communicate, in the media, the importance of these species to sustain healthy ecosystems and human well-being, to encourage the social support for conservation policies, and to alleviate future potential conflicts.

Humans are constantly undergoing changes that influence the conservation of nature. We encourage that further research should evaluate not only how environmental changes affect biodiversity, but also how these changes affect humans' relations with nature, and thus human well-being, from a multidisciplinary approach, including environmental, sociological, and anthropological dimensions. These assessments will provide empirical information that will help to shape human-wildlife coexistence in human dominated ecosystems.

REFERENCES

Acevedo, P., M. Á. Farfán, A. L. Márquez, M. Delibes-Mateos, R. Real, and J. M. Vargas. 2011. Past, present and future of wild ungulates in relation to changes in land use. *Landscape Ecology* 26: 19–31. doi:10.1007/s10980-010-9538-2.

Aguilera-Alcalá, N., Z. Morales-Reyes, B. Martín-López, M. Moleón, and J. A. Sánchez-Zapata. 2020. Role of scavengers in providing non-material contributions to people. *Ecological Indicators* 117. Elsevier: 106643. doi:10.1016/j.ecolind.2020.106643.

Aguilera-Alcalá, N., E. Arrondo, R. Pascual-Rico, Z. Morales-Reyes, J. M. Gil-Sánchez, J. A. Donázar, M. Moleón, and J. A. Sánchez-Zapata. 2021. The value of transhumance for biodiversity conservation: Vulture foraging in relation to livestock movements. *Ambio*. doi:10.1007/s13280-021-01668-x.

Alarcón, P. A. E., and S. A. Lambertucci. 2018. A three-decade review of telemetry studies on vultures and condors. *Movement Ecology* 6. Movement Ecology: 1–13. doi:10.1186/s40462-018-0133-5.

Apollonio, M., R. Andersen, and R. Putman. 2010. *European ungulates and their management in the 21st century*. Edited by Marco Apollonio, Reidar Andersen, and Rory Putman. New York: Cambridge University Press.

Arrondo, E., M. Moleón, A. Cortés-Avizanda, J. Jiménez, P. Beja, J. A. Sánchez-Zapata, and J. A. Donázar. 2018. Invisible barriers: Differential sanitary regulations constrain vulture movements across country borders. *Biological Conservation* 219: 46–52. doi:10.1016/j.biocon.2017.12.039.

Becker, N., M. Inbar, O. Bahat, Y. Choresh, G. Ben-Noon, and O. Yaffe. 2005. Estimating the economic value of viewing griffon vultures *Gyps fulvus*: A Travel Cost Model study at Gamla Nature Reserve, Israel. *Oryx* 39: 429–434. doi:10.1109/SENSOR.2007.4300616.

Buckley, R. C., J. G. Castley, F. D. V. Pegas, A. C. Mossaz, and R. Steven. 2012. A Population Accounting Approach to Assess Tourism Contributions to Conservation of IUCN-Redlisted Mammal Species. *PLoS ONE* 7: e44134. doi:10.1371/journal.pone.0044134.

Carpio, A. J., M. Apollonio, and P. Acevedo. 2021. Wild ungulate overabundance in Europe: contexts, causes, monitoring and management recommendations. *Mammal Review* 51: 95–108. doi:10.1111/mam.12221.

Donázar, J. A., O. Ceballos, and A. Cortés-Avizanda. 2018. Tourism in protected areas: Disentangling road and traffic effects on intra-guild scavenging processes. *Science of the Total Environment* 630. Elsevier B.V.: 600–608. doi:10.1016/j.scitotenv.2018.02.186.

Fernández-Gil, A., J. Naves, A. Ordiz, M. Quevedo, E.

Revilla, and M. Delibes. 2016. Conflict misleads large carnivore management and conservation: Brown bears and wolves in Spain. *PLoS ONE* 11. doi:10.1371/journal.pone.0151541.

García-Jiménez, R., Z. Morales-Reyes, J. M. Pérez-García, and A. Margalida. 2021. Economic valuation of non-material contributions to people provided by avian scavengers: Harmonizing conservation and wildlife-based tourism. *Ecological Economics* 187. Elsevier B.V.: 107088. doi:10.1016/j.ecolecon.2021.107088.

García-Jiménez, R., J. M. Pérez-García, A. Margalida, and Z. Morales-Reyes. 2022. Avian scavengers contributions to people: The cultural dimension of wildlife-based tourism. *Science of the Total Environment* 806. The Authors: 150419. doi:10.1016/j.scitotenv.2021.150419.

Gil-Sánchez, J. M., N. Aguilera-Alcalá, M. Moleón, E. Sebastián-González, A. Margalida, Z. Morales-Reyes, C. J. Durá-Alemañ, P. Oliva-Vidal, et al. 2021. Biases in the Detection of Intentionally Poisoned Animals: Public Health and Conservation Implications from a Field Experiment. *International Journal of Environmental Research and Public Health* 18: 1201. doi:https:// doi.org/10.3390/ijerph18031201 Academic.

González-Delgado, A., A. Cortés-Avizanda, D. Serrano, E. Arrondo, O. Duriez, A. Margalida, M. Carrete, P. Oliva-Vidal, et al. 2022. Apex scavengers from different European populations converge at threatened savannah landscapes. *Scientific Reports* 12. Nature Publishing Group UK: 2500. doi:10.1038/s41598-022-06436-9.

Ilea, R. C. 2009. Intensive livestock farming: Global trends, increased environmental concerns, and ethical solutions. *Journal of Agricultural and Environmental Ethics* 22: 153–167. doi:10.1007/s10806-008-9136-3.

Kosanic, A., and J. Petzold. 2020. A systematic review of cultural ecosystem services and human wellbeing. *Ecosystem Services* 45. Elsevier B.V.: 101168. doi:10.1016/j.ecoser.2020.101168.

De la Bodega, D., C. Cano, and E. Mínguez. 2020. *El veneno en España. Evolución del envenenamiento de fauna silvestre (1992-2017)*. Edited by SEO/BirdLife and WWF. Madrid.

Lambertucci, S. A., A. Margalida, K. L. Speziale, A. Amar, F. Ballejo, K. L. Bildstein, G. Blanco, A. J. Botha, et al. 2021. Presumed killers? Vultures, stakeholders, misperceptions, and fake news. *Conservation Science and Practice* 3: e415. doi:10.1111/csp2.415.

Li, Shicheng, J. Wu, J. Gong, and Shaowei Li. 2018. Human footprint in Tibet: Assessing the spatial layout and effectiveness of nature reserves. *Science of the Total Environment* 621. Elsevier B.V.: 18–29. doi:10.1016/j.scitotenv.2017.11.216.

Llorent-Bedmar, V., V. C. Cobano-Delgado Palma, and M. Navarro-Granados. 2021. The rural exodus of young people from empty Spain. Socio-educational aspects. *Journal of Rural Studies* 82: 303–314. doi:10.1016/j.jrurstud.2021.01.014.

Ma, Z., Y. Cheng, J. Wang, and X. Fu. 2013. The rapid development of birdwatching in mainland China: a new force for bird study and conservation. *Bird Conservation International* 23: 259–269. doi:10.1017/S0959270912000378.

Margalida, A., and M. À. Colomer. 2012. Modelling the effects of sanitary policies on European vulture conservation. *Scientific Reports* 2. doi:10.1038/srep00753.

Martín-López, B., I. Iniesta-Arandia, M. García-Llorente, I. Palomo, I. Casado-Arzuaga, D. G. Del Amo, E. Gómez-Baggethun, E. Oteros-Rozas, et al. 2012. Uncovering ecosystem service bundles through social preferences. *PLoS ONE* 7. doi:10.1371/journal.pone.0038970.

Massei, G., J. Kindberg, A. Licoppe, D. Gacic, N. Šprem, J. Kamler, E. Baubet, U. Hohmann, et al. 2015. Wild boar populations up , numbers of hunters down ? A review of trends and implications for Europe. *Pest Management Science* 71: 492–500. doi:10.1002/ps.3965.

Di Minin, E., H. Tenkanen, and T. Toivonen. 2015. Prospects and challenges for social media data in conservation science. *Frontiers in Ecology and the Environment Science* 3: 1–6. doi:10.3389/fenvs.2015.00063.

Morales-Reyes, Z., J. M. Pérez-García, M. Moleón, F. Botella, M. Carrete, C. Lazcano, R. Moreno-Opo, A. Margalida, et al. 2015. Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. *Scientific Reports* 5: 7811. doi:10.1038/srep07811.

Morales-Reyes, Z., J. M. Pérez-García, M. Moleón, F. Botella, M. Carrete, J. A. Donázar, A. Cortés-Avizanda, E. Arrondo, et al. 2017. Evaluation of the network of protection areas for the feeding of scavengers in Spain: from biodiversity conservation to greenhouse gas emission savings. *Journal of Applied Ecology* 54: 1120–1129. doi:10.1111/1365-2664.12833.

Nielsen, H., and A. Spenceley. 2010. *The success of tourims in Rwanda – Gorillas and more*. The Hague, The Netherlands.

Oteros-Rozas, E., B. Martín-López, C. A. López, I. Palomo, and J. A. González. 2013. Envisioning the future of transhumant pastoralism through participatory scenario planning: a case study in Spain. *The Rangeland Journal* 35: 251–272. doi:http://dx.doi.org/10.1071/RJ12092.

Oteros-Rozas, E., B. Martín-López, N. Fagerholm, C. Bieling, and T. Plieninger. 2018. Using social media photos to explore the relation between cultural ecosystem services and landscape features across five European sites. *Ecological Indicators* 94. Elsevier Ltd: 74–86. doi:10.1016/j.ecolind.2017.02.009.

Perona, A. M., V. Urios, and P. López-López. 2019. Holidays? Not for all. Eagles have larger home ranges on holidays as a consequence of human disturbance. *Biological Conservation* 231. Elsevier: 59–66. doi:10.1016/j.biocon.2019.01.010.

Russell, R., A. D. Guerry, P. Balvanera, R. K. Gould, X. Basurto, K. M. A. Chan, S. Klain, J. Levine, et al. 2013. Humans and Nature: How Knowing and Experiencing Nature Affect Well-Being. *Annual Review of Environment and Resources* 38: 473–502. doi:10.1146/annurev-environ-012312-110838.

Santangeli, A., V. Arkumarev, N. Rust, and M. Girardello. 2016. Understanding, quantifying and mapping the use of poison by commercial farmers in Namibia – Implications for scavengers' conservation and ecosystem health. *Biological Conservation* 204. Elsevier Ltd: 205–211. doi:10.1016/j.biocon.2016.10.018.

Schwartz, H. A., J. C. Eichstaedt, M. L. Kern, L. Dziurzynski, S. M. Ramones, M. Agrawal, A. Shah, M. Kosinski, et al. 2013. Personality, Gender, and Age in the Language of Social Media: The Open-Vocabulary Approach. *PLoS ONE* 8: e73791. doi:10.1371/journal.pone.0073791.

Silva, J. P., J. Eldridge, S. Nottinghan, and C. Travagnin. 2018. *LIFE & Wildlife Crime*. Luxembourg. doi:10.2779/96643.

Steven, R., C. Morrison, and J. G. Castley. 2014. Birdwatching and avitourism: a global review of research into its participant markets , distribution and impacts , highlighting future research priorities to inform sustainable avitourism management. *Journal of Sustainable Tourism*: 37–41. doi:10.1080/09669582.2014.924955.

Taff, B. D., J. Benfield, Z. D. Miller, A. D'antonio, and F. Schwartz. 2019. The role of tourism impacts on cultural ecosystem services. *Environments* 6: 1–12. doi:10.3390/environments6040043.

Wilson, C., and C. Tisdell. 2003. Conservation and Economic Benefits of Wildlife-Based Marine Tourism : Sea Turtles and Whales as Case Studies. *Human Dimensions of Wildlife: An International Journal* 8: 49–58. doi:10.1080/10871200390180145.

Conclusions / Conclusiones

Photo by Pilar Oliva Vidal.
Bearded vulture (*Gypaetus barbatus*) in Pyrenees of Lleida.

CONCLUSIONS

I Despite the widespread decline of extensive livestock farming, the presence of transhumant herds still has an effect in the foraging activity of obligate scavengers in southeastern Spain. Preserving traditional, as opposed to industrial, farming systems may contribute to biodiversity conservation.

II Official databases about wildlife poisoning in Spain are biased, with several facultative scavenger species being underrepresented. More exhaustive monitoring of poison detection protocols is needed in order to be able to estimate the real impact of this activity, and to establish the appropriate corrective measures.

III In Spain, scavengers play a major role in providing different non-material contributions to people, such as aesthetic enjoyment, recreational activities, contribution to knowledge for both society and the scientific community, and supporting identity. These contributions are mediated both by the ecological traits of the species and by the sociocultural context of the stakeholders.

IV The scavengers' non-material contributions are heterogeneously distributed throughout peninsular Spain. In particular, they are linked to natural areas, specially to National Parks, so that proper management of these areas is essential to ensure that human presence does not compromise scavenger populations and the provision of their contributions.

V The poisoning of wildlife and the abandonment of traditional livestock practices in favour to more intensive ones can be a threat not only to scavenger populations, but also to the important and diverse non-material contributions that scavengers provide to society.

CONCLUSIONES

I Pese al declive generalizado de la ganadería extensiva, la presencia de rebaños trashumantes todavía tiene un efecto en el uso del espacio por parte de los carroñeros obligados en el sureste de España. Preservar los sistemas agroganaderos tradicionales, frente a los más industrializados, puede contribuir a la conservación de la biodiversidad.

II Las bases de datos oficiales sobre envenenamiento de fauna silvestre en España presentan sesgos, estando infrarrepresentadas algunas especies de carroñeros facultativos. Se hace necesaria una vigilancia más exhaustiva en los protocolos de detección de veneno, con el fin de poder estimar el impacto real de esta actividad y establecer las medidas correctoras oportunas.

III En España, los carroñeros desempeñan un papel importante en la provisión de diferentes contribuciones no materiales para las personas, como el disfrute estético, las actividades recreativas, la contribución al conocimiento para la sociedad y para la comunidad científica, y son base para la construcción de identidades. Estas contribuciones se relacionan tanto con los rasgos ecológicos de las especies como con el contexto sociocultural de los agentes implicados.

IV La provisión de contribuciones no materiales por parte de las especies carroñeras se distribuye heterogéneamente a lo largo de la España peninsular. En particular, está vinculada a los espacios naturales, especialmente a los parques nacionales, por lo que una gestión adecuada de estos espacios es esencial para que la presencia humana no perjudique ni a las poblaciones de carroñeros ni a la provisión de sus contribuciones.

V El envenenamiento de fauna silvestre y el abandono de las prácticas ganaderas tradicionales por otras más intensivas pueden ser una amenaza no solo para las poblaciones de carroñeros, sino también para las importantes y diversas contribuciones no materiales que éstos proporcionan a la sociedad.

Annexes

Photo by Pilar Oliva Vidal.
Griffon vulture (*Gyps fulvus*) and Egyptian vulture (*Neophron percnopterus*)
in Pre-Pyrenees of Lleida

SUPPLEMENTARY MATERIAL TO CHAPTER 1: THE VALUE OF TRANSHUMANCE FOR BIODIVERSITY CONSERVATION: VULTURE FORAGING IN RELATION TO LIVESTOCK MOVEMENTS

THIS MATERIAL INCLUDES:

Table S1. GPS device settings and time elapsed between consecutive locations.

Table S2. Details of griffon vultures tagged and tracking.

Table S1. GPS device settings and time elapsed between consecutive locations. Devices were activated one hour before sunrise and turned off one hour after sunset. High-performance settings were active continuously except if we detected a low battery status for several days. We then activated the low-performance setting until the battery recovered normal status. During the study period, the time between consecutive locations ranged from 5 seconds to 14.9 h with a median of 5 min.

	Battery status			
	Full	**Non-full**	**Close to security level**	**Under security level**
Low-performance setting	10 min	30 min	1 h	1 day
High-performance setting	5 min	20 min	30 min	1 day

Table S2. Details of griffon vultures tagged and tracking. The table shows fixes recorded during the period 2015-2018, the number of monitored months and the number of breeding years for each tagged individual.

Individual	Sex	No. fixes	No. months	No. breeding years
L73	Male	35539	49	4
L8J	Male	5552	45	1
T00	Female	11043	49	4
T01	Female	10185	45	3
T02	Male	14850	22	2
T03	Male	6764	40	3
T05	Male	49161	49	4
T06	Male	8965	9	0
T07	Male	3177	14	1
T08	Female	22062	47	4
T09	Male	42442	49	4
T0A	Male	20769	46	3
T0C	Male	56490	49	3
T0H	Male	31780	49	1
T0J	Female	37920	49	3
T0L	Male	11991	9	0
T0U	Female	18603	25	2
T0V	Male	5551	43	3
T0W	Female	9778	14	2
T0X	Male	15831	22	2
T10	Female	6030	11	1
T11	Male	21468	49	0
T12	Male	8197	33	3
T14	Male	6747	43	1
T15	Female	36000	49	3
T16	Male	779	33	1
T17	Male	22698	49	0
T19	Female	9471	23	2
T1C	Female	5751	32	3
T1J	Female	20640	49	3

SUPPLEMENTARY MATERIAL TO CHAPTER 2: BIASES IN THE DETECTION OF INTENTIONALLY POISONED ANIMALS: PUBLIC HEALTH AND CONSERVATION IMPLICATIONS FROM A FIELD EXPERIMENT

THIS MATERIAL INCLUDES:

Table S1. Species traits considered in the GLMM.

Table S2. Species and individuals recorded in the "Antídoto Program" database and observed feeding upon baits in the field experiment, by study area.

Table S3. AICc-based model selection.

Table S1. Species traits considered in the GLMM. We included species weight (mean adult weight in Spain, in kg), color (conspicuous – with presence of black and white or bright black patches – / cryptic – otherwise –), mobility (aerial – birds – / terrestrial – mammals and reptiles –), sociality (social – foraging in large groups or familiar groups – / solitary – foraging alone or in pairs –), and conservation status (endangered / non-endangered).

Group	Species	Weight (kg)	Log weight	Color	Mobility	Sociality	Conservation status
Wild carnivores	*Canis lupus*	30	1.48	cryptic	terrestrial	social	endangered
	Felis silvestris silvestris	4	0.60	cryptic	terrestrial	solitary	endangered
	Genetta genetta	1.9	0.28	conspicuous	terrestrial	solitary	non-endangered
	Martes foina	1.75	0.24	cryptic	terrestrial	solitary	non-endangered
	Martes martes	1.75	0.24	cryptic	terrestrial	solitary	non-endangered
	Meles meles	7.5	0.88	conspicuous	terrestrial	social	non-endangered
	Vulpes vulpes	6	0.78	cryptic	terrestrial	solitary	non-endangered
Domestic carnivores	*Canis lupus familiaris*	15	1.18	cryptic	terrestrial	solitary	non-endangered
	Felis silvestris catus	4	0.60	cryptic	terrestrial	solitary	non-endangered
Suids	*Sus scrofa*	52.98	1.72	cryptic	terrestrial	social	non-endangered
Small mammals	*Apodemus sylvaticus*	0.025	-1.60	cryptic	terrestrial	solitary	non-endangered
	Crocidura russula	0.008	-2.10	cryptic	terrestrial	solitary	non-endangered
	Eliomys quercinus	0.09	-1.05	conspicuous	terrestrial	solitary	non-endangered
	Erinaceus europaeus	0.8	-0.10	cryptic	terrestrial	solitary	non-endangered
	Rattus spp.	0.3	-0.52	cryptic	terrestrial	solitary	non-endangered
Corvids	*Corvus corax*	2	0.30	conspicuous	aerial	social	non-endangered
	Corvus corone	0.6	-0.22	conspicuous	aerial	social	non-endangered
	Cyanopica cooki	0.07	-1.15	conspicuous	aerial	social	non-endangered

Table S1. (Cont.)

Group	Species	Weight (kg)	Log weight	Color	Mobility	Sociality	Conservation status
	Garrulus glandarius	0.19	-0.72	conspicuous	aerial	solitary	non-endangered
	Pica pica	0.24	-0.62	conspicuous	aerial	social	non-endangered
Vultures	*Aegypius monachus*	9.8	0.99	conspicuous	aerial	social	endangered
	Gypaetus barbatus	6	0.78	conspicuous	aerial	solitary	endangered
	Gyps fulvus	8.5	0.93	cryptic	aerial	social	non-endangered
	Neophron percnopterus	2	0.30	conspicuous	aerial	solitary	endangered
Other raptors	*Accipiter gentilis*	1	0.00	cryptic	aerial	solitary	non-endangered
	Aquila chrysaetos	4	0.60	cryptic	aerial	solitary	endangered
	Aquila fasciata	2.2	0.34	cryptic	aerial	solitary	endangered
	Bubo bubo	1.75	0.24	cryptic	aerial	solitary	non-endangered
	Buteo buteo	0.73	-0.14	cryptic	aerial	solitary	non-endangered
	Falco tinnunculus	0.225	-0.65	cryptic	aerial	solitary	non-endangered
	Hieraaetus pennatus	0.8	-0.10	cryptic	aerial	solitary	non-endangered
	Milvus migrans	0.75	-0.12	cryptic	aerial	social	non-endangered
	Milvus milvus	1	0.00	cryptic	aerial	social	endangered
Other birds	*Ciconia ciconia*	3.5	0.54	conspicuous	aerial	social	non-endangered
	Erithacus rubecula	0.019	-1.72	cryptic	aerial	solitary	non-endangered
	Parus major	0.018	-1.74	conspicuous	aerial	solitary	non-endangered
	Phoenicurus ochruros	0.016	-1.80	cryptic	aerial	solitary	non-endangered
	Turdus viscivorus	0.13	-0.89	cryptic	aerial	solitary	non-endangered
Reptiles	*Timon lepidus*	0.25	-0.60	cryptic	terrestrial	solitary	non-endangered
	Lacerta schreiberi	0.026	-1.59	cryptic	terrestrial	solitary	endangered

Table S2. Species and individuals recorded in the "Antídoto Program" database ("Dat.") and observed feeding upon baits in the field experiment ("Exp."), by study area. Species considered as endangered according to Spanish national and/or regional laws are indicated by an asterisk.

		Cabrera		**Cameros**		**Pre-Pyrenees**		**Harana**		**Cazorla**		**Escalona**		**Total**	
Group	**Species**	**Dat.**	**Exp.**	**Dat.**	**Exp.**	**Dat.**	**Exp.**	**Dat.**	**Exp.**	**Dat.**	**Exp.**	**Dat.**	**Exp.**	**Dat.**	**Exp.**
Wild carnivores	*Canis lupus**	9	0	0	0	0	0	0	0	0	0	0	0	**9**	**0**
	*Felis silvestris silvestris**	0	0	0	0	0	0	0	0	1	0	0	0	**1**	**0**
	Genetta genetta	0	0	0	0	1	0	0	0	0	1	0	0	**1**	**1**
	Martes foina	0	0	0	9	6	6	10	2	2	6	0	0	**18**	**23**
	Martes martes	0	1	0	0	0	0	0	0	0	0	0	0	**0**	**1**
	Meles meles	0	0	0	1	1	1	2	1	0	0	0	0	**3**	**3**
	Vulpes vulpes	3	7	7	13	2	16	22	13	22	10	6	1	**62**	**59**
Domestic carnivores	*Canis lupus familiaris*	17	0	5	1	20	2	26	0	23	0	17	0	**108**	**3**
	Felis silvestris catus	0	0	0	1	3	0	10	0	3	0	1	1	**17**	**2**
Suids	*Sus scrofa*	0	2	1	0	0	2	2	2	0	1	1	6	**4**	**13**
Small mammals	*Apodemus sylvaticus*	0	9	0	0	0	2	1	4	0	1	2	3	**3**	**19**
	Crocidura russula	0	0	0	0	0	0	1	0	0	0	0	0	**1**	**0**
	Eliomys quercinus	0	3	0	0	0	0	0	3	0	0	0	25	**0**	**31**
	Erinaceus europaeus	0	1	0	0	0	0	0	0	0	0	0	0	**0**	**1**
	Rattus spp.	0	0	0	0	0	0	0	0	0	0	0	1	**0**	**1**
Corvids	*Corvus corax*	0	0	9	5	1	6	1	0	4	0	0	0	**15**	**11**
	Corvus corone	0	0	0	3	0	0	0	4	2	5	0	0	**2**	**12**
	Cyanopica cooki	0	0	0	0	0	0	1	2	0	0	0	0	**1**	**2**
	Garrulus glandarius	0	3	0	4	0	7	0	5	0	5	0	0	**0**	**24**
	Pica pica	2	0	0	0	0	0	9	4	0	0	0	1	**11**	**5**

Table S2. (Cont.)

		Cabrera		Cameros		Pre-Pyrenees		Harana		Cazorla		Escalona		Total	
Group	**Species**	**Dat.**	**Exp.**	**Dat.**	**Exp.**	**Dat.**	**Exp.**	**Dat.**	**Exp.**	**Dat.**	**Exp.**	**Dat.**	**Exp.**	**Dat.**	**Exp.**
Vultures	*Aegypius monachus**	0	0	0	0	0	1	0	0	0	0	0	0	**0**	**1**
	*Gypaetus barbatus**	0	0	0	0	1	0	0	0	4	0	0	0	**5**	**0**
	Gyps fulvus	0	0	64	2	7	5	3	0	30	0	0	0	**104**	**7**
	*Neophron percnopterus**	0	0	7	0	0	4	0	0	3	0	0	0	**10**	**4**
Other raptors	*Accipiter gentilis*	0	0	0	0	1	0	1	0	0	0	1	0	**3**	**0**
	*Aquila chrysaetos**	0	0	1	0	0	0	0	0	0	0	0	0	**1**	**0**
	*Aquila fasciata**	0	0	0	0	0	0	0	0	0	0	5	0	**5**	**0**
	Bubo bubo	0	0	1	0	0	0	0	0	0	0	2	0	**3**	**0**
	Buteo buteo	0	0	4	0	2	0	0	0	0	0	2	0	**8**	**0**
	Falco tinnunculus	0	0	0	0	0	0	0	0	1	0	1	1	**2**	**1**
	Hieraaetus pennatus	0	0	1	0	0	0	0	0	0	0	0	0	**1**	**0**
	Milvus migrans	0	0	0	1	1	0	0	0	0	0	0	0	**1**	**1**
	*Milvus milvus**	2	0	10	0	4	1	0	0	0	0	0	0	**16**	**1**
Other birds	*Ciconia ciconia*	0	0	6	0	0	0	0	0	0	0	0	0	**6**	**0**
	Erithacus rubecula	0	0	0	0	0	0	0	0	0	0	0	2	**0**	**2**
	Parus major	0	0	0	0	0	0	0	1	0	0	0	4	**0**	**5**
	Phoenicurus ochruros	0	0	0	0	0	0	0	0	0	0	0	1	**0**	**1**
	Turdus viscivorus	0	1	0	0	0	0	0	0	0	0	0	0	**0**	**1**
Reptiles	*Lacerta schreiberi**	0	2	0	0	0	0	0	0	0	0	0	0	**0**	**2**
	Timon lepidus	0	0	0	0	0	0	1	1	0	1	5	2	**6**	**4**
Total		**33**	**29**	**116**	**40**	**50**	**53**	**90**	**42**	**95**	**30**	**43**	**48**	**427**	**237**

Table S3. AICc-based model selection to assess the effect of study area (random factor) and weight, color, mobility, sociality, and conservation status of the species on the difference between a) the number of poisoned individuals included in the "Antídoto Program" database and b) the number of individuals recorded consuming the baits in the field experiment. Number of estimated parameters (k), AICc values, AICc differences (delta-AICc) with the highest ranked model (i.e., the one with the lowest AICc), and the variability of the response variable that is explained by the fixed factors (R2) are shown. The selected model is in bold.

Model	**k**	**AIC_c**	**delta-AIC_c**	**marginal *R2***
weight + color + mobility (+ 1|area)	**4**	**721.6**	**0**	**19.69**
weight + color + mobility + status (+ 1|area)	5	723.8	2.21	
weight + color + mobility + sociality (+ 1|area)	5	723.9	2.28	
weight + color (+ 1|area)	3	724.5	2.88	
weight (+ 1|area)	2	725.9	4.31	
weight + mobility (+ 1|area)	3	726.0	4.38	
weight + color + sociality (+ 1|area)	4	726.1	4.50	
weight + color + mobility + sociality + status (+ 1|area)	6	726.2	4.55	
weight + color + status (+ 1|area)	4	726.7	5.09	
weight + mobility + sociality (+ 1|area)	4	728.1	6.51	
weight + mobility + status (+ 1|area)	4	728.1	6.51	
weight + sociality (+ 1|area)	3	728.1	6.51	
weight + status (+ 1|area)	3	728.2	6.52	
weight + color + sociality + status (+ 1|area)	5	728.4	6.73	
weight + mobility + sociality + status (+ 1|area)	5	730.2	8.57	
weight + sociality + status (+ 1|area)	4	730.4	8.77	
color + sociality (+ 1|area)	3	731.7	10.04	
color + mobility + sociality (+ 1|area)	4	732.5	10.89	
color + mobility (+ 1|area)	3	733.4	11.81	
color + sociality + status (+ 1|area)	4	733.5	11.88	
color (+ 1|area)	2	733.6	11.95	
color + mobility + sociality + status (+ 1|area)	5	734.7	13.03	
color + status (+ 1|area)	3	735.3	13.71	
color + mobility + status (+ 1|area)	4	735.6	13.94	
(1|area)	1	737.2	15.53	
sociality (+ 1|area)	2	737.7	16.04	
mobility (+ 1|area)	2	739.1	17.50	
status (+ 1|area)	2	739.1	17.50	
sociality + status (+ 1|area)	3	739.7	18.08	
mobility + sociality (+ 1|area)	3	739.8	18.21	
mobility + status (+ 1|area)	3	741.2	19.53	
mobility + sociality + status (+ 1|area)	4	742.0	20.33	

SUPPLEMENTARY MATERIAL TO CHAPTER 3: ROLE OF SCAVENGERS IN PROVIDING NON-MATERIAL CONTRIBUTIONS TO PEOPLE

THIS MATERIAL INCLUDES:

Appendix A. Search strings used in this study.

Appendix B. List of references of the scientific articles included in the review.

Appendix C. Detailed description of the calculation of indicators and indices.

Figure C1. Graphical description of the indices calculation.

Appendix D. Supplementary tables.

Table D1. List of scavenger species included in this study and traits used as explanatory variables in the canonical correspondence analysis.

Table D2. List of functional traits for which data were collected on the scavenger species.

Table D3. Summary statistics and results of the canonical correspondence analysis showing the associations between the indices representing non-material nature's contributions to people (NCP) provided by scavenger species and the ecological variables.

APPENDIX A.
SEARCH STRINGS USED IN THIS STUDY

Search string for webs offering wildlife watching tours in Google

Species	Search string
Aegypius monachus	”black vulture” OR “cinereous vulture” OR “Aegypius monachus” AND “wildlife watching” AND “Spain”
Gypaetus barbatus	“bearded vulture” OR ”lammergeier” OR “Gypaetus barbatus” AND ”wildlife watching” AND “Spain”
Gyps fulvus	”griffon vulture” OR “Gyps fulvus” AND “wildlife watching” AND “Spain”
Neophron percnopterus	”egyptian vulture” OR “Neophron percnopterus” AND “wildlife watching” AND “Spain”
Aquila adalberti	“imperial eagle” OR Adalbert’s eagle” OR “Aquila adalberti” AND “wildlife watching” AND “Spain”
Aquila chrysaetos	“golden eagle” OR “Aquila chrysaetos” AND “wildlife watching” AND “Spain”
Milvus migrans	“black kite” OR “Milvus migrans” AND “wildlife watching” AND “Spain”
Milvus milvus	“red kite” OR “Milvus milvus” AND “wildlife watching” AND “Spain”
Buteo buteo	“common buzzard” OR eurasian buzzard” OR “Buteo buteo” AND “wildlife watching” AND “Spain”
Circus aeruginosus	“marsh harrier” OR “Circus aeruginosus” AND “wildlife watching” AND “Spain”
Corvus corax	“raven” OR “Corvus corax” AND wildlife watching” AND “Spain”
Corvus corone	“carrion crow” OR “Corvus corone” AND “wildlife watching” AND “Spain”
Pica pica	“magpie” OR “Pica pica” AND “wildlife watching” AND “Spain”
Canis lupus	“gray wolf” OR “wolf” OR “Canis lupus” AND “wildlife watching” AND “Spain”
Ursus arctos	“brown bear” OR “Ursus arctos” AND “wildlife watching” AND “Spain”
Vulpes vulpes	“red fox” OR fox” OR “Vulpes vulpes” AND “wildlife watching” AND “Spain”
Martes foina	“stone marten” OR “beech marten” OR “Martes foina” AND “wildlife watching” AND “Spain”
Martes martes	“pine marten” OR “Martes martes” AND “wildlife watching” AND “Spain”
Genetta genetta	“common genet” OR “Genetta genetta” AND “wildlife watching” AND “Spain”
Meles meles	“eurasian badger” OR badger” OR “Meles meles” AND “wildlife watching” AND “Spain”
Herpestes ichneumon	“egyptian mongoose” OR “Herpestes ichneumon” AND “wildlife watching” AND “Spain”
Sus scrofa	“wild boar” OR “Sus scrofa” AND “wildlife watching” AND “Spain”

Search string for Web of Science

Search data: 12/06/2017

Topic: “scaveng*” OR “vulture” OR “Gypaetus barbatus” OR “Gyps fulvus” OR “Neophron percnopterus” OR “Aegypius monachus” OR “Aquila chrysaetos” OR “Aquila adalberti” OR “Milvus migrans” OR “Milvus milvus” OR “Buteo buteo” OR “Circus aeruginosus” OR “Corvus corax” OR “Pica pica” OR “Corvus corone” OR “Canis lupus” OR “Ursus arctos” OR “Vulpes vulpes” OR “Martes foina” OR “Martes martes” OR “Genetta genetta” OR “Meles meles” OR “Herpestes ichneumon” OR “Sus scrofa”

Topic: “Spain”

Refined by:

Type of document: article

Language: English

Research area: biodiversity conservation

Time period: 2000-2016.

APPENDIX B.
LIST OF REFERENCES OF THE SCIENTIFIC ARTICLES INCLUDED IN THE REVIEW.

Acevedo, P., Farfán, M.Á., Márquez, A.L., Delibes-Mateos, M., Real, R., Vargas, J.M., 2011. Past, present and future of wild ungulates in relation to changes in land use. Landsc. Ecol. 26, 19–31. https://doi.org/10.1007/s10980-010-9538-2

Acevedo, P., González-Quirós, P., Prieto, J.M., Etherington, T.R., Gortázar, C., Balseiro, A., 2014a. Generalizing and transferring spatial models: A case study to predict Eurasian badger abundance in Atlantic Spain. Ecol. Modell. 275, 1–8. https://doi.org/10.1016/j.ecolmodel.2013.12.011

Acevedo, P., Quirós-Fernández, F., Casal, J., Vicente, J., 2014b. Spatial distribution of wild boar population abundance: Basic information for spatial epidemiology and wildlife management. Ecol. Indic. 36, 594–600. https://doi.org/10.1016/j.ecolind.2013.09.019

Agudo, R., Alcaide, M., Rico, C., Lemus, J.A., Blanco, G., Hiraldo, F., Donázar, J.A., 2011a. Major histocompatibility complex variation in insular populations of the Egyptian vulture: Inferences about the roles of genetic drift and selection. Mol. Ecol. 20, 2329–2340. https://doi.org/10.1111/j.1365-294X.2011.05107.x

Agudo, R., Rico, C., Hiraldo, F., Donázar, J.A., 2011b. Evidence of connectivity between continental and differentiated insular populations in a highly mobile species. Divers. Distrib. 17, 1–12. https://doi.org/10.1111/j.1472-4642.2010.00724.x

Agudo, R., Rico, C., Vilà, C., Hiraldo, F., Donzar, J.A., 2010. The role of humans in the diversification of a threatened island raptor. BMC Evol. Biol. 10. https://doi.org/10.1186/1471-2148-10-384

Alvarez-Rodríguez, M., Alvarez, M., Anel-López, L., Martínez-Rodríguez, C., Martínez-Pastor, F., Borragan, S., Anel, L., De Paz, P., 2013a. The antioxidant effects of soybean lecithin- or low-density lipoprotein-based extenders for the cryopreservation of brown-bear (*Ursus arctos*) spermatozoa. Reprod. Fertil. Dev. 25, 1185–1193. https://doi.org/10.1071/RD12181

Alvarez-Rodríguez, M., Alvarez, M., Borragan, S., Martinez-Pastor, F., Holt, W. V., Fazeli, A., de Paz, P., Anel, L., 2013b. The addition of heat shock protein HSPA8 to cryoprotective media improves the survival of brown bear (*Ursus arctos*) spermatozoa during chilling and after cryopreservation. Theriogenology 79, 541–550. https://doi.org/10.1016/j.theriogenology.2012.11.006

Anderson, L.G., Gortázar, C., Vicente, J., Hutchings, M.R., White, P.C.L., 2013. Modelling the effectiveness of vaccination in controlling bovine tuberculosis in wild boar. Wildl. Res. 40, 367–376. https://doi.org/10.1071/WR12139

Arrondo, E., Cortés-Avizanda, A., Donázar, J.A., 2015. Temporally unpredictable supplementary feeding may benefit endangered scavengers. Ibis (Lond. 1859). 157, 648–651. https://doi.org/10.1111/ibi.12267

Arshad, M., Pedall, I., Gonzalez, J., Wink, M., Hatzofe, O., Khan, A.A., Osborne, T., 2009. Genetic Variation of Four *Gyps* Species (*Gyps bengalensis*, *G. africanus*, *G. indicus* and *G. fulvus*) based on microsatellite analysis. J. Raptor Res. 43, 227–236. https://doi.org/10.3356/JRR-08-91.1

Astobiza, I., Barral, M., Ruiz-Fons, F., Barandika, J.F., Gerrikagoitia, X., Hurtado, A., García-Pérez, A.L., 2011. Molecular investigation of the occurrence of *Coxiella burnetii* in wildlife and ticks in an endemic area. Vet. Microbiol. 147, 190–194. https://doi.org/10.1016/j.vetmic.2010.05.046

Balseiro, A., Oleaga, Á., Polledo, L., Aduriz, G., Atxaerandio, R., Kortabarria, N., Marín, J.F.G., 2013. *Clostridium sordellii* in a Brown Bear (*Ursus arctos*) from Spain. J. Wildl. Dis. 49, 1047–1051. https://doi.org/10.7589/2013-03-065

Banos-González, I., Martínez-Fernández, J., Esteve-Selma, M.A., 2016. Using dynamic sustainability indicators to assess environmental policy measures in Biosphere Reserves. Ecol. Indic. 67, 565–576. https://doi.org/10.1016/j.ecolind.2016.03.021

Barasona, J.A., VerCauteren, K.C., Saklou, N., Gortazar, C., Vicente, J., 2013. Effectiveness of cattle operated bump gates and exclusion fences in preventing ungulate multi-host sanitary interaction. Prev. Vet. Med. 111, 42–50. https://doi.org/10.1016/j.prevetmed.2013.03.009

Barea-Azcón, J.M., Virgós, E., Ballesteros-Duperón, E., Moleón, M., Chirosa, M., 2007. Surveying carnivores at large spatial scales: A comparison of four broad-applied methods. Biodivers. Conserv. 16, 1213–1230. https://doi.org/10.1007/s10531-006-9114-x

Barja, I., 2005. Winter distribution of European pine marten (*Martes martes*) scats in a protected area of Galicia, Spain. Mammalia 69, 435–438.

Barrientos, R., Arroyo, B., 2014. Nesting habitat selection of Mediterranean raptors in managed pinewoods: Searching for common patterns to derive conservation recommendations. Bird Conserv. Int. 24, 138–151. https://doi.org/10.1017/S0959270913000270

Barrientos, R., Ponce, C., Palacín, C., Martín, C.A., Martín, B., Alonso, J.C., 2012. Wire marking results in a small but significant reduction in avian mortality at power lines: a BACI designed study. PLoS One 7, e32569. https://doi.org/10.1371/journal.pone.0032569

Barrios, L., Rodríguez, A., 2004. Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. J. Appl. Ecol. 41, 72–81.

Barrull, J., Mate, I., Casanovas, J.G., Salicrú, M., Gosàlbez, J., 2011. Selectivity of mammalian predator control in managed hunting areas: An example in a Mediterranean environment. Mammalia 75, 363–369. https://doi.org/10.1515/MAMM.2011.052

Barrull, J., Mate, I., Ruiz-Olmo, J., Casanovas, J.G., Gosàlbez, J., Salicrú, M., 2014a. Factors and mechanisms that explain coexistence in a Mediterranean carnivore assemblage: An integrated study based on camera trapping and diet. Mamm. Biol. 79, 123–131. https://doi.org/10.1016/j.mambio.2013.11.004

Barrull, J., Mate, I., Salicrú, M., Palet, J., Casanovas, J.G., Gosàlbez, J., Ruiz-Olmo, J., 2014b. Differential response of a carnivore community to predator control: a spatio-temporal observational study. Ital. J. Zool. 81, 271–279. https://doi.org/10.1080/11250003.2014.893378

Bautista, L.M., García, J.T., Calmaestra, R.G., Palacín, C., Martín, C.A., Morales, M.B., Bonal, R., Viñuela, J., 2004. Effect of weekend road traffic on the use of space by raptors. Conserv. Biol. 18, 726–732. https://doi.org/10.1111/j.1523-1739.2004.00499.x

Belda, A., Martinez-Perez, J.E., Peiro, V., Seva, E., Arques, J., 2011. Main landscape metrics affecting abundance and diversity of game species in a semi-arid agroecosystem in the Mediterranean region. Spanish J. Agric. Res. 9, 1197–1212. https://doi.org/10.5424/sjar/20110904-470-10

Belda, A., Zaragozí, B., Martínez-Pérez, J.E., Peiró, V., Ramón, A., Seva, E., Arques, J., 2012. Use of GIS to predict potential distribution areas for wild boar (*Sus scrofa* Linnaeus 1758) in

Mediterranean regions (SE Spain). Ital. J. Zool. 79, 252–265. https://doi.org/10.1080/11250003.2011.631944

Bisson, I.A., Ferrer, M., Bird, D.M., 2002. Factors influencing nest-site selection by Spanish Imperial Eagles. J. F. Ornithol. 73, 298–302. https://doi.org/10.1648/0273-8570-73.3.298

Blanco, G., 2015. Multiresistant *Salmonella* Serovar Typhimurium Monophasic in Wintering Red Kites (Milvus milvus) in Segovia, Central Spain. J. Raptor Res. 49, 337–341. https://doi.org/10.3356/JRR-14-56.1

Blanco, G., 2014. Can livestock carrion availability influence diet of wintering red kites? Implications of sanitary policies in ecosystem services and conservation. Popul. Ecol. 56, 593–604. https://doi.org/10.1007/s10144-014-0445-2

Blanco, G., Junza, A., Segarra, D., Barbosa, J., Barrón, D., 2016. Wildlife contamination with fluoroquinolones from livestock: Widespread occurrence of enrofloxacin and marbofloxacin in vultures. Chemosphere 144, 1536–1543. https://doi.org/10.1016/j.chemosphere.2015.10.045

Blanco, G., Lemus, J.A., García-Montijano, M., 2011. When conservation management becomes contraindicated: Impact of food supplementation on health of endangered wildlife. Ecol. Appl. 21, 2469–2477. https://doi.org/10.1890/11-0038.1

Blanco, G., Sergio, F., Sanchéz-Zapata, J.A., Pérez-García, J.M., Botella, F., Martínez, F., Zuberogoitia, I., Frías, O., Roviralta, F., Martínez, J.E., Hiraldo, F., 2012. Safety in numbers? Supplanting data quality with fanciful models in wildlife monitoring and conservation. Biodivers. Conserv. 21, 3269–3276. https://doi.org/10.1007/s10531-012-0344-9

Blas, J., Sergio, F., Hiraldo, F., 2009. Age-related improvement in reproductive performance in a long-lived raptor: A cross-sectional and longitudinal study. Ecography (Cop.). 32, 647–657. https://doi.org/10.1111/j.1600-0587.2008.05700.x

Boadella, M., Acevedo, P., Vicente, J., Mentaberre, G., Balseiro, A., Arnal, M.C., Martínez, D., García-Bocanegra, I., Casal, C., Álvarez, J., Oleaga, Á., Lavín, S., Muñoz, M., Sáez-Llorente, J.L., de la Fuente, J., Gortázar, C., 2011a. Spatio-temporal trends of Iberian wild boar contact with *Mycobacterium tuberculosis* complex detected by ELISA. Ecohealth 8, 478–484. https://doi.org/10.1007/s10393-011-0713-y

Boadella, M., Barasona, J.A., Pozio, E., Montoro, V., Vicente, J., Gortazar, C., Acevedo, P., 2012a. Spatio-temporal trends and risk factors for Trichinella species infection in wild boar (Sus scrofa) populations of central Spain: A long-term study. Int. J. Parasitol. 42, 739–745. https://doi.org/10.1016/j.ijpara.2012.05.003

Boadella, M., Díez-Delgado, I., Gutiérrez-Guzmán, A.V., Höfle, U., Gortázar, C., 2012b. Do Wild Ungulates Allow Improved Monitoring of Flavivirus Circulation in Spain? Vector-Borne Zoonotic Dis. 12, 490–495. https://doi.org/10.1089/vbz.2011.0843

Boadella, M., Lyashchenko, K., Greenwald, R., Esfandiari, J., Jaroso, R., Carta, T., Garrido, J.M., Vicente, J., De La Fuente, J., Gortá Zar, C., 2011b. Serologic tests for detecting antibodies against *Mycobacterium bovis* and *Mycobacterium avium* subspecies *paratuberculosis* in Eurasian wild boar (*Sus scrofa scrofa*). J. Vet. Diagnostic Investig. 23.

Boadella, M., Vicente, J., Ruiz-Fons, F., de la Fuente, J., Gortázar, C., 2012c. Effects of culling Eurasian wild boar on the prevalence of Mycobacterium bovis and Aujeszky's disease virus. Prev. Vet. Med. 107, 214–221. https://doi.org/10.1016/j.prevetmed.2012.06.001

Bodewes, R., Ruiz-Gonzalez, A., Schapendonk, C.M.E., Van Den Brand, J.M.A., Osterhaus, A.D.M.E., Smits, S.L., 2014. Viral metagenomic analysis of feces of wild small carnivores. Virol. J. 11, 89. https://doi.org/10.1186/1743-422X-11-89

Bosch, J., Mardones, F., Pérez, A., De la Torre, A., Muñoz, M.J., 2014. A maximum entropy model for predicting wild boar distribution in Spain. Spanish J. Agric. Res. 12, 984–999. https://doi.org/10.5424/sjar/2014124-5717

Bosch, J., Peris, S., Fonseca, C., Martinez, M., De La Torre, A., Iglesias, I., Muñoz, M.J., 2012. Distribution, abundance and density oh the wild boar on the Iberian Peninsula, based on the CORINE program and hunting statistics. Folia Zool. 61, 138–151.

Bueno, C.G., Alados, C.L., Gómez-García, D., Barrio, I.C., García-González, R., 2009. Understanding the main factors in the extent and distribution of wild boar rooting on alpine grasslands. J. Zool. 279, 195–202. https://doi.org/10.1111/j.1469-7998.2009.00607.x

Bueno, C.G., Barrio, I.C., García-González, R., Alados, C.L., Gómez-García, D., 2010. Does wild boar rooting affect livestock grazing areas in alpine grasslands? Eur. J. Wildl. Res. 56, 765–770. https://doi.org/10.1007/s10344-010-0372-2

Bueno, C.G., Jiménez, J.J., 2014. Livestock grazing activities and wild boar rooting affect alpine earthworm communities in the Central Pyrenees (Spain). Appl. Soil Ecol. 88, 71–78. https://doi.org/10.1016/j.apsoil.2014.04.013

Bueno, C.G., Reiné, R., Alados, C.L., Gómez-García, D., 2011. Effects of large wild boar disturbances on alpine soil seed banks. Basic Appl. Ecol. 12, 125–133. https://doi.org/10.1016/j.baae.2010.12.006

Cabezas-Díaz, S., Virgós, E., Mangas, J.G., Lozano, J., 2011. The presence of a “competitor pit effect” compromises wild rabbit (*Orcytolagus cuniculus*) conservation. Anim. Biol. 61, 319–334. https://doi.org/10.1163/157075511X584254

Cabezón, O., García-Bocanegra, I., Molina-López, R., Marco, I., Blanco, J.M., Höfle, U., Margalida, A., Bach-Raich, E., Darwich, L., Echeverría, I., Obón, E., Hernández, M., Lavín, S., Dubey, J.P., Almería, S., 2011. Seropositivity and risk factors associated with *Toxoplasma gondii* infection in wild birds from Spain. PLoS One 6, e29549. https://doi.org/10.1371/journal.pone.0029549

Cahill, S., Llimona, F., Cabañeros, L., Calomardo, F., 2012. Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. Anim. Biodivers. Conserv. 35, 221–233.

Calero-Bernal, R., Gómez-Gordo, L., Saugar, J.M., Frontera, E., Pérez-Martín, J.E., Reina, D., Serrano, F.J., Fuentes, I., 2013. Congenital Toxoplasmosis in Wild Boar (*Sus scrofa*) and Identification of the *Toxoplasma gondii* Types Involved. J. Wildl. Dis. 49, 1019–1023. https://doi.org/10.7589/2013-01-024

Calero-Bernal, R., Saugar, J.M., Frontera, E., Pérez-Martín, J.E., Habela, M.A., Serrano, F.J., Reina, D., Fuentes, I., 2015. Prevalence and Genotype Identification of *Toxoplasma gondii* in Wild Animals from Southwestern Spain. J. Wildl. Dis. 51, 233–238. https://doi.org/10.7589/2013-09-233

Camiña, A., Montelío, E., 2006. Griffon Vulture *Gyps fulvus* food shortages in the Ebro Valley (NE Spain) caused by regulations against Bovine Spongiform Encephalopathy (BSE). Acta Ornithol. 41, 7–13. https://doi.org/10.3161/068.041.0106

Camiña, A., Yosef, R., 2012. Effect of European Union BSE-Related Enactments on Fledgling Eurasian Griffons *Gyps fulvus*. Acta Ornithol. 47, 101–109. https://doi.org/10.3161/000164512X662205

Camps, D., Alldredge, J.R., 2013. Multi-scale habitat use and selection of common genet *Genetta genetta* (Viverridae, Carnivora) in a Mediterranean environment. Mammalia 285–295. https://doi.org/10.1515/mammalia-2012-0023

Cancio, I., González-Robles, A., Bastida, J.M., Manzaneda, A.J., Salido, T., Rey, P.J., 2016. Habitat loss exacerbates regional extinction risk of the keystone semiarid shrub Ziziphus lotus through collapsing the seed dispersal service by foxes (*Vulpes vulpes*). Biodivers. Conserv. 25, 693–709. https://doi.org/10.1007/s10531-016-1085-y

Cano-Manuel, F.J., López-Olvera, J., Fandos, P., Soriguer, R.C., Pérez, J.M., Granados, J.E., 2014. Long-term monitoring of 10 selected pathogens in wild boar (*Sus scrofa*) in Sierra Nevada National Park, southern Spain. Vet. Microbiol. 174, 148–154. https://doi.org/10.1016/j.vetmic.2014.06.017

Carbonero, A., Paniagua, J., Torralbo, A., Arenas-Montes, A., Borge, C., García-Bocanegra, I., 2014. *Campylobacter* infection in wild artiodactyl species from southern Spain: Occurrence, risk factors and antimicrobial susceptibility. Comp. Immunol. Microbiol. Infect. Dis. 37, 155–121. https://doi.org/10.1016/j.cimid.2014.01.001

Cardador, L., Carrete, M., Mañosa, S., 2012a. Inter-individual variability and conspecific densities: consequences for population regulation and range expansion. PLoS One 7, e33375. https://doi.org/10.1371/journal.pone.0033375

Cardador, L., Carrete, M., Mañosa, S., 2011. Can intensive agricultural landscapes favour some raptor species? The Marsh harrier in north-eastern Spain. Anim. Conserv. 14, 382–390. https://doi.org/10.1111/j.1469-1795.2011.00449.x

Cardador, L., Planas, E., Varea, A., Mañosa, S., 2012b. Feeding behaviour and diet composition of Marsh Harriers *Circus aeruginosus* in agricultural landscapes. Bird Study 59, 228–235. https://doi.org/10.1080/00063657.2011.648165

Cardador, L., Sardà-Palomera, F., Carrete, M., Mañosa, S., 2014. Incorporating spatial constraints in different periods of the annual cycle improves species distribution model performance for a highly mobile bird species. Divers. Distrib. 20, 515–528. https://doi.org/10.1111/ddi.12156

Carneiro, M., Colaço, B., Brandão, R., Azorín, B., Nicolas, O., Colaço, J., Pires, M.J. oã., Agustí, S., Casas-Díaz, E., Lavin, S., Oliveira, P.A., 2015. Assessment of the exposure to heavy metals in Griffon vultures (*Gyps fulvus*) from the Iberian Peninsula. Ecotoxicol. Environ. Saf. 113, 295–301. https://doi.org/10.1016/j.ecoenv.2014.12.016

Carneiro, M.A., Oliveira, P.A., Brandão, R., Nicolas Francisco, O., Velarde, R., Lavín, S., Colaço, B., 2016. Lead Poisoning Due to Lead-Pellet Ingestion in Griffon Vultures (*Gyps fulvus*) From the Iberian Peninsula. J. Avian Med. Surg. 30, 274–279. https://doi.org/10.1647/2014-051

Caro, J., Ontiveros, D., Pizarro, M., Pleguezuelos, J.M., 2011. Habitat features of settlement areas used by floaters of Bonellis and Golden Eagles. Bird Conserv. Int. 21, 59–71. https://doi.org/10.1017/S0959270910000213

Carpio, A.J., Castro-López, J., Guerrero-Casado, J., Ruiz-Aizpurua, L., Vicente, J., Tortosa, F.S., 2014a. Effect of wild ungulate density on invertebrates in a Mediterranean ecosystem. Anim. Biodivers. Conserv. 37, 115–125.

Carpio, A.J., Guerrero-Casado, J., Ruiz-Aizpurua, L., Vicente, J., Tortosa, F.S., 2014b. The high abundance of wild ungulates in a Mediterranean region: is this compatible with the European rabbit? Wildlife Biol. 20, 161–166. https://doi.org/10.2981/wlb.13113

Carpio, A.J., Oteros, J., Lora, Á., Tortosa, F.S., 2015a. Effects of the overabundance of wild ungulates on natural grassland in Southern Spain. Agrofor. Syst. https://doi.org/10.1007/s10457-015-9801-2

Carpio, A.J., Oteros, J., Vicente, J., Tortosa, F.S., Guerrero-Casado, J., 2015b. Factors Affecting Red-Legged Partridge *Alectoris rufa* Abundance on Big-Game Hunting

Estates: Implications for Management and Conservation. Ardeola 62, 283–297. https://doi.org/10.13157/arla.62.2.2015.283

Carpio, A.J., Tortosa, F.S., Barrio, I.C., 2015c. Rabbit Abundance Influences Predation on Bird Nests in Mediterranean Olive Orchards. Acta Ornithol. 50, 171–179. https://doi.org/10.3161/00016454AO2015.50.2.005

Carrete, M., Bortolotti, G.R., Sánchez-Zapata, J.A., Delgado, A., Cortés-Avizanda, A., Grande, J.M., Donázar, J.A., 2013. Stressful conditions experienced by endangered Egyptian vultures on African wintering areas. Anim. Conserv. 16, 353–358. https://doi.org/10.1111/acv.12001

Carrete, M., Donázar, J.A., 2005. Application of central-place foraging theory shows the importance of Mediterranean dehesas for the conservation of the cinereous vulture, *Aegypius monachus*. Biol. Conserv. 126, 582–590. https://doi.org/10.1016/j.biocon.2005.06.031

Carrete, M., Donázar, J.A., Margalida, A., 2006a. Density-dependent productivity depression in Pyrenean Bearded Vultures: Implications for conservation. Ecol. Appl. 16, 1674–1682. https://doi.org/10.1890/1051-0761(2006)016[1674:DPDIPB]2.0.CO;2

Carrete, M., Donázar, J.A., Margalida, A., Bertran, J., 2006b. Linking ecology, behaviour and conservation: does habitat saturation change the mating system of bearded vultures? Biol. Lett. 2, 624–627. https://doi.org/10.1098/rsbl.2006.0498

Carrete, M., Grande, J.M., Tella, J.L., Sánchez-Zapata, J.A., Donázar, J.A., Díaz-Delgado, R., Romo, A., 2007. Habitat, human pressure, and social behavior: Partialling out factors affecting large-scale territory extinction in an endangered vulture. Biol. Conserv. 136, 143–154. https://doi.org/10.1016/j.biocon.2006.11.025

Carrete, M., Sánchez-Zapata, J.A., Benítez, J.R., Lobón, M., Donázar, J.A., 2009. Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. Biol. Conserv. 142, 2954–2961. https://doi.org/10.1016/j.biocon.2009.07.027

Carrete, M., Sánchez-Zapata, J.A., Benítez, J.R., Lobón, M., Montoya, F., Donázar, J.A., 2012. Mortality at wind-farms is positively related to large-scale distribution and aggregation in griffon vultures. Biol. Conserv. 145, 102–108. https://doi.org/10.1016/j.biocon.2011.10.017

Carrete, M., Sánchez-Zapata, J.A., Calvo, J.F., Lande, R., 2005. Demography and habitat availability in territorial occupancy of two competing species. Oikos 108, 125–136. https://doi.org/10.1111/j.0030-1299.2005.12942.x

Carrete, M., Sánchez-Zapata, J.A., Martínez, J.E., Sánchez, M.Á., Calvo, J.F., 2002. Factors influencing the decline of a Bonelli's eagle *Hieraaetus fasciatus* population in southeastern Spain: demography, habitat or competition? Biodivers. Conserv. 11, 975–985. https://doi.org/10.1023/A:1015856924451

Carril González-Barros, S.T., Alvarez Piñeiro, M.E., Lozano, J.S., Lage Yusty, M.A., 2000. Organochlorine pesticides in wolves from Galicia. Ecotoxicol. Environ. Saf. 47, 247–252. https://doi.org/10.1006/eesa.1999.1856

Casas-Díaz, E., Closa-Sebastià, F., Marco, I., Lavín, S., Bach-Raich, E., Cuenca, R., 2015. Hematologic and biochemical reference intervals for Wild Boar (Sus scrofa) captured by cage trap. Vet. Clin. Pathol. 44, 215–222. https://doi.org/10.1111/vcp.12250

Casas-Díaz, E., Cristòfol, C., Cuenca, R., Agustí, S., Carneiro, M., Marco, I., Lavín, S., Margalida, A., 2016. Determination of fluoroquinolone antibiotic residues in the plasma of Eurasian griffon vultures (*Gyps fulvus*) in Spain. Sci. Total Environ. 557–558, 620–626. https://doi.org/10.1016/j.scitotenv.2016.03.083

Castaño, J.P., Sánchez, J.F., Díaz-Portero, M.A., Robles, M., 2015. Dispersal and Survival of Juvenile Black Vultures *Aegypius monachus* in

Central Spain. Ardeola 62, 351–361. https://doi.org/10.13157/arla.62.2.2015.351

Castro-Hermida, A., García-Presedo, I., González-Warleta, M., Mezo, M., 2011. Prevalence of *Cryptosporidium* and *Giardia* in roe deer (*Capreolus capreolus*) and wild boars (*Sus scrofa*) in Galicia (NW, Spain). Vet. Parasitol. 179, 216–219. https://doi.org/10.1016/j.vetpar.2011.02.023

Celedón-Neghme, C., Traveset, A., Calviño-Cancela, M., 2013. Contrasting patterns of seed dispersal between alien mammals and native lizards in a declining plant species. Plant Ecol. 214, 657–667. https://doi.org/10.1007/s11258-013-0197-7

Che'Amat, A., Armenteros, J.A., González-Barrio, D., Lima, J.F., Díez-Delgado, I., Barasona, J.A., Romero, B., Lyashchenko, K.P., Ortiz, J.A., Gortázar, C., 2016. Is targeted removal a suitable means for tuberculosis control in wild boar? Prev. Vet. Med. https://doi.org/10.1016/j.prevetmed.2016.11.002

Closa-Sebastià, F., Casas-Díaz, E., Cuenca, R., Lavín, S., Mentaberre, G., Marco, I., 2011. Antibodies to selected pathogens in wild boar (*Sus scrofa*) from Catalonia (NE Spain). Eur. J. Wildl. Res. 57, 977–981. https://doi.org/10.1007/s10344-010-0491-9

Colino-Rabanal, V.J., Lizana, M., Peris, S.J., 2011. Factors influencing wolf *Canis lupus* roadkills in Northwest Spain. Eur. J. Wildl. Res. 57, 399–409. https://doi.org/10.1007/s10344-010-0446-1

Colino-Rabanal, V.J., Peris, S.J., Bosch, J., Muñoz, M.J., 2012. Influence of new irrigated croplands on wild boar (*Sus scrofa*) road kills in NW Spain. Anim. Biodivers. Conserv. 35, 247–252.

Colomer, M.À., Margalida, A., Sanuy, D., Pérez-Jiménez, M.J., 2011. A bio-inspired computing model as a new tool for modeling ecosystems: The avian scavengers as a case study. Ecol. Modell. 222, 33–47. https://doi.org/10.1016/j.ecolmodel.2010.09.012

Cortés-Avizanda, A., Almaraz, P., Carrete, M., Sánchez-Zapata, J.A., Delgado, A., Hiraldo, F., Donázar, J.A., 2011. Spatial heterogeneity in resource distribution promotes facultative sociality in two trans-saharan migratory birds. PLoS One 6, e21016. https://doi.org/10.1371/journal.pone.0021016

Cortés-Avizanda, A., Carrete, M., Donázar, J.A., 2010. Managing supplementary feeding for avian scavengers: Guidelines for optimal design using ecological criteria. Biol. Conserv. 143, 1707–1715. https://doi.org/10.1016/j.biocon.2010.04.016

Cortés-Avizanda, A., Carrete, M., Serrano, D., Donázar, J.A., 2009a. Carcasses increase the probability of predation of ground-nesting birds: A caveat regarding the conservation value of vulture restaurants. Anim. Conserv. 12, 85–88. https://doi.org/10.1111/j.1469-1795.2008.00231.x

Cortés-Avizanda, A., Ceballos, O., Donázar, J.A., 2009b. Long-term trends in population size and breeding success in Egyptian vulture (*Neophron percnopterus*) in Northern Spain. J. Raptor Res. 43, 43–49. https://doi.org/10.3356/JRR-08-24.1

Cortés-Avizanda, A., Colomer, M.À., Margalida, A., Ceballos, O., Donázar, J.A., 2015. Modeling the consequences of the demise and potential recovery of a keystone-species: Wild rabbits and avian scavengers in Mediterranean landscapes. Sci. Rep. 5, 17033. https://doi.org/10.1038/srep17033

Cortés, O., Martinez, A.M., Cañon, J., Sevane, N., Gama, L.T., Ginja, C., Landi, V., Zaragoza, P., Carolino, N., Vicente, A., Sponenberg, P., Delgado, J. V., Pons, Á., Alvarado, A.P.P., Vasquez, A.S., Peinado Ramón, B., Barba Capote, C., Pérez Pineda, E., Martín Burriel, I., Carril Gonzalez-Barros, J.A., Vega-Pla, J.L., Montes-Sánchez, J.J., Alvarez, L.A., Carolino, M.I., Gómez, M., Llambí, S., Montenegro, M., Revidatti, M.A., Galíndez, R., 2016. Conservation priorities of Iberoamerican pig breeds and their ancestors based on microsatellite information. Heredity (Edinb). 117, 14–24. https://doi.org/10.1038/hdy.2016.21

Cowie, C.E., Gortázar, C., White, P.C.L., Hutchings, M.R., Vicente, J., 2015. Stakeholder opinions on the practicality of management interventions to control bovine tuberculosis. Vet. J. 204, 179–185. https://doi.org/10.1016/j.tvjl.2015.02.022

Cuesta Gerveno, J.M., Risco Pérez, D., Gonçalves Blanco, P., García Jiménez, W.L., Gil Molino, M., Fernandez-Llario, P., Hermoso de Mendoza Salcedo, J., Gómez Gordo, L.J., 2013. Fatal infection due to *Haemophilus parasuis* in a young wild boar (*Sus scrofa*). J. Vet. Diagnostic Investig. 25, 297–300. https://doi.org/10.1177/1040638713479348

D'Amico, M., Périquet, S., Román, J., Revilla, E., 2016. Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. J. Appl. Ecol. 53, 181–190. https://doi.org/10.1111/1365-2664.12572

de la Fuente, J., Naranjo, V., Ruiz-Fons, F., Vicente, J., Estrada-Peña, A., Almazán, C., Kocan, K.M., Martín, M.P., Gortázar, C., 2004. Prevalence of tick-borne pathogens in ixodid ticks (Acari: Ixodidae) collected from European wild boar (*Sus scrofa*) and Iberian red deer (*Cervus elaphus hispanicus*) in central Spain. Eur. J. Wildl. Res. 50, 187–196. https://doi.org/10.1007/s10344-004-0060-1

de Lucas, M., Ferrer, M., Bechard, M.J., Muñoz, A.R., 2012a. Griffon vulture mortality at wind farms in southern Spain: Distribution of fatalities and active mitigation measures. Biol. Conserv. 147, 184–189. https://doi.org/10.1016/j.biocon.2011.12.029

de Lucas, M., Ferrer, M., Janss, G.F.E., 2012b. Using Wind Tunnels to Predict Bird Mortality in Wind Farms: The Case of Griffon Vultures. PLoS One 7, e48092. https://doi.org/10.1371/journal.pone.0048092

De Lucas, M., Janss, G.F.E., Whitfield, D.P., Ferrer, M., 2008. Collision fatality of raptors in wind farms does not depend on raptor abundance. J. Appl. Ecol. 45, 1695–1703. https://doi.org/10.1111/j.1365-2664.2008.01549.x

Delibes-Mateos, M., Díaz-Fernández, S., Ferreras, P., Viñuela, J., Arroyo, B., 2013. The role of economic and social factors driving predator control in small-game estates in central Spain. Ecol. Soc. 18, 28. https://doi.org/10.5751/ES-05367-180228

Delibes-Mateos, M., Farfán, M.Á., Olivero, J., Márquez, A.L., Vargas, J.M., 2009. Long-term changes in game species over a long period of transformation in the iberian mediterranean landscape. Environ. Manage. 43, 1256–1268. https://doi.org/10.1007/s00267-009-9297-5

Delibes-Mateos, M., Fernandez De Simon, J., Villafuerte, R., Ferreras, P., 2008. Feeding responses of the red fox (*Vulpes vulpes*) to different wild rabbit (*Oryctolagus cuniculus*) densities: a regional approach. Eur. J. Wildl. Res. 54, 71–78. https://doi.org/10.1007/s10344-007-0111-5

Delibes-Mateos, M., Redpath, S.M., Angulo, E., Ferreras, P., Villafuerte, R., 2007. Rabbits as a keystone species in southern Europe. Biol. Conserv. 137, 149–156. https://doi.org/10.1016/j.biocon.2007.01.024

Díaz-Ruiz, F., Delibes-Mateos, M., Ferreras, P., 2016. Can Cage-Trap Performance in Capturing Red Foxes Be Improved by Using Different Baits and Scent Attractants? Ann. Zool. Fennici 51, 91–102. https://doi.org/10.5735/086.053.0208

Díaz-Ruiz, F., García, J.T., Pérez-Rodríguez, L., Ferreras, P., 2010. Experimental evaluation of live cage-traps for black-billed magpies *Pica pica* management in Spain. Eur. J. Wildl. Res. 56, 239–248. https://doi.org/10.1007/s10344-009-0310-3

Díaz, M., Torre, I., Peris, A., Tena, L., 2005. Foraging behavior of wood mice as related to presence and activity of genets. J. Mammal. 86, 1178–1185.

Domingo-Roura, X., Marmi, J., Ferrando, A., López-Giráldez, F., Macdonald, D.W., Jansman, H.A.H., 2006. Badger hair in shaving brushes comes from protected Eurasian badgers. Biol. Conserv. 128, 425–430. https://doi.org/10.1016/j.biocon.2005.08.013

Domínguez, G., 2004. North Spain (Burgos) wild mammals ectoparasites. Parasite 11, 267–272. https://doi.org/10.1051/parasite/2004113267

Donázar, J.A., Blanco, G., Hiraldo, F., Soto-Largo, E., Oria, J., 2002. Effects of forestry and other land-use practices on the conservation of cinereous vultures. Ecol. Appl. 12, 1445–1456.

Echegaray, J., Vilà, C., 2010. Noninvasive monitoring of wolves at the edge of their distribution and the cost of their conservation. Anim. Conserv. 13, 157–161. https://doi.org/10.1111/j.1469-1795.2009.00315.x

Escribano-Avila, G., Calviño-Cancela, M., Pías, B., Virgós, E., Valladares, F., Escudero, A., 2014. Diverse guilds provide complementary dispersal services in a woodland expansion process after land abandonment. J. Appl. Ecol. 51, 1701–1711. https://doi.org/10.1111/1365-2664.12340

Escribano-Ávila, G., Pías, B., Sanz-Pérez, V., Virgós, E., Escudero, A., Valladares, F., 2013. Spanish juniper gain expansion opportunities by counting on a functionally diverse dispersal assemblage community. Ecol. Evol. 3, 3751–3763. https://doi.org/10.1002/ece3.753

Escribano-Avila, G., Sanz-Pérez, V., Pías, B., Virgós, E., Escudero, A., Valladares, F., 2012. Colonization of Abandoned Land by *Juniperus thurifera* Is Mediated by the Interaction of a Diverse Dispersal Assemblage and Environmental Heterogeneity. PLoS One 7, e46993. https://doi.org/10.1371/journal.pone.0046993

Espín, S., Martínez-López, E., Jiménez, P., María-Mojica, P., García-Fernández, A.J., 2014. Effects of heavy metals on biomarkers for oxidative stress in Griffon vulture (*Gyps fulvus*). Environ. Res. 129, 59–68. https://doi.org/10.1016/j.envres.2013.11.008

Fedriani, J.M., Delibes, M., 2013. Pulp feeders alter plant interactions with subsequent animal associates. J. Ecol. 101, 1581–1588. https://doi.org/10.1111/1365-2745.12146

Fedriani, J.M., Delibes, M., 2009. Functional diversity in fruit-frugivore interactions: A field experiment with Mediterranean mammals. Ecography (Cop.). 32, 983–992. https://doi.org/10.1111/j.1600-0587.2009.05925.x

Fedriani, J.M., Wiegand, T., 2014. Hierarchical mechanisms of spatially contagious seed dispersal in complex seed-disperser networks. Ecology 95, 514–526. https://doi.org/10.1890/13-0718.1

Fedriani, J.M., Wiegand, T., Delibes, M., 2010. Spatial pattern of adult trees and the mammal-generated seed rain in the Iberian pear. Ecography (Cop.). 33, 545–555. https://doi.org/10.1111/j.1600-0587.2009.06052.x

Fernandez-de-Mera, I.G., Gortazar, C., Vicente, J., Höfle, U., Fierro, Y., 2003. Wild boar helminths: risks in animal translocations. Vet. Parasitol. 115, 335–341. https://doi.org/10.1016/S0304-4017(03)00211-5

Fernández-Gil, A., Naves, J., Delibes, M., 2006. Courtship of brown bears *Ursus arctos* in northern Spain: phenology, weather, habitat and durable mating areas. Wildlife Biol. 12, 367–373. https://doi.org/10.2981/0909-6396(2006)12[367:COBBUA]2.0.CO;2

Fernández-Gil, A., Naves, J., Ordiz, A., Quevedo, M., Revilla, E., Delibes, M., 2016. Conflict misleads large carnivore management and conservation: Brown bears and wolves in Spain. PLoS One 11. https://doi.org/10.1371/journal.pone.0151541

Fernández-Juricic, E., 2000. Local and regional effects of pedestrians in forest birds in a fragmented landscape. Condor 102, 247–255. https://doi.org/10.1650/0010-5422(2000)102[0247:LAREOP]2.0.CO;2

Fernández-Juricic, E., Jimenez, M.D., Lucas, E., 2001. Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. Environ. Conserv. 28, 263–269.

Fernández-Juricic, E., Tellería, J.L., 2000. Effects of human disturbance on spatial and temporal feeding patterns of Blackbird *Turdus merula* in urban parks in Madrid, Spain. Bird Study 47, 13–21. https://doi.org/10.1080/00063650009461156

Fernández-Llario, P., Mateos-Quesada, P., 2003. Population structure of the wild boar (*Sus scrofa*) in two Mediterranean habitats in the western Iberian Peninsula. Folia Zool. 52, 143–148.

Fernández-Llario, P., Mateos-Quesada, P., Silvério, A., Santos, P., 2003. Habitat effects and shooting techniques on two wild boar (*Sus scrofa*) populations in Spain and Portugal. Z. Jagdwiss. 49, 120–129. https://doi.org/10.1007/BF02190452

Fernández-López, J., Fandos, G., Cano, L.S., Garcia, F.J., Tellería, J.L., 2014. Effect of wildlife refuges on small carnivores in a hunting area in Mediterranean habitat. Hystrix, Ital. J. Mammal. 25, 45–46. https://doi.org/10.4404/hystrix-25.1-9437

Fernández, J.M., de Azua, N.R., 2010. Historical dynamics of a declining wolf population: Persecution vs. prey reduction. Eur. J. Wildl. Res. 56, 169–179. https://doi.org/10.1007/s10344-009-0300-5

Fernández, J.M., Gurrutxaga, M., 2010. Habitat suitability models for assessing bird conservation goals in "special protection areas." Ardeola 57, 79–91.

Ferrer, M., de Lucas, M., Janss, G.F.E., Casado, E., Muñoz, A.R., Bechard, M.J., Calabuig, C.P., 2012. Weak relationship between risk assessment studies and recorded mortality in wind farms. J. Appl. Ecol. 49, 38–46. https://doi.org/10.1111/j.1365-2664.2011.02054.x

Ferrer, M., Newton, I., Muriel, R., 2013. Rescue of a small declining population of Spanish imperial eagles. Biol. Conserv. 159, 32–36. https://doi.org/10.1016/j.biocon.2012.10.011

Ferrer, M., Newton, I., Muriel, R., Báguena, G., Bustamante, J., Martini, M., Morandini, V., 2014. Using manipulation of density-dependent fecundity to recover an endangered species: The bearded vulture Gypaetus barbatus as an example. J. Appl. Ecol. 51, 1255–1263. https://doi.org/10.1111/1365-2664.12308

Ferrer, M., Newton, I., Pandolfi, M., 2009. Small populations and offspring sex-ratio deviations in eagles. Conserv. Biol. 23, 1017–1025. https://doi.org/10.1111/j.1523-1739.2009.01215.x

Ferrer, M., Otalora, F., García-Ruiz, J.M., 2004. Density-dependent age of first reproduction as a buffer affecting persistence of small populations. Ecol. Appl. 14, 616–624. https://doi.org/10.1890/02-5361

Ferrer, M., Penteriani, V., 2008. Non-independence of demographic parameters: Positive density-dependent fecundity in eagles. J. Appl. Ecol. 45, 1453–1459. https://doi.org/10.1111/j.1365-2664.2008.01497.x

Ferrer, M., Penteriani, V., Balbontín, J., Pandolfi, M., 2003. The proportion of immature breeders as a reliable early warning signal of population decline: evidence from the Spanish imperial eagle in Doñana. Biol. Conserv. 114, 463–466. https://doi.org/10.1016/S0006-3207(03)00085-5

Ferreras, P., Travaini, A., Cristina Zapata, S., Delibes, M., 2011. Short-term responses of mammalian carnivores to a sudden collapse of rabbits in Mediterranean Spain. Basic Appl. Ecol. 12, 116–124. https://doi.org/10.1016/j.baae.2011.01.005

Fonseca-Salamanca, F., Nogal-Ruiz, J.J., García-Sánchez, R.N., Bolas-Fernandez, F., Jiménez, S., Álamo, R., Gárate, T., Martínez-Fernandez, A.R., 2009. Prevalence of *Trichinella* spp. in North Spain wild fauna and new variety of *Trichinella britovi* identification. Vet. Parasitol. 159, 222–224. https://doi.org/10.1016/j.vetpar.2008.10.040

Fortes, G.G., Grandal-d'Anglade, A., Kolbe, B., Fernandes, D., Meleg, I.N., García-Vázquez, A., Pinto-Llona, A.C., Constantin, S., de Torres, T.J., Ortiz, J.E., Frischauf, C., Rabeder, G., Hofreiter, M., Barlow, A., 2016. Ancient DNA reveals differences in behaviour and sociality between brown bears and extinct cave bears. Mol. Ecol. 25, 4907–4918. https://doi.org/10.1111/mec.13800

Frati, F., Lovari, S., 2000. Does protection from hunting favour genetic uniformity in the red fox? Zeitschrift für Säugetierkd. 65, 76–83.

Galindo, R.C., Ayoubi, P., Naranjo, V., Gortazar, C., Kocan, K.M., de la Fuente, J., 2009. Gene expression profiles of European wild boar naturally infected with *Mycobacterium bovis*. Vet. Immunol. Immunopathol. 129, 119–125. https://doi.org/10.1016/j.vetimm.2008.12.012

García-Bocanegra, I., Busquets, N., Napp, S., Alba, A., Zorrilla, I., Villalba, R., Arenas, A., 2011. Serosurvey of West Nile Virus and Other Flaviviruses of the Japanese Encephalitis Antigenic Complex in Birds from Andalusia, Southern Spain. Vector-Borne Zoonotic Dis. 11, 1107–1113. https://doi.org/10.1089/vbz.2009.0237

García-Bocanegra, I., de Val, B.B., Arenas-Montes, A., Paniagua, J., Boadella, M., Gortázar, C., Arenas, A., 2012. Seroprevalence and risk factors associated to *Mycobacterium bovis* in Wild Artiodactyl species from Southern Spain, 2006-2010. PLoS One 7, e34908. https://doi.org/10.1371/journal.pone.0034908

Garcia-Fernandez, A.J., Martinez-Lopez, E., Romero, D., Maria-Mojica, P., Godino, A., Jimenez, P., 2005. High levels of blood lead in griffon vultures (*Gyps fulvus*) from Cazorla Natural Park (southern Spain). Environ. Toxicol. 20, 459–463. https://doi.org/10.1002/tox.20132

García-González, Á.M., Pérez-Martín, J.E., Gamito-Santos, J.A., Calero-Bernal, R., Alonso, M.A., Carrión, E.M.F., 2013. Epidemiologic Study of Lung Parasites (*Metastrongylus* spp.) in Wild Boar (*Sus scrofa*) in Southwestern Spain. J. Wildl. Dis. 49, 157–162. https://doi.org/10.7589/2011-07-217

García-Jiménez, W.L., Benítez-Medina, J.M., Fernández-Llario, P., Abecia, J.A., García-Sánchez, A., Martínez, R., Risco, D., Ortiz-Peláez, A., Salguero, F.J., Smith, N.. H., Gómez, L., Hermoso de Mendoza, J., 2013a. Comparative Pathology of the Natural infections by *Mycobacterium bovis* and by *Mycobacterium caprae* in Wild Boar (*Sus scrofa*). Transbound. Emerg. Dis. 60, 102–109. https://doi.org/10.1111/j.1865-1682.2012.01321.x

García-Jiménez, W.L., Benítez-Medina, J.M., Martínez, R., Carranza, J., Cerrato, R., García-Sánchez, A., Risco, D., Moreno, J.C., Sequeda, M., Gómez, L., Fernández-Llario, P., Hermoso-de-Mendoza, J., 2015. Non-tuberculous mycobacteria in wild boar (sus scrofa) from southern Spain: Epidemiological, clinical and diagnostic concerns. Transbound. Emerg. Dis. 62, 72–80. https://doi.org/10.1111/tbed.12083

García-Jiménez, W.L., Cortés, M., Benítez-Medina, J.M., Hurtado, I., Martínez, R., García-Sánchez, A., Risco, D., Cerrato, R., Sanz, C., Hermoso-de-Mendoza, M., Fernández-Llario, P., Hermoso-de-Mendoza, J., 2016. Spoligotype diversity and 5-year trends of bovine tuberculosis in Extremadura, southern Spain. Trop. Anim. Health Prod. https://doi.org/10.1007/s11250-016-1124-4

García-Jiménez, W.L., Fernández-Llario, P., Benítez-Medina, J.M., Cerrato, R., Cuesta, J., García-Sánchez, A., Gonçalves, P., Martínez, R., Risco, D., Salguero, F.J., Serrano, E., Gómez, L., Hermoso-de-Mendoza, J., 2013b. Reducing Eurasian wild boar (*Sus scrofa*) population density as a measure for bovine tuberculosis control: Effects in wild boar and a sympatric fallow deer (*Dama dama*) population in Central Spain. Prev. Vet. Med. 110, 435–446. https://doi.org/10.1016/j.prevetmed.2013.02.017

García-Montijano, M., García, A., Lemus, J.A., Montesinos, A., Canales, R., Luaces, I., Pereira, P., 2002. Blood chemistry, protein electrophoresis, and hematologic values of captive Spanish Imperial Eagles (*Aquila adalberti*). J. Zoo Wildl. Med. 33, 112–117. https://doi.org/10.1638/1042-7260(2002)033[0112:BCPEAH]2.0.CO;2

García-Presedo, I., Pedraza-Díaz, S., González-Warleta, M., Mezo, M., Gómez-Bautista, M., Ortega-Mora, L.M., Castro-Hermida, J.A., 2013. Presence of *Cryptosporidium scrofarum*, *C. suis* and *C. parvum* subtypes IIaA16G2R1 and IIaA13G1R1 in Eurasian wild boars (*Sus scrofa*). Vet. Parasitol. 196, 497–502. https://doi.org/10.1016/j.vetpar.2013.04.017

García-Ripollés, C., López-López, P., 2011. Integrating effects of supplementary feeding, poisoning, pollutant ingestion and wind farms of two vulture species in Spain using a population viability analysis. J. Ornithol. 152, 879–888. https://doi.org/10.1007/s10336-011-0671-8

García-Ripollés, C., López-López, P., 2006. Population size and breeding performance of Egyptian Vultures (*Neophron percnopterus*) in eastern Iberian Peninsula. J. Raptor Res. 40, 217–221. https://doi.org/10.3356/0892-1016(2006)40[217:PSABPO]2.0.CO;2

García-Sánchez, R.N., Nogal-Ruiz, J.J., Manzano-Lorenzo, R., Díaz, J.M.A., López, G.P., Ruano, F.J.S., Casas, A.R., Bascón, C.C., Bolás-Fernández, F., Martínez-Fernández, A.R., 2009. Trichinellosis survey in the wild boar from the Toledo mountains in south-western Spain (2007-2008): Molecular characterization of *Trichinella* isolates by ISSR-PCR. J. Helminthol. 83, 117–120. https://doi.org/10.1017/S0022149X09349469

García, C.B., Gil, J.A., Alcántara, M., González, J., Cortés, M.R., Bonafonte, J.I., Arruga, M. V., 2012. The present Pyrenean population of bearded vulture (*Gypaetus barbatus*): Its genetic characteristics. J. Biosci. 37, 689–694. https://doi.org/10.1007/s12038-012-9229-z

García, J., Miguélez, D., Astiárraga, H., Zumalacárregui, C., 2015. Factors determining the occupation of Marsh Harrier *Circus aeruginosus* breeding grounds in a Mediterranean environment. Bird Study 62, 331–338. https://doi.org/10.1080/00063657.2015.1032887

Gassó, D., Feliu, C., Ferrer, D., Mentaberre, G., Casas-Díaz, E., Velarde, R., Fernández-Aguilar, X., Colom-Cadena, A., Navarro-Gonzalez, N., López-Olvera, J.R., Lavín, S., Fenández-Llario, P., Segalés, J., Serrano, E., 2015. Uses and limitations of faecal egg count for assessing worm burden in wild boars. Vet. Parasitol. 209, 133–137. https://doi.org/10.1016/j.vetpar.2015.02.006

Gassó, D., Serrano, E., Castillo-Contreras, R., Fernández Aguilar, X., Colom Cadena, A., Velarde, R., Mentaberre, G., López-Olvera, J.R., Risco, D., Gonçalves, P., Lavín, S., Fernandez-Llário, P., Segalés, J., Ferrer, D., 2016. Coprological tests underestimate Macracanthorhynchus hirudinaceus burden in wild boar. Parasitol. Res. 115, 2103–2105. https://doi.org/10.1007/s00436-016-4976-7

Gaubert, P., Del Cerro, I., Centeno-Cuadros, A., Palomares, F., Fournier, P., Fonseca, C., Paillat, J.P., Godoy, J.A., 2015. Tracing historical introductions in the Mediterranean Basin: the success story of the common genet (*Genetta genetta*) in Europe. Biol. Invasions. https://doi.org/10.1007/s10530-015-0846-y

Gaubert, P., Godoy, J.A., Del Cerro, I., Palomares, F., 2009. Early phases of a successful invasion: Mitochondrial phylogeography of the common genet (*Genetta genetta*) within the Mediterranean Basin. Biol. Invasions 11, 523–546. https://doi.org/10.1007/s10530-008-9268-4

Gaubert, P., Machordom, A., Morales, A., López-Bao, J.V., Veron, G., Amin, M., Barros, T., Basuony, M., Djagoun, C.A.M.S., San, E.D.L., Fonseca, C., Geffen, E., Ozkurt, S.O., Cruaud, C., Couloux, A., Palomares, F., 2011. Comparative phylogeography of two African carnivorans presumably introduced into Europe: Disentangling natural versus human-mediated dispersal across the Strait of Gibraltar. J. Biogeogr. 38, 341–358. https://doi.org/10.1111/j.1365-2699.2010.02406.x

Gautschi, B., Müller, J.P., Schmid, B., Shykoff, J.A., 2003. Effective number of breeders and maintenance of genetic diversity in the captive bearded vulture population. Heredity (Edinb). 91, 9–16. https://doi.org/10.1038/sj.hdy.6800278

Gil-Tena, A., Saura, S., Brotons, L., 2007. Effects of forest composition and structure on bird species richness in a Mediterranean context: Implications for forest ecosystem management. For. Ecol. Manage. 242, 470–476. https://doi.org/10.1016/j.foreco.2007.01.080

Gil, J.A., Báguena, G., Sánchez-Castilla, E., Antor, R.J., Alcántara, M., López-López, P., 2014. Home ranges and movements of non-breeding bearded vultures tracked by satellite telemetry in the Pyrenees. Ardeola 61, 379–387. https://doi.org/10.13157/arla.61.2.2014.379

Giménez-Anaya, A., Herrero, J., Rosell, C., Couto, S., García-Serrano, A., 2008. Food habits of wild boars (*Sus scrofa*) in a mediterranean coastal wetland. Wetlands 28, 197–203.

Godinho, R., Llaneza, L., Blanco, J.C., Lopes, S., Álvares, F., García, E.J., Palacios, V., Cortés, Y., Talegón, J., Ferrand, N., 2011. Genetic evidence for multiple events of hybridization between wolves and domestic dogs in the Iberian Peninsula. Mol. Ecol. 20. https://doi.org/10.1111/j.1365-294X.2011.05345.x

Godinho, R., López-Bao, J.V., Castro, D., Llaneza, L., Lopes, S., Silva, P., Ferrand, N., 2015. Real-time assessment of hybridization between wolves and dogs: combining noninvasive samples with ancestry informative markers. Mol. Ecol. Resour. 15, 317–328. https://doi.org/10.1111/1755-0998.12313

Godoy, J.A., Negro, J.J., Hiraldo, F., Donázar, J.A., 2004. Phylogeography, genetic structure and diversity in the endangered bearded vulture (*Gypaetus barbatus* , L.) as revealed by mitochondrial DNA. Mol. Ecol. 13, 371–390. https://doi.org/10.1046/j.1365-294X.2003.02075.x

Gómara, B., González, M.J., Baos, R., Hiraldo, F., Abad, E., Rivera, J., Jiménez, B., 2008. Unexpected high PCB and total DDT levels in the breeding population of red kite (*Milvus milvus*) from Doñana National Park, south-western Spain. Environ. Int. 34, 73–78. https://doi.org/10.1016/j.envint.2007.07.002

Gómez-Ramírez, P., Shore, R.F., van den Brink, N.W., van Hattum, B., Bustnes, J.O., Duke, G., Fritsch, C., García-Fernández, A.J., Helander, B.O., Jaspers, V., Krone, O., Martínez-López, E., Mateo, R., Movalli, P., Sonne, C., 2014. An overview of existing raptor contaminant monitoring activities in Europe. Environ. Int. 67, 12–21. https://doi.org/10.1016/j.envint.2014.02.004

Gómez De Segura, A., Mart inez, J.M., Aĺcantara, M., 2012. Population size of the endangered Bearded Vulture *Gypaetus barbatus* in Aragon (Spain): An approximation to the pyrenean population. Ardeola 59, 43–55.

Gómez, J.M., Hódar, J.A., 2008. Wild boars (*Sus scrofa*) affect the recruitment rate and spatial distribution of holm oak (*Quercus ilex*). For. Ecol. Manage. 256, 1384–1389. https://doi.org/10.1016/j.foreco.2008.06.045

Gonçalves, P., Risco, D., Fernández-Llario, P., Barquero-Pérez, O., Serrano, E., Hermoso-

De-Mendoza, J., Mateos, C., 2016. A new method for ageing wild boar using dental measures. Ecol. Indic. 62, 328–332. https://doi.org/10.1016/j.ecolind.2015.11.013

González-Barrio, D., Martín-Hernando, M.P., Ruiz-Fons, F., 2015. Shedding patterns of endemic Eurasian wild boar (*Sus scrofa*) pathogens. Res. Vet. Sci. 102, 206–211. https://doi.org/10.1016/j.rvsc.2015.08.014

González-Rodríguez, V., Villar, R., 2012. Post-dispersal seed removal in four Mediterranean oaks: species and microhabitat selection differ depending on large herbivore activity. Ecol. Res. 27, 587–594. https://doi.org/10.1007/s11284-012-0927-7

González-Varo, J.P., López-Bao, J. V., Guitián, J., 2013. Functional diversity among seed dispersal kernels generated by carnivorous mammals. J. Anim. Ecol. 83, 562–571. https://doi.org/10.1111/1365-2656.12024

González, L. M., Arroyo, B.E., Margalida, A., Sánchez, R., Oria, J., 2006. Effect of human activities on the behaviour of breeding Spanish imperial eagles (*Aquila adalberti*): management implications for the conservation of a threatened species. Anim. Conserv. 9, 85–93. https://doi.org/10.1111/j.1469-1795.2005.00016.x

González, L.M., Margalida, A., Mañosa, S., Sánchez, R., Oria, J., Molina, J.I., Caldera, J., Aranda, A., Prada, L., 2007. Causes and spatio-temporal variations of non-natural mortality in the Vulnerable Spanish imperial eagle *Aquila adalberti* during a recovery period. ORYX 41, 495–502. https://doi.org/10.1017/S0030605307414119

González, Luis Mariano, Margalida, A., Sánchez, R., Oria, J., 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (*Aquila adalberti*). Biol. Conserv. 129, 477–486. https://doi.org/10.1016/j.biocon.2005.11.014

Gortázar, C., Ferreras, P., Villafuerte, R., Martín, M., Blanco, J.C., 2003. Habitat related differences in age structure and reproductive parameters of red foxes. Acta Theriol. (Warsz). 48, 93–100. https://doi.org/10.1007/BF03194269

Gortázar, C., Herrero, J., Villafuerte, R., Marco, J., 2000. Historical examination of the status of large mammals in Aragon, Spain. Mammalia 64, 411–422. https://doi.org/10.1515/mamm.2000.64.4.411

Gortazar, C., Torres, M.J., Acevedo, P., Aznar, J., Negro, J.J., De La Fuente, J., Vicente, J., 2011. Fine-tuning the space, time, and host distribution of mycobacteria in wildlife. BMC Microbiol. 11. https://doi.org/10.1186/1471-2180-11-27

Green, R.E., Donázar, J.A., Sánchez-Zapata, J.A., Margalida, A., 2016. Potential threat to Eurasian griffon vultures in Spain from veterinary use of the drug diclofenac. J. Appl. Ecol. 53, 993–1003. https://doi.org/10.1111/1365-2664.12663

Guerrero-Casado, J., Arenas, R., Tortosa, F.S., 2013a. Modelling the nesting-habitat of the Cinereous Vulture *Aegypius monachus* on a fine scale for conservation purposes. Bird Study 60, 533–538. https://doi.org/10.1080/00063657.2013.849657

Guerrero-Casado, J., Ruiz-Aizpurua, L., S. Tortosa, F., 2013b. The short-term effect of total predation exclusion on wild rabbit abundance in restocking plots. Acta Theriol. (Warsz). 58, 415–418. https://doi.org/10.1007/s13364-013-0140-2

Guerrero, I., Morales, M.B., Oñate, J.J., Geiger, F., Berendse, F., Snoo, G. de, Eggers, S., Pärt, T., Bengtsson, J., Clement, L.W., Weisser, W.W., Olszewski, A., Ceryngier, P., Hawro, V., Liira, J., Aavik, T., Fischer, C., Flohre, A., Thies, C., Tscharntke, T., 2012. Response of ground-nesting farmland birds to agricultural intensification across Europe: Landscape and field level management factors. Biol. Conserv. 152, 74–80. https://doi.org/10.1016/j.biocon.2012.04.001

Guil, F., Fernández-Olalla, M., Moreno-Opo, R., Mosqueda, I., Gómez, M.E., Aranda, A., Arredondo, Á., Guzmán, J., Oria, J., González, L.M., Margalida, A., 2011. Minimising mortality in endangered raptors due to power lines: The importance of spatial aggregation to optimize the application of mitigation measures. PLoS One 6, e28212. https://doi.org/10.1371/journal.pone.0028212

Guitián, J., Munilla, I., 2010. Responses of mammal dispersers to fruit availability: Rowan (*Sorbus aucuparia*) and carnivores in mountain habitats of northern Spain. Acta Oecologica 36, 242–247. https://doi.org/10.1016/j.actao.2010.01.005

Gurrutxaga, M., Lozano, P.J., del Barrio, G., 2010. GIS-based approach for incorporating the connectivity of ecological networks into regional planning. J. Nat. Conserv. 18, 318–326. https://doi.org/10.1016/j.jnc.2010.01.005

Gutiérrez-Guzmán, A.V., Vicente, J., Sobrino, R., Perez-Ramírez, E., Llorente, F., Höfle, U., 2012. Antibodies to West Nile virus and related flaviviruses in wild boar, red foxes and other mesomammals from Spain. Vet. Microbiol. 159, 291–297. https://doi.org/10.1016/j.vetmic.2012.04.019

Hernández, M., González, L.M., Oria, J., Sánchez, R., Arroyo, B., 2008. Influence of contamination by organochlorine pesticides and polychlorinated biphenyls on the breeding of the Spanish Imperial Eagle (*Aquila adalberti*). Environ. Toxicol. Chem. 27, 433–441. https://doi.org/10.1897/07-308R.1

Hernández, M., Margalida, A., 2010. HEMATOLOGY AND BLOOD CHEMISTRY REFERENCE VALUES AND AGE-RELATED CHANGES IN WILD BEARDED VULTURES (*GYPAETUS BARBATUS*). J. Wildl. Dis. 46, 390–400. https://doi.org/10.7589/0090-3558-46.2.390

Hernández, M., Margalida, A., 2009a. Assessing the risk of lead exposure for the conservation of the endangered Pyrenean bearded vulture (*Gypaetus barbatus*) population. Environ. Res. 109, 837–842. https://doi.org/10.1016/j.envres.2009.05.001

Hernández, M., Margalida, A., 2009b. Poison-related mortality effects in the endangered Egyptian vulture (*Neophron percnopterus*) population in Spain. Eur. J. Wildl. Res. 55, 415–423. https://doi.org/10.1007/s10344-009-0255-6

Hernández, M., Margalida, A., 2008. Pesticide abuse in Europe: Effects on the Cinereous vulture (*Aegypius monachus*) population in Spain. Ecotoxicology 17, 264–272. https://doi.org/10.1007/s10646-008-0193-1

Herrero-Medrano, J.M., Megens, H.J., Groenen, M.A.M., Ramis, G., Bosse, M., Pérez-Enciso, M., Crooijmans, R.P.M.A., 2013. Conservation genomic analysis of domestic and wild pig populations from the Iberian Peninsula. BMC Genet. 14. https://doi.org/10.1186/1471-2156-14-106

Herrero, J., García-Serrano, A., Couto, S., Ortuño, V.M., García-González, R., 2006. Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. Eur. J. Wildl. Res. 52, 245–250. https://doi.org/10.1007/s10344-006-0045-3

Herrero, J., García-Serrano, A., García-González, R., 2008. Reproductive and demographic parameters in two Iberian wild boar *Sus scrofa* populations. Acta Theriol. (Warsz). 53, 355–364.

Herruzo, C., Martinez-Jauregui, M., 2013. Trends in hunters, hunting grounds and big game harvest in Spain. For. Syst. 22, 114–122. https://doi.org/10.5424/fs/2013221-03371

Iglesias-Merchán, C., Diaz-Balteiro, L., de la Puente, J., 2016. Road traffic noise impact assessment in a breeding colony of cinereous vultures (*Aegypius monachus*) in Spain. J. Acoust. Soc. Am. 139, 1124–1131. https://doi.org/10.1121/1.4943553

Jaroso, R., Vicente, J., Fernandez-de-Mera, I.G., Aranaz, A., Gortazar, C., 2010. Eurasian wild boar response to skin-testing with mycobacterial and non-mycobacterial antigens. Prev. Vet. Med. 96, 211–217. https://doi.org/10.1016/j.prevetmed.2010.06.011

Jiménez-Franco, M. V., Martínez, J.E., Calvo, J.F., 2014. Lifespan analyses of forest raptor nests: Patterns of creation, persistence and reuse. PLoS One 9, e93628. https://doi.org/10.1371/journal.pone.0093628

Jiménez, J., García, E.J., Llaneza, L., Palacios, V., González, L.M., García-Domínguez, F., Múñoz-Igualada, J., López-Bao, J.V., 2016. Multimethod, multistate Bayesian hierarchical modeling approach for use in regional monitoring of wolves. Conserv. Biol. 30, 883–893. https://doi.org/10.1111/cobi.12685

Jokimäki, J., Kaisanlahti-Jokimäki, M.L., Sorace, A., Fernández-Juricic, E., Rodriguez-Prieto, I., Jimenez, M.D., 2005. Evaluation of the "safe nesting zone" hypothesis across an urban gradient: a multi-scale study. Ecography (Cop.). 28, 59–70. https://doi.org/10.1111/j.0906-7590.2005.04001.x

Jordano, P., Garcia, C., Godoy, J.A., Garcia-Castano, J.L., 2007. Differential contribution of frugivores to complex seed dispersal patterns. Proc. Natl. Acad. Sci. 104, 3278–3282. https://doi.org/10.1073/pnas.0606793104

Kretzmann, M.B., Capote, N., Gautschi, B., Godoy, J.A., Donázar, J.A., Negro, J.J., 2003. Genetically distinct island populations of the Egyptian vulture (*Neophron percnopterus*). Conserv. Genet. 4, 697–706.

Kukielka, D., Rodriguez-Prieto, V., Vicente, J., Sánchez-Vizcaíno, J.M., 2015. Constant Hepatitis E Virus (HEV) Circulation in Wild Boar and Red Deer in Spain: An Increasing Concern Source of HEV Zoonotic Transmission. Transbound. Emerg. Dis. 63, 360–368. https://doi.org/10.1111/tbed.12311

Kukielka, E., Barasona, J.A., Cowie, C.E., Drewe, J.A., Gortazar, C., Cotarelo, I., Vicente, J., 2013. Spatial and temporal interactions between livestock and wildlife in South Central Spain assessed by camera traps. Prev. Vet. Med. 112, 231–221. https://doi.org/10.1016/j.prevetmed.2013.08.008

Lado, L.R., Tapia, L., 2012. Suitable breeding habitat for Golden Eagle (Aquila chrysaetos) in a border of distribution area in Northwestern Spain: Advantages of using remote sensing information vs. land use maps. Vie Milieu 62, 77–85.

Lagos, L., Bárcena, F., 2015. EU Sanitary Regulation on Livestock Disposal: Implications for the Diet of Wolves. Environ. Manage. 56, 890–902. https://doi.org/10.1007/s00267-015-0571-4

Lagos, L., Picos, J., Valero, E., 2012. Temporal pattern of wild ungulate-related traffic accidents in northwest Spain. Eur. J. Wildl. Res. 58, 661–668. https://doi.org/10.1007/s10344-012-0614-6

LaHue, N.P., Baños, J.V., Acevedo, P., Gortázar, C., Martínez-López, B., 2016. Spatially explicit modeling of animal tuberculosis at the wildlife-livestock interface in Ciudad Real province, Spain. Prev. Vet. Med. 128, 101–111. https://doi.org/10.1016/j.prevetmed.2016.04.011

Lara-Romero, C., Virgós, E., Escribano-Ávila, G., Mangas, J.G., Barja, I., Pardavila, X., 2012. Habitat selection by European badgers in Mediterranean semi-arid ecosystems. J. Arid Environ. 76, 43–48. https://doi.org/10.1016/j.jaridenv.2011.08.004

Leverkus, A.B., Castro, J., Puerta-Piñero, C., Rey Benayas, J.M., 2013. Suitability of the management of habitat complexity, acorn burial depth, and a chemical repellent for post-fire reforestation of oaks. Ecol. Eng. 53, 15–22. https://doi.org/10.1016/j.ecoleng.2013.01.003

Leverkus, A.B., Rojo, M., Castro, J., 2015. Habitat complexity and individual acorn protectors enhance the post-fire restoration of oak forests via seed sowing. Ecol. Eng. 83, 276–280. https://doi.org/10.1016/j.ecoleng.2015.06.033

Llaneza, L., García, E.J., Palacios, V., Sazatornil, V., López-Bao, J.V., 2016. Resting in risky environments: the importance of cover for wolves to cope with exposure risk in human-dominated landscapes. Biodivers. Conserv. 25, 1515–1528. https://doi.org/10.1007/s10531-016-1134-6

Llaneza, L., López-Bao, J. V., 2015. Indirect effects of changes in environmental and agricultural policies on the diet of wolves. Eur. J. Wildl. Res. 61, 895–902. https://doi.org/10.1007/s10344-015-0966-9

Llaneza, L., López-Bao, J. V., Sazatornil, V., 2012. Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. Divers. Distrib. 18, 495–469. https://doi.org/10.1111/j.1472-4642.2011.00869.x

Lledó, L., Domínguez-Peñafiel, G., Giménez-Pardo, C., Gegúndez, I., González, R., Saz, J.V., 2014. Molecular and Serological Study of Rickettsial Infection in Humans, and in Wild and Farm Animals, in the Province of Burgos, Spain. Vector-Borne Zoonotic Dis. 14, 383–388. https://doi.org/10.1089/vbz.2013.1513

Lledó, L., Giménez-Pardo, C., Domínguez-Peñafiel, G., Sousa, R., Gegúndez, M.I., Casado, N., Criado, A., 2010. Molecular Detection of Hemoprotozoa and *Rickettsia* Species in Arthropods Collected from Wild Animals in the Burgos Province, Spain. Vector-Borne Zoonotic Dis. 10, 735–738. https://doi.org/10.1089/vbz.2009.0114

Lledó, L., Serrano, J.L., Isabel Gegúndez, M., Giménez-Pardo, C., Vicente Saz, J., 2016. Antibodies to *Rickettsia* spp . and *Borrelia burgdorferi* in Spanish Wild Red Foxes (*Vulpes vulpes*). J. Wildl. Dis. 52, 122–125. https://doi.org/10.7589/2015-03-074

López-Bao, J. V., González-Varo, J.P., Guitián, J., 2015. Mutualistic relationships under landscape change: Carnivorous mammals and plants after 30 years of land abandonment. Basic Appl. Ecol. 16, 152–161. https://doi.org/10.1016/j.baae.2014.12.001

López-López, P., Ferrer, M., Madero, A., Casado, E., McGrady, M., 2011. Solving man-induced large-scale conservation problems: The Spanish Imperial Eagle and power lines. PLoS One 6, e17196. https://doi.org/10.1371/journal.pone.0017196

López-López, P., García-Ripollés, C., Soutullo, Á., Cadahía, L., Urios, V., 2007. Identifying potentially suitable nesting habitat for golden eagles applied to “important bird areas” design. Anim. Conserv. 10, 208–218. https://doi.org/10.1111/j.1469-1795.2006.00089.x

López-López, P., García-Ripollés, C., Urios, V., 2014. Food predictability determines space use of endangered vultures: implications for management of supplementary feeding. Ecol. Appl. 24, 938–949.

López-López, P., García-Ripollés, C., Verdejo, J., 2004. Population status and reproductive performance or eurasian griffons (*Gyps fulvus*) in eastern Spain. J. Raptor Res. 38, 350–356.

López-López, P., Gilmanuel Alcántara, J.A., 2014. Post-fledging dependence period and onset of natal dispersal in Bearded Vultures (*Gypaetus barbatus*): new insights from GPS satellite telemetry. J. Raptor Res. 48, 173–181. https://doi.org/10.3356/JRR-13-00072.1JRR-13-00072.1

López-López, P., Soutullo, A., García-Ripollés, C., Urios, V., Cadahía, L., Ferrer, M., 2009. Markov models of territory occupancy: Implications for the management and conservation of competing species. Biodivers. Conserv. 18, 1389–1402. https://doi.org/10.1007/s10531-008-9469-2

López-López, P., Zuberogoitia, Í., Alcántara, M., Gil, J.A., 2013. Philopatry, natal dispersal, first settlement and age of first breeding of bearded vultures *Gypaetus barbatus* in central Pyrenees. Bird Study 60, 555–560. https://doi.org/10.1080/00063657.2013.842537

López-Perea, J.J., Camarero, P.R., Molina-López, R.A., Parpal, L., Obón, E., Solá, J., Mateo, R., 2015. Interspecific and geographical differences in anticoagulant rodenticide residues of predatory wildlife from the Mediterranean region of Spain. Sci. Total Environ. 511, 259–267. https://doi.org/10.1016/j.scitotenv.2014.12.042

López y López-Leitón, T.J., Alvarez Piñeiro, M.E., Lage Yusty, M.A., Simal Lozano, J., 2001. Aliphatic hydrocarbons in birds of prey from Galicia (NW Spain). Ecotoxicol. Environ. Saf. 50, 44–47. https://doi.org/10.1006/eesa.2001.2066

Lozano, J., Virgós, E., Cabezas-Díaz, S., Mangas, J.G., 2007. Increase of large game species in Mediterranean areas: Is the European wildcat (*Felis silvestris*) facing a new threat? Biol. Conserv. 138. https://doi.org/10.1016/j.biocon.2007.04.027

Luzardo, O.P., Ruiz-Suárez, N., Henríquez-Hernández, L.A., Valerón, P.F., Camacho, M., Zumbado, M., Boada, L.D., 2014. Assessment of the exposure to organochlorine pesticides, PCBs and PAHs in six species of predatory birds of the Canary Islands, Spain. Sci. Total Environ. 472, 146–153. https://doi.org/10.1016/j.scitotenv.2013.11.021

Lyashchenko, K.P., Greenwald, R., Esfandiari, J., Chambers, M.A., Vicente, J., Gortazar, C., Santos, N., Correia-Neves, M., Buddle, B.M., Jackson, R., O'Brien, D.J., Schmitt, S., Palmer, M. V., Delahay, R.J., Waters, W.R., 2008. Animal-side serologic assay for rapid detection of *Mycobacterium* bovis infection in multiple species of free-ranging wildlife. Vet. Microbiol. 132, 283–292. https://doi.org/10.1016/j.vetmic.2008.05.029

Malo, J.E., Suárez, F., Díez, A., 2004. Can we mitigate animal-vehicle accidents using predictive models? J. Appl. Ecol. 41, 701–710.

Mangas, J.G., Lozano, J., Cabezas-Díaz, S., Virgós, E., 2008. The priority value of scrubland habitats for carnivore conservation in Mediterranean ecosystems. Biodivers. Conserv. 17, 43–51. https://doi.org/10.1007/s10531-007-9229-8

Mangas, J.G., Rodríguez-Estival, J., 2010. Logging and livestock influence the abundance of common mammal species in Mediterranean forested environments. For. Ecol. Manage. 260, 1274–1281. https://doi.org/10.1016/j.foreco.2010.07.001

Margalida, A., 2010. Supplementary feeding during the chick-rearing period is ineffective in increasing the breeding success in the bearded vulture (*Gypaetus barbatus*). Eur. J. Wildl. Res. 56, 673–678. https://doi.org/10.1007/s10344-010-0366-0

Margalida, A., Benítez, J.R., Sánchez-Zapata, J.A., Ávila, E., Arenas, R., Donázar, J.A., 2012. Long-term relationship between diet breadth and breeding success in a declining population of Egyptian Vultures *Neophron percnopterus*. Ibis (Lond. 1859). 154, 184–188.

Margalida, A., Bertran, J., Heredia, R., 2009a. Diet and food preferences of the endangered Bearded Vulture *Gypaetus barbatus*: a basis for their conservation. Ibis (Lond. 1859). 151, 235–243. https://doi.org/10.1111/j.1474-919X.2008.00904.x

Margalida, A., Campión, D., Donázar, J.A., 2014a. Vultures vs livestock: Conservation relationships in an emerging conflict between humans and wildlife. ORYX 48, 172–176. https://doi.org/10.1017/S0030605312000889

Margalida, A., Carrete, M., Hegglin, D., Serrano, D., Arenas, R., Donázar, J.A., 2013. Uneven Large-Scale Movement Patterns in Wild and Reintroduced Pre-Adult Bearded Vultures: Conservation Implications. PLoS One 8, e65857. https://doi.org/10.1371/journal.pone.0065857

Margalida, A., Colomer, M.À., Oro, D., 2014b.

Man-induced activities modify demographic parameters in a long-lived species: Effects of poisoning and health policies. Ecol. Appl. 24, 436–444. https://doi.org/10.1890/13-0414.1

Margalida, A., Colomer, M.À., Oro, D., Arlettaz, R., Donázar, J.A., 2015. Assessing the impact of removal scenarios on population viability of a threatened, long-lived avian scavenger. Sci. Rep. 5, 16962. https://doi.org/10.1038/srep16962

Margalida, A., Colomer, M.À., Sanuy, D., 2011a. Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. PLoS One 6, e20248. https://doi.org/10.1371/journal.pone.0020248

Margalida, A., Donázar, J.A., Bustamante, J., Hernández, F.J., Romero-Pujante, M., 2008. Application of a predictive model to detect long-term changes in nest-site selection in the Bearded Vulture *Gypaetus barbatus*: conservation in relation to territory shrinkage. Ibis (Lond. 1859). 150, 242–249.

Margalida, A., Garcia, D., Bertran, J., Heredia, R., 2003. Breeding biology and success of the Bearded Vulture *Gypaetus barbatus* in the eastern Pyrenees. Ibis (Lond. 1859). 145, 244–252. https://doi.org/10.1046/j.1474-919X.2003.00148.x

Margalida, A., García, D., Heredia, R., Bertran, J., 2010. Video-monitoring helps to optimize the rescue of second-hatched chicks in the endangered bearded vulture *Gypaetus barbatus*. Bird Conserv. Int. 20, 55–61. https://doi.org/10.1017/S0959270909990165

Margalida, A., Mañosa, S., Bertran, J., García, D., 2007. Biases in studying the diet of the Bearded Vulture. J. Wildl. Manage. 71, 1621–1625. https://doi.org/10.2193/2006-049

Margalida, A., Marín-Arroyo, A.B., 2013. Dietary habits in the endangered Bearded Vulture *Gypaetus barbatus* from Upper Pleistocene to modern times in Spain: A paleobiological conservation perspective. Bird Conserv. Int. 23, 469–476. https://doi.org/10.1017/S0959270912000500

Margalida, A., Moreno-Opo, R., Arroyo, B.E., Arredondo, A., 2011b. Reconciling the conservation of endangered species with economically important anthropogenic activities: Interactions between cork exploitation and the cinereous vulture in Spain. Anim. Conserv. 14, 167–174. https://doi.org/10.1111/j.1469-1795.2010.00412.x

Margalida, A., Pérez-García, J.M., Afonso, I., Moreno-Opo, R., 2016. Spatial and temporal movements in Pyrenean bearded vultures (*Gypaetus barbatus*): Integrating movement ecology into conservation practice. Sci. Rep. 6. https://doi.org/10.1038/srep35746

Margalida, A., Sánchez-Zapata, J.A., Eguía, S., Arroyo, A.B.M., Hernández, F.J., Bautista, J., 2009b. Assessing the diet of breeding bearded vultures (*Gypaetus barbatus*) in mid-20th century in Spain: A comparison to recent data and implications for conservation. Eur. J. Wildl. Res. 55, 443–448. https://doi.org/10.1007/s10344-009-0269-0

Mariano González, L., Oria, J., Margalida, A., Sánchez, R., Prada, L., Caldera, J., Aranda, A., Ignacio Molina, J., 2006. Effective natal dispersal and age of maturity in the threatened Spanish Imperial Eagle <i>Aquila adalberti<i>: conservation implications. Bird Study 53, 285–293. https://doi.org/10.1080/00063650609461444doi.org/10.1080/00063650609461444

Márquez, C., Vargas, J.M., Villafuerte, R., Fa, J.E., 2013a. Understanding the propensity of wild predators to illegal poison baiting. Anim. Conserv. 16, 118–129. https://doi.org/10.1111/j.1469-1795.2012.00581.x

Márquez, C., Vargas, J.M., Villafuerte, R., Fa, J.E., 2013b. Risk mapping of illegal poisoning of avian and mammalian predators. J. Wildl. Manage. 77, 75–83. https://doi.org/10.1002/jwmg.424

Martín-López, B., Montes, C., Benayas, J., 2007. The non-economic motives behind the willingness to pay for biodiversity conservation. Biol. Conserv. 139, 67–82. https://doi.org/10.1016/j.biocon.2007.06.005

Martín, B., Onrubia, A., de la Cruz, A., Ferrer, M., 2016. Trends of autumn counts at Iberian migration bottlenecks as a tool for monitoring continental populations of soaring birds in Europe. Biodivers. Conserv. 25, 295–309. https://doi.org/10.1007/s10531-016-1047-4

Martín, B., Onrubia, A., Ferrer, M.A., 2014. Effects of climate change on the migratory behaviour oh the common buzzard *Buteo buteo*. Clim. Res. 60, 187–197. https://doi.org/10.3354/cr01233

Martin, J., Revilla, E., Quenette, P.Y., Naves, J., Allainé, D., Swenson, J.E., 2012. Brown bear habitat suitability in the Pyrenees: transferability across sites and linking scales to make the most of scarce data. J. Appl. Ecol. 49, 621–631. https://doi.org/10.1111/j.1365-2664.2012.02139.x

Martínez-Abraín, A., Crespo, J., Jiménez, J., Gómez, J.A., Oro, D., 2009. Is the historical war against wildlife over in southern Europe? Anim. Conserv. 12, 204–208. https://doi.org/10.1111/j.1469-1795.2009.00239.x

Martínez-Abraín, A., Tavecchia, G., Regan, H.M., Jiménez, J., Surroca, M., Oro, D., 2012. Effects of wind farms and food scarcity on a large scavenging bird species following an epidemic of bovine spongiform encephalopathy. J. Appl. Ecol. 49, 109–117. https://doi.org/10.1111/j.1365-2664.2011.02080.x

Martínez-Cruz, B., Godoy, J.A., Negro, J.J., 2007. Population fragmentation leads to spatial and temporal genetic structure in the endangered Spanish imperial eagle. Mol. Ecol. 16, 477–486. https://doi.org/10.1111/j.1365-294X.2007.03147.x

Martínez-Cruz, B., Godoy, J.A., Negro, J.J., 2004. Population genetics after fragmentation: the case of the endangered Spanish imperial eagle (*Aquila adalberti*). Mol. Ecol. 13, 2243–2255. https://doi.org/10.1111/j.1365-294X.2004.02220.x

Martínez-Díaz, R.A., Ponce-Gordo, F., Rodríguez-Arce, I., del Martínez-Herrero, M.C., González, F.G., Molina-López, R.Á., Gómez-Muñoz, M.T., 2015. *Trichomonas gypaetinii* n. sp., a new trichomonad from the upper gastrointestinal tract of scavenging birds of prey. Parasitol. Res. 144, 101–112. https://doi.org/10.1007/s00436-014-4165-5

Martínez-Herrero, M.C., Sansano-Maestre, J., López Márquez, I., Obón, E., Ponce, C., González, J., Garijo-Toledo, M.M., Gómez-Muñoz, M.T., 2014. Genetic characterization of oropharyngeal trichomonad isolates from wild birds indicates that genotype is associated with host species, diet and presence of pathognomonic lesions. Avian Pathol. 43, 535–546. https://doi.org/10.1080/03079457.2014.967660

Martinez-Jauregui, M., Herruzo, A.C., Campos, P., 2015. What does hunting market price reflect? The role of species, landscape and management. Wildl. Res. 42, 280–289. https://doi.org/10.1071/WR14206

Martínez-Jauregui, M., Herruzo, A.C., Campos, P., Soliño, M., 2016. Shedding light on the self-consumption value of recreational hunting in European Mediterranean forests. For. Policy Econ. 69, 83–89. https://doi.org/10.1016/j.forpol.2016.05.002

Martínez-López, B., Barasona, J.A., Gortázar, C., Rodríguez-Prieto, V., Sánchez-Vizcaíno, J.M., Vicente, J., 2014. Farm-level risk factors for the occurrence, new infection or persistence of tuberculosis in cattle herds from South-Central Spain. Prev. Vet. Med. 116, 268–278. https://doi.org/10.1016/j.prevetmed.2013.11.002

Martínez, A., Crespo, D., Fernández, J.Á., Aboal, J.R., Carballeira, A., 2012. Selection of flight feathers from *Buteo buteo* and *Accipiter gentilis* for use in biomonitoring heavy metal contamination. Sci. Total Environ. 425, 254–261. https://doi.org/10.1016/j.scitotenv.2012.03.017

Martínez Cano, I., Taboada, F.G., Naves, J., Fernández-Gil, A., Wiegand, T., 2016. Decline and recovery of a large carnivore: environmental change and long-term trends in an endangered brown bear population. Proc. R. Soc. B Biol. Sci. 283. https://doi.org/10.6084/m9

Martínez, J.E., Calvo, J.F., Martínez, J.A., Zuberogoitia, I., Cerezo, E., Manrique, J., Gómez, G.J., Nevado, J.C., Sánchez, M., Sánchez, R., Bayo, J., Pallarés, A., González, C., Gómez, J.M., Pérez, P., Motos, J., 2010. Potential impact of wind farms on territories of large eagles in southeastern Spain. Biodivers. Conserv. 19, 3757–3767. https://doi.org/10.1007/s10531-010-9925-7

Mateo-Moriones, A., Villafuerte, R., Ferreras, P., 2012. Does fox control improve red–legged partridge (*Alectoris rufa*) survival? An experimental study in Northern Spain. Anim. Biodivers. Conserv. 35, 395–404.

Mateo-Sánchez, María C., Balkenhol, N., Cushman, S., Pérez, T., Domínguez, A., Saura, S., 2015. A comparative framework to infer landscape effects on population genetic structure: are habitat suitability models effective in explaining gene flow? Landsc. Ecol. 30, 1405–1420. https://doi.org/10.1007/s10980-015-0194-4

Mateo-Sánchez, M. C., Balkenhol, N., Cushman, S., Pérez, T., Domínguez, A., Saura, S., 2015. Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data. Ecosphere 6, 59. https://doi.org/10.1890/ES14-00387.1

Mateo-Sánchez, M.C., Cushman, S.A., Saura, S., 2014. Connecting endangered brown bear subpopulations in the Cantabrian Range (north-western Spain). Anim. Conserv. 17, 430–440. https://doi.org/10.1111/acv.12109

Mateo-Sánchez, M.C., Gastón, A., Ciudad, C., García-Viñas, J.I., Cuevas, J., López-Leiva, C., Fernández-Landa, A., Algeet-Abarquero, N., Marchamalo, M., Fortin, M.J., Saura, S., 2016. Seasonal and temporal changes in species use of the landscape: how do they impact the inferences from multi-scale habitat modeling? Landsc. Ecol. 31, 1261–1276. https://doi.org/10.1007/s10980-015-0324-z

Mateo-Tomás, P., Olea, P.P., 2015. Livestock-driven land use change to model species distributions: Egyptian vulture as a case study. Ecol. Indic. 57, 331–340. https://doi.org/10.1016/j.ecolind.2015.05.017

Mateo-Tomás, P., Olea, P.P., 2010a. Anticipating knowledge to inform species management: Predicting spatially explicit habitat suitability of a colonial vulture spreading its range. PLoS One 5, e12374. https://doi.org/10.1371/journal.pone.0012374

Mateo-Tomás, P., Olea, P.P., 2010b. When hunting benefits raptors: A case study of game species and vultures. Eur. J. Wildl. Res. 56, 519–528. https://doi.org/10.1007/s10344-009-0341-9

Mateo-Tomás, P., Olea, P.P., 2010c. Diagnosing the causes of territory abandonment by the Endangered Egyptian vulture *Neophron percnopterus*: The importance of traditional pastoralism and regional conservation. ORYX 44, 424–433. https://doi.org/10.1017/S0030605310000189

Mateo-Tomás, P., Olea, P.P., 2009. Combining scales in habitat models to improve conservation planning in an endangered vulture. Acta Oecologica 35, 489–498. https://doi.org/10.1016/j.actao.2009.03.004

Mateo-Tomás, P., Olea, P.P., Fombellida, I., 2010. Status of the Endangered Egyptian vulture *Neophron percnopterus* in the Cantabrian Mountains, Spain, and assessment of threats. ORYX 44, 434–440. https://doi.org/10.1017/S0030605310000505

Mateo-Tomás, P., Olea, P.P., Moleón, M., Vicente, J., Botella, F., Selva, N., Viñuela, J., Sánchez-Zapata, J.A., 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Divers. Distrib. 21, 913–924. https://doi.org/10.1111/ddi.12330

Mateo-Tomás, P., Olea, P.P., Sánchez-Barbudo, I.S., Mateo, R., 2012. Alleviating human-wildlife conflicts: identifying the causes and mapping the risk of illegal poisoning of wild fauna. J. Appl. Ecol. 49, 376–385. https://doi.org/10.1111/j.1365-2664.2012.02119.x

Mateo, R., Millán, J., Rodríguez-Estival, J., Camarero, P.R., Palomares, F., Ortiz-Santaliestra, M.E., 2012. Levels of organochlorine pesticides and polychlorinated biphenyls in the critically endangered Iberian lynx and other sympatric carnivores in Spain. Chemosphere 86, 691–700. https://doi.org/10.1016/j.chemosphere.2011.10.037

Mateo, R., Sánchez-Barbudo, I.S., Camarero, P.R., Martínez, J.M., 2015. Risk assessment of bearded vulture (*Gypaetus barbatus*) exposure to topical antiparasitics used in livestock within an ecotoxicovigilance framework. Sci. Total Environ. 536, 704–712. https://doi.org/10.1016/j.scitotenv.2015.07.109

Matías, L., Zamora, R., Mendoza, I., Hódar, J.A., 2010. Seed Dispersal Patterns by Large Frugivorous Mammals in a Degraded Mosaic Landscape. Restor. Ecol. 18, 619–627. https://doi.org/10.1111/j.1526-100X.2008.00475.x

Melero, Y., Plaza, M., Santulli, G., Saavedra, D., Gosàlbez, J., Ruiz-Olmo, J., Palazón, S., 2012. Evaluating the effect of American mink, an alien invasive species, on the abundance of a native community: is coexistence possible? Biodivers. Conserv. 21, 1795–1809. https://doi.org/10.1007/s10531-012-0277-3

Meli, M.L., Simmler, P., Cattori, V., Martínez, F., Vargas, A., Palomares, F., López-Bao, J. V., Simón, M.A., López, G., León-Vizcaino, L., Hofmann-Lehmann, R., Lutz, H., 2010. Importance of canine distemper virus (CDV) infection in free-ranging Iberian lynxes (*Lynx pardinus*). Vet. Microbiol. 146, 132–137. https://doi.org/10.1016/j.vetmic.2010.04.024

Menéndez, J., Goyache, F., Beja-Pereira, A., Fernández, I., Menéndez-Arias, N.A., Godinho, R., Álvarez, I., 2016. Genetic characterisation of the endangered Gochu Asturcelta pig breed using microsatellite and mitochondrial markers: Insights for the composition of the Iberian native pig stock. Livest. Sci. 187, 162–167. https://doi.org/10.1016/j.livsci.2016.03.013

Mentaberre, G., Porrero, M.C., Navarro-Gonzalez, N., Serrano, E., Domínguez, L., Lavín, S., 2013. Cattle Drive *Salmonella* Infection in the Wildlife-Livestock Interface. Zoonoses Public Health 60, 510–518. https://doi.org/10.1111/zph.12028

Merino, S., Peirce, M.A., Fernández, M., Lanzarot, P., 2002. Redescription of *Babesia moshkovskii* (Schurenkova) from the griffon vulture *Gyps fulvus* (Hablizl). J. Nat. Hist. 36, 1635–1638. https://doi.org/10.1080/00222930110097653

Mezo, M., González-Warleta, M., Castro-Hermida, J.A., Manga-González, M.Y., Peixoto, R., Mas-Coma, S., Valero, M.A., 2013. The wild boar (Sus scrofa Linnaeus, 1758) as secondary reservoir of *Fasciola hepatica* in Galicia (NW Spain). Vet. Parasitol. 198, 174–283. https://doi.org/10.1016/j.vetpar.2013.09.009

Millán, J., Candela, M.G., Palomares, F., Cubero, M.J., Rodríguez, A., Barral, M., de la Fuente, J., Almería, S., León-Vizcaíno, L., 2009. Disease threats to the endangered Iberian lynx (*Lynx pardinus*). Vet. J. 182, 114–124. https://doi.org/10.1016/j.tvjl.2008.04.005

Millán, J., Casanova, J.C., 2007. Helminth parasites of the endangered Iberian lynx (*Lynx pardinus*) and sympatric carnivores. J. Helminthol. 81, 377–380. https://doi.org/10.1017/S0022149X07869203

Millán, J., López-Bao, J.V., García, E.J., Oleaga, Á., Llaneza, L., Palacios, V., De La Torre, A., Rodríguez, A., Dubovi, E.J., Esperón, F., 2016.

Patterns of exposure of iberian wolves (*Canis lupus*) to canine viruses in human-dominated landscapes. Ecohealth 13, 123–134. https://doi.org/10.1007/s10393-015-1074-8

Millán, J., Mateo, R., Taggart, M.A., López-Bao, J. V., Viota, M., Monsalve, L., Camarero, P.R., Blázquez, E., Jiménez, B., 2008. Levels of heavy metals and metalloids in critically endangered Iberian lynx and other wild carnivores from Southern Spain. Sci. Total Environ. 399, 193–201. https://doi.org/10.1016/j.scitotenv.2008.03.038

Millán, J., Negre, N., Castellanos, E., de Juan, L., Mateos, A., Parpal, L., Aranaz, A., 2010. Avian mycobacteriosis in free-living raptors in Majorca Island, Spain. Avian Pathol. 39, 1–6. https://doi.org/10.1080/03079450903389945

Millán, J., Ruiz-Fons, F., Márquez, F.J., Viota, M., López-Bao, J. V., Martín-Mateo, M.P., 2007. Ectoparasites of the endangered Iberian lynx *Lynx pardinus* and sympatric wild and domestic carnivores in Spain. Med. Vet. Entomol. 21, 248–254.

Molina-López, R.A., Casal, J., Darwich, L., 2015a. Prognostic indicators associated with early mortality of wild raptors admitted to a wildlife rehabilitation centre in Spain. Vet. Q. 35, 9–15. https://doi.org/10.1080/01652176.2014.985856

Molina-López, R.A., Vidal, A., Obón, E., Martín, M., Darwich, L., 2015b. Multidrug-resistant *Salmonella enterica* Serovar Typhimurium Monophasic Variant 4,12:i:- Isolated from Asymptomatic Wildlife in a Catalonian Wildlife Rehabilitation Center, Spain. J. Wildl. Dis. 51, 759–763. https://doi.org/10.7589/2015-01-019

Montesdeoca, N., Calabuig, P., Corbera, J.A., Orós, J., 2016. Causes of Admission for Raptors to the Tafira Wildlife Rehabilitation Center, Gran Canaria Island, Spain: 2003–2013. J. Wildl. Dis. 52. https://doi.org/10.7589/2015-09-255

Morán-López, Ricardo, Sánchez Guzmán, J.M., Costillo Borrego, E., Villegas Sánchez, A., 2006. Nest-site selection of endangered cinereous vulture (*Aegypius monachus*) populations affected by anthropogenic disturbance: Present and future conservation implications. Anim. Conserv. 9, 29–37. https://doi.org/10.1111/j.1469-1795.2005.00003.x

Morán-López, R., Sánchez, J.M., Costillo, E., Corbacho, C., Villegas, A., 2006. Spatial variation in anthropic and natural factors regulating the breeding success of the cinereous vulture (*Aegypius monachus*) in the SW Iberian Peninsula. Biol. Conserv. 130, 169–182. https://doi.org/10.1016/j.biocon.2005.12.011

Moreno-Opo, R., Afonso, I., Jiménez, J., Fernández-Olalla, M., Canut, J., García-Ferré, D., Piqué, J., García, F., Roig, J., Muñoz-Igualada, J., González, L.M., López-Bao, J.V., 2015a. Is It Necessary Managing Carnivores to Reverse the Decline of Endangered Prey Species? Insights from a Removal Experiment of Mesocarnivores to Benefit Demographic Parameters of the Pyrenean Capercaillie. PLoS One 10. https://doi.org/10.1371/journal.pone.0139837

Moreno-Opo, R., Fernández-Olalla, M., Margalida, A., Arredondo, Á., Guil, F., 2013. Influence of environmental factors on the breeding success of Cinereous Vultures *Aegypius monachus*. Acta Ornithol. 48, 187–193. https://doi.org/10.3161/000164513X678838

Moreno-Opo, R., Margalida, A., 2013. Carcasses provide resources not exclusively to scavengers: Patterns of carrion exploitation by passerine birds. Ecosphere 4. https://doi.org/10.1890/ES13-00108.1

Moreno-Opo, R., Margalida, A., Arredondo, Á., Guil, F., Martín, M., Higuero, R., Soria, C., Guzmán, J., 2010. Factors influencing the presence of the cinereous vulture *Aegypius monachus* at carcasses: food preferences and implications for the management of supplementary feeding sites. Wildlife Biol. 16, 25–34. https://doi.org/10.2981/09-037

Moreno-Opo, R., Margalida, A., García, F., Arredondo, Á., Rodríguez, C., González, L.M., 2012. Linking sanitary and ecological requirements in the management of avian scavengers: effectiveness of fencing against mammals in supplementary feeding sites. Biodivers. Conserv. 21, 1673–1685. https://doi.org/10.1007/s10531-012-0270-x

Moreno-Opo, R., Trujillano, A., Arredondo, Á., González, L.M., Margalida, A., 2015b. Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. Biol. Conserv. 181, 27–35. https://doi.org/10.1016/j.biocon.2014.10.022

Moreno-Opo, R., Trujillano, A., Margalida, A., 2015c. Optimization of supplementary feeding programs for European vultures depends on environmental and management factors. Ecosphere 8, 127. https://doi.org/10.1890/ES15-00009.1

Moreno-Rueda, G., Pizarro, M., Ontiveros, D., Pleguezuelos, J.M., 2009. The coexistence of the eagles *Aquila chrysaetos* and *Hieraaetus fasciatus* increases with low human population density, intermediate temperature, and high prey diversity. Ann. Zool. Fennici 46, 283–290. https://doi.org/10.5735/086.046.0405

Müller, T., Klupp, B.G., Freuling, C., Hoffmann, B., Mojcicz, M., Capua, I., Palfi, V., Toma, B., Lutz, W., Ruiz-Fon, F., Gortrzar, C., Hlinak, A., Schaarschmidt, U., Zimmer, K., Conraths, F.J., Hahn, E.C., Mettenleiter, T.C., 2010. Characterization of pseudorabies virus of wild boar origin from Europe. Epidemiol. Infect. 138, 1590–1600. https://doi.org/10.1017/S0950268810000361

Muñoz-Igualada, J., Shivik, J.A., Domínguez, F.G., Lara, J., González, L.M., 2008. Evaluation of cage-traps and cable restraint devices to capture red foxes in Spain. J. Wildl. Manage. 72, 830–836. https://doi.org/10.2193/2007-198

Muñoz-Igualada, J., Shivik, J.A., Domínguez, F.G., Mariano González, L., Aranda Moreno, A., Fernández Olalla, M., Alves García, C., 2010. Traditional and New Cable Restraint Systems to Capture Fox in Central Spain. J. Wildl. Manage. 74, 181–187. https://doi.org/10.2193/2008-603

Muñoz, A., Bonal, R., Díaz, M., 2009. Ungulates, rodents, shrubs: interactions in a diverse Mediterranean ecosystem. Basic Appl. Ecol. 10, 151–160. https://doi.org/10.1016/j.baae.2008.01.003

Mur, L., Boadella, M., Martínez-López, B., Gallardo, C., Gortazar, C., Sánchez-Vizcaíno, J.M., 2012. Monitoring of African Swine Fever in the Wild Boar Population of the Most Recent Endemic Area of Spain. Transbound. Emerg. Dis. 59, 526–531. https://doi.org/10.1111/j.1865-1682.2012.01308.x

Muriel, R., Morandini, V., Ferrer, M., Balbontín, J., 2015. Independence and juvenile dispersal distances in wild and reintroduced Spanish imperial eagles. Biol. Conserv. 191, 300–305. https://doi.org/10.1016/j.biocon.2015.07.020

Muriel, R., Morandini, V., Ferrer, M., Balbontín, J., Morlanes, V., 2016. Juvenile dispersal behaviour and conspecific attraction: an alternative approach with translocated Spanish imperial eagles. Anim. Behav. 116, 17–29. https://doi.org/10.1016/j.anbehav.2016.03.023

Navarro-González, N., Casas-Díaz, E., Porrero, C.M., Mateos, A., Domínguez, L., Lavín, S., Serrano, E., 2013a. Food-borne zoonotic pathogens and antimicrobial resistance of indicator bacteria in urban wild boars in Barcelona, Spain. Vet. Microbiol. 167, 686–689. https://doi.org/10.1016/j.vetmic.2013.07.037

Navarro-González, N., Fernández-Llario, P., Pérez-Martín, J.E., Mentaberre, G., López-Martín, J.M., Lavín, S., Serrano, E., 2013b. Supplemental feeding drives endoparasite infection in wild boar in Western Spain. Vet. Parasitol. 196, 114–123. https://doi.org/10.1016/j.vetpar.2013.02.019

Navarro-González, N., Mentaberre, G., Porrero, C.M., Serrano, E., Mateos, A., López-Martín, J.M., Lavín, S., Domínguez, L., 2012. Effect of Cattle on *Salmonella Carriage*, Diversity and Antimicrobial Resistance in Free-Ranging Wild Boar (*Sus scrofa*) in Northeastern Spain. PLoS One 7, e51614. https://doi.org/10.1371/journal.pone.0051614

Navarro-González, N., Porrero, M.C., Mentaberre, G., Serrano, E., Mateos, A., Domínguez, L., Lavín, S., 2013c. Antimicrobial resistance in indicator Escherichia coli isolates from free-ranging livestock and sympatric wild ungulates in a natural environment (Northeastern Spain). Appl. Environ. Microbiol. 79, 6184–6186. https://doi.org/10.1128/AEM.01745-13

Navarro-González, N., Ugarte-Ruiz, M., Porrero, M.C., Zamora, L., Mentaberre, G., Serrano, E., Mateos, A., Lavín, S., Domínguez, L., 2014. Campylobacter shared between free-ranging cattle and sympatric wild ungulates in a natural environment (NE Spain). Ecohealth 11, 333–342. https://doi.org/10.1007/s10393-014-0921-3

Naves, J., Wiegand, T., Revilla, E., Delibes, M., Luisa, M., 2003. Endangered Species Constrained by Natural and Human Factors: the Case of Brown Bears in Northern Spain. Conserv. Biol. 17, 1276–1289.

Nicolas, M., Alvarez, M., Anel, E., Martínez, F., Borragán, S., Martínez-Pastor, F., de Paz, P., Anel, L., 2012. Spermatozoa recovery and post-thawing quality of brown bear ejaculates is affected for centrifugation regimes. Eur. J. Wildl. Res. 58, 77–84. https://doi.org/10.1007/s10344-011-0544-8

Noguera, J.C., Pérez, I., Mínguez, E., 2010. Impact of terrestrial wind farms on diurnal raptors: Developing a spatial vulnerability index and potential vulnerability maps. Ardeola 57, 41–53.

Olano, M., Beñaran, H., Laso, M., Arizaga, J., 2016. Exotic Pine Plantations and the Conservation of the Threatened Red Kite *Milvus milvus* in Gipuzkoa, Northern Iberia. Ardeola 63, 369–374. https://doi.org/10.13157/arla.63.2.2016.sc3

Olea, P.P., Mateo-Tomás, P., 2014. Living in risky landscapes: Delineating management units in multithreat environments for effective species conservation. J. Appl. Ecol. 51, 42–52. https://doi.org/10.1111/1365-2664.12176

Olea, P.P., Mateo-Tomás, P., 2013. Assessing Species Habitat Using Google Street View: A Case Study of Cliff-Nesting Vultures. PLoS One 8, e54582. https://doi.org/10.1371/journal.pone.0054582

Olea, P.P., Mateo-Tomás, P., 2011. Spatially explicit estimation of occupancy, detection probability and survey effort needed to inform conservation planning. Divers. Distrib. 17, 714–724. https://doi.org/10.1111/j.1472-4642.2011.00777.x

Olea, P.P., Mateo-Tomás, P., 2009. The role of traditional farming practices in ecosystem conservation: The case of transhumance and vultures. Biol. Conserv. 142, 1844–1853. https://doi.org/10.1016/j.biocon.2009.03.024

Oleaga, A., Alasaad, S., Rossi, L., Casais, R., Vicente, J., Maione, S., Soriguer, R.C., Gortázar, C., 2013. Genetic epidemiology of *Sarcoptes scabiei* in the Iberian wolf in Asturias, Spain. Vet. Parasitol. 196, 453–459. https://doi.org/10.1016/j.vetpar.2013.04.016

Oleaga, Á., Casais, R., Balseiro, A., Espí, A., Llaneza, L., Hartasánchez, A., Gortázar, C., 2011. New techniques for an old disease: Sarcoptic mange in the Iberian wolf. Vet. Parasitol. 181, 255–266. https://doi.org/10.1016/j.vetpar.2011.04.036

Oleaga, A., Vicente, J., Ferroglio, E., Pegoraro de Macedo, M.R., Casais, R., del Cerro, A., Espí, A., García, E.J., Gortázar, C., 2015.

Concomitance and interactions of pathogens in the Iberian wolf (*Canis lupus*). Res. Vet. Sci. 101, 22–27. https://doi.org/10.1016/j.rvsc.2015.05.010

Ordiz, A., Rodríguez, C., Naves, J., Fernández, A., Huber, D., Kaczensky, P., Mertens, A., Mertzanis, Y., Mustoni, A., Palazón, S., Quenette, P.Y., Rauer, G., Swenson, J.E., 2007. Distance-based criteria to identify minimum number of brown bear females with cubs in Europe. Ursus 18, 158–167. https://doi.org/10.2192/1537-6176(2007)18[158:DCTIMN]2.0.CO;2

Oro, D., Margalida, A., Carrete, M., Heredia, R., Donázar, J.A., 2008. Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. PLoS One 3, e4084. https://doi.org/10.1371/journal.pone.0004084

Ortega, E., Mañosa, S., Margalida, A., Sánchez, R., Oria, J., González, L.M., 2009. A demographic description of the recovery of the vulnerable spanish imperial eagle *Aquila adalberti*. ORYX 43, 113–121. https://doi.org/10.1017/S0030605307991048

Pain, D.J., Meharg, A.A., Ferrer, M., Taggart, M., Penteriani, V., 2005. Lead concentrations in bones and feathers of the globally threatened Spanish imperial eagle. Biol. Conserv. 121, 603–610. https://doi.org/10.1016/j.biocon.2004.06.012

Palacio, S., Bueno, C.G., Azorín, J., Maestro, M., Gómez-García, D., 2013. Wild-boar disturbance increases nutrient and C stores of geophytes in subalpine grasslands. Am. J. Bot. 100, 1790–1799. https://doi.org/10.3732/ajb.1300002

Palacios, V., López-Bao, J.V., Llaneza, L., Fernández, C., Font, E., 2016. Decoding Group Vocalizations: The Acoustic Energy Distribution of Chorus Howls Is Useful to Determine Wolf Reproduction. PLoS One 11. https://doi.org/10.1371/journal.pone.0153858

Palomares, F., Godoy, J.A., Piriz, A., O'Brien, S.J., Johnson, W.E., 2002. Faecal genetic analysis to determine the presence and distribution of elusive carnivores: design and feasibility for the Iberian lynx. Mol. Ecol. 11, 2171–2182. https://doi.org/10.1046/j.1365-294X.2002.01608.x

Palomero, G., Ballesteros, F., Nores, C., Blanco, J.C., Herrero, J., García-Serrano, A., 2007. Trends in number and distribution of brown bear females with cubs-of-the-year in the Cantabrian Mountains, Spain. Ursus 18, 145–157. https://doi.org/10.2192/1537-6176(2007)18[145:TINADO]2.0.CO;2

Palomino, D., Carrascal, L.M., 2007. Habitat associations of a raptor community in a mosaic landscape of Central Spain under urban development. Landsc. Urban Plan. 83, 268–274. https://doi.org/10.1016/j.landurbplan.2007.04.011

Palomo, I., Martín-López, B., Alcorlo, P., Montes, C., 2014. Limitations of Protected Areas Zoning in Mediterranean Cultural Landscapes Under the Ecosystem Services Approach. Ecosystems 17, 1202–1215. https://doi.org/10.1007/s10021-014-9788-y

Paracuellos, M., 2006. Relationships of songbird occupation with habitat configuration and bird abundance in patchy reed beds. Ardea 94, 87–98.

Patón, D., Romero, F., Cuenca, J., Escudero, J.C., 2012. Tolerance to noise in 91 bird species from 27 urban gardens of Iberian Peninsula. Landsc. Urban Plan. 104, 1–8. https://doi.org/10.1016/j.landurbplan.2011.09.002

Penteriani, V., Otalora, F., Ferrer, M., 2008. Floater mortality within settlement areas can explain the Allee effect in breeding populations. Ecol. Modell. 213, 98–104. https://doi.org/10.1016/j.ecolmodel.2007.11.009

Penteriani, V., Otalora, F., Sergio, F., Ferrer, M., 2005. Environmental stochasticity in dispersal areas can explain the "mysterious" disappearance of breeding populations. Proc.

R. Soc. B Biol. Sci. 275, 1265–1269. https://doi.org/10.1098/rspb.2005.3075

Perea, R., Delibes, M., Polko, M., Suárez-Esteban, A., Fedriani, J.M., 2013. Context-dependent fruit-frugivore interactions: Partner identities and spatio-temporal variations. Oikos 122, 943–951. https://doi.org/10.1111/j.1600-0706.2012.20940.x

Perea, R., Gil, L., 2014. Tree regeneration under high levels of wild ungulates: The use of chemically vs. physically-defended shrubs. For. Ecol. Manage. 312, 47–54. https://doi.org/10.1016/j.foreco.2013.10.022

Peredo, A., Martínez, D., Rodríguez-Pérez, J., García, D., 2013. Mammalian seed dispersal in Cantabrian woodland pastures: Network structure and response to forest loss. Basic Appl. Ecol. 14, 378–386. https://doi.org/10.1016/j.baae.2013.05.003

Pereira, M., Rodríguez, A., 2010. Conservation value of linear woody remnants for two forest carnivores in a Mediterranean agricultural landscape. J. Appl. Ecol. 47, 611–620. https://doi.org/10.1111/j.1365-2664.2010.01804.x

Pérez-García, J.M., Sebastián-González, E., Botella, F., Sánchez-Zapata, J.A., 2016. Selecting indicator species of infrastructure impacts using network analysis and biological traits: Bird electrocution and power lines. Ecol. Indic. 60, 428–433. https://doi.org/10.1016/j.ecolind.2015.07.020

Pérez, T., Naves, J., Vázquez, J.F., Fernández-Gil, A., Seijas, J., Albornoz, J., Revilla, E., Delibes, M., Domínguez, A., 2014. Estimating the population size of the endangered Cantabrian brown bear through genetic sampling. Wildlife Biol. 20, 300–309. https://doi.org/10.2981/wlb.00069

Pérez, T., Naves, J., Vázquez, J.F., Seijas, J., Corao, A., Albornoz, J., Domínguez, A., 2010. Evidence for improved connectivity between Cantabrian brown bear subpopulations. Ursus 21, 104–108. https://doi.org/10.2192/09SC018.1

Pérez, T., Vázquez, F., Naves, J., Fernández, A., Corao, A., Albornoz, J., Domínguez, A., 2009. Non-invasive genetic study of the endangered Cantabrian brown bear (*Ursus arctos*). Conserv. Genet. 10, 291–301. https://doi.org/10.1007/s10592-008-9578-1

Peris, S., Morales, J., 2004. Use of passages across a canal by wild mammals and related mortality. Eur. J. Wildl. Res. 50, 67–72. https://doi.org/10.1007/s10344-004-0045-0

Piñeiro, A., Barja, I., Otero, G.P., Silván, G., Illera, J.C., 2015. No Effects of Habitat, Prey Abundance and Competitor Carnivore Abundance on Fecal Cortisol Metabolite Levels in Wildcats (*Felis silvestris*). Ann. Zool. Fennici 52, 90–102. https://doi.org/10.5735/086.052.0208

Pita, M., Casas, S., Herrero, J., Prada, C., García, R., 2012. Game Reserves in Spain: the public management of hunting. For. Syst. 21, 398–404. https://doi.org/10.5424/fs/2012213-02343

Portillo, A., Pérez-Martínez, L., Santibáñez, S., Santibáñez, P., Palomar, A.M., Oteo, J.A., 2011. *Anaplasma* spp. in Wild Mammals and *Ixodes ricinus* from the North of Spain. Vector-Borne Zoonotic Dis. 11, 3–8. https://doi.org/10.1089/vbz.2009.0214

Puerta-Piñero, C., 2010. Intermediate spatial variations on acorn predation shapes Holm oak establishment within a Mediterranean landscape context. Plant Ecol. 210, 213–224. https://doi.org/10.1007/s11258-010-9750-9

Puerta-Piñero, C., Sánchez-Miranda, A., Leverkus, A., Castro, J., 2010. Management of burnt wood after fire affects post-dispersal acorn predation. For. Ecol. Manage. 260, 345–352. https://doi.org/10.1016/j.foreco.2010.04.023

Puig, J., Ariño, A.H., Sanz, L., 2012. The link between roadkills distribution and the surrounding landscape in two highways in Navarre, Spain. Environ. Eng. Manag. J. 11, 1171–1178.

Ramirez, O., Altet, L., Enseñat, C., Vilà, C., Sanchez, A., Ruiz, A., 2006. Genetic assessment of the Iberian wolf *Canis lupus* signatus captive breeding program. Conserv. Genet. 7, 861–878. https://doi.org/10.1007/s10592-006-9123-z

Ramírez, O., Burgos-Paz, W., Casas, E., Ballester, M., Bianco, E., Olalde, I., Santpere, G., Novella, V., Gut, M., Lalueza-Fox, C., Saña, M., Pérez-Enciso, M., 2015. Genome data from a sixteenth century pig illuminate modern breed relationships. Heredity (Edinb). 114, 175–184. https://doi.org/10.1038/hdy.2014.81

Rasero, R., Rossi, L., Soglia, D., Maione, S., Sacchi, P., Rambozzi, L., Sartore, S., Soriguer, R.C., Spalenza, V., Alasaad, S., 2010. Host taxon-derived *Sarcoptes* mite in European wild animals revealed by microsatellite markers. Biol. Conserv. 143, 1269–1277. https://doi.org/10.1016/j.biocon.2010.03.001

Recio, M.R., Arija, C.M., Cabezas-Díaz, S., Virgós, E., 2015. Changes in Mediterranean mesocarnivore communities along urban and ex-urban gradients. Curr. Zool. 61, 793–801. https://doi.org/10.1093/czoolo/61.5.793

Recio, M.R., Virgós, E., 2010. Predictive niche modelling to identify potential areas of conflicts between human activities and expanding predator populations: A case study of game management and the grey mongoose, *Herpestes ichneumon*, in Spain. Wildl. Res. 37, 343–354. https://doi.org/10.1071/WR09096

Reque, J.A., Martin, E., 2015. Designing acorn protection for direct seeding of quercus species in high predation areas. For. Syst. 24, 5 pages. https://doi.org/http://dx.doi.org/10.5424/fs/2015241-05632

Requena-Mullor, J.M., López, E., Castro, A.J., Cabello, J., Virgós, E., González-Miras, E., Castro, H., 2014. Modeling spatial distribution of European badger in arid landscapes: an ecosystem functioning approach. Landsc. Ecol. 29, 843–855. https://doi.org/10.1007/s10980-014-0020-4

Revilla, E., Palomares, F., Delibes, M., 2001. Edge-core effects and the effectiveness of traditional reserves in conservation: Eurasian badgers in Doñana National Park. Conserv. Biol. 15, 148–158. https://doi.org/10.1046/j.1523-1739.2001.99431.x

Revilla, E., Palomares, F., Delibes, M., 2000. Defining key habitats for low density populations of Eurasian badgers in Mediterranean environments. Biol. Conserv. 95, 269–277. https://doi.org/10.1016/S0006-3207(00)00043-4

Risco, D., Salguero, F.J., Cerrato, R., Gutierrez-Merino, J., Lanham-New, S., Barquero-Pérez, O., Hermoso De Mendoza, J., Fernández-Llario, P., 2016. Association between vitamin D supplementation and severity of tuberculosis in wild boar and red deer. Res. Vet. Sci. 108, 116–119. https://doi.org/10.1016/j.rvsc.2016.08.003

Rivière, J., Carabin, K., Le Strat, Y., Hendrikx, P., Dufour, B., 2014. Bovine tuberculosis surveillance in cattle and free-ranging wildlife in EU Member States in 2013: A survey-based review. Vet. Microbiol. 173, 323–331. https://doi.org/10.1016/j.vetmic.2014.08.013

Rodríguez-Freire, M., Crecente-Maseda, R., 2008. Directional connectivity of wolf (<i>Canis lupus<i>) populations in northwest Spain and anthropogenic effects on dispersal patterns. Environ. Model. Assess. 13. https://doi.org/10.1007/s10666-006-9078-y

Rodriguez-Ramos Fernandez, J., Höfle, U., Mateo, R., Nicolas De Francisco, O., Abbott, R., Acevedo, P., Blanco, J.M., 2011. Assessment of lead exposure in Spanish imperial eagle (*Aquila adalberti*) from spent ammunition in central Spain. Ecotoxicology 20, 670–681. https://doi.org/10.1007/s10646-011-0607-3

Rodríguez, B., Rodríguez, A., Siverio, F., Siverio, M., 2010. Causes of Raptor Admissions to a Wildlife Rehabilitation Center in Tenerife (Canary Islands). J. Raptor Res. 44, 30–39.

https://doi.org/10.3356/JRR-09-40.1

Rodríguez, B., Siverio, F., Siverio, M., Barone, R., Rodríguez, A., 2015. Nectar and pollen of the invasive century plant Agave americana as a food resource for endemic birds. Bird Study 1–11. https://doi.org/10.1080/00063657.2015.1015484

Rodríguez, C., Naves, J., Fernández-Gil, A., Obeso, J.R., Delibes, M., 2007. Long-term trends in food habits of a relict brown bear population in northern Spain: the influence of climate and local factors. Environ. Conserv. 34, 36–44. https://doi.org/10.1017/S0376892906003535

Romero, B., Aranaz, A., Sandoval, Á., Álvarez, J., de Juan, L., Bezos, J., Sánchez, C., Galka, M., Fernández, P., Mateos, A., Domínguez, L., 2008. Persistence and molecular evolution of *Mycobacterium bovis* population from cattle and wildlife in Doñana National Park revealed by genotype variation. Vet. Microbiol. 132, 87–95. https://doi.org/10.1016/j.vetmic.2008.04.032

Romero, D., Olivero, J., Brito, J.C., Real, R., 2016. Comparison of approaches to combine species distribution models based on different sets of predictors. Ecography (Cop.). 39, 561–571. https://doi.org/10.1111/ecog.01477

Roques, S., Negro, J.J., 2005. MtDNA genetic diversity and population history of a dwindling raptorial bird, the red kite (*Milvus milvus*). Biol. Conserv. 126, 41–50. https://doi.org/10.1016/j.biocon.2005.04.020

Rosell, C., Navàs, F., Romero, S., 2012. Reproduction of wild boar in a cropland and coastal wetland area: implications for management. Anim. Biodivers. Conserv. 35, 209–217.

Rost, J., Pons, P., Bas, J.M., 2012. Seed dispersal by carnivorous mammals into burnt forests: An opportunity for non-indigenous and cultivated plant species. Basic Appl. Ecol. 13, 623–630. https://doi.org/10.1016/j.baae.2012.08.016

Rotllan-Puig, X., Traveset, A., 2016. Declining relict plants: Climate effect or seed dispersal disruption? A landscape-scale approach. Basic Appl. Ecol. 17, 81–91. https://doi.org/10.1016/j.baae.2015.08.003

Ruiz-Capillas, P., Mata, C., Malo, J.E., 2013. Community Response of Mammalian Predators and Their Prey to Motorways: Implications for Predator-Prey Dynamics. Ecosystems 16, 617–626. https://doi.org/10.1007/s10021-013-9634-7

Ruiz-Fons, F., Vidal, D., Vicente, J., Acevedo, P., Fernández-De-Mera, I.G., Montoro, V., Gortázar, C., 2008. Epidemiological risk factors of Aujeszky's disease in wild boars (*Sus scrofa*) and domestic pigs in Spain. Eur. J. Wildl. Res. 54, 549–555. https://doi.org/10.1007/s10344-008-0179-6

Ruiz-González, A., Gurrutxaga, M., Cushman, S.A., Madeira, M.J., Randi, E., Gómez-Moliner, B.J., 2014. Landscape genetics for the empirical assessment of resistance surfaces: The European pine marten (*Martes martes*) as a target-species of a regional ecological network. PLoS One 9. https://doi.org/10.1371/journal.pone.0110552

Ruiz-Olmo, J., Blanch, F., Vidal, F., 2003. Relationships between the Red Fox and Waterbirds in the Ebro Delta Natural Park, N.E. Spain. Waterbirds 26, 217–225.

Ruiz-Suárez, N., Henríquez-Hernández, L.A., Valerón, P.F., Boada, L.D., Zumbado, M., Camacho, M., Almeida-González, M., Luzardo, O.P., 2014. Assessment of anticoagulant rodenticide exposure in six raptor species from the Canary Islands (Spain). Sci. Total Environ. 485–486, 371–376. https://doi.org/10.1016/j.scitotenv.2014.03.094

Sáenz-de-Santa-María, A., Tellería, J.L., 2015. Wildlife-vehicle collisions in Spain. Eur. J. Wildl. Res. https://doi.org/10.1007/s10344-015-0907-7

Salinas, J., Caro, M.R., Vicente, J., Cuello, F., Reyes-Garcia, A.R., Buendía, A.J., Rodolakis, A., Gortázar, C., 2009. High prevalence of antibodies against *Chlamydiaceae* and *Chlamydophila abortus* in wild ungulates using two "in house" blocking-ELISA tests. Vet. Microbiol. 135, 46–53. https://doi.org/10.1016/j.vetmic.2008.10.001

Salvatori, V., Mertens, A.D., 2012. Damage prevention methods in Europe: experiences from LIFE nature projects. Hystrix, Ital. J. Mammal. 23, 73–79. https://doi.org/10.4404/hystrix-23.1-4548

Sánchez-Oliver, J.S., Rey Benayas, J.M., Carrascal, L.M., 2014. Local habitat and landscape influence predation of bird nests on afforested Mediterranean cropland. Acta Oecologica 58, 35–43. https://doi.org/10.1016/j.actao.2014.05.001

Santos, T., Tellería, J.L., Díaz, M., Carbonell, R., 2006. Evaluating the benefits of CAP reforms: Can afforestations restore bird diversity in Mediterranean Spain? Basic Appl. Ecol. 7, 483–495. https://doi.org/10.1016/j.baae.2005.11.001

Sanz-Aguilar, A., Sánchez-Zapata, J.A., Carrete, M., Benítez, J.R., Ávila, E., Arenas, R., Donázar, J.A., 2015. Action on multiple fronts, illegal poisoning and wind farm planning, is required to reverse the decline of the Egyptian vulture in southern Spain. Biol. Conserv. 187, 10–18. https://doi.org/10.1016/j.biocon.2015.03.029

Sarasa, M., Sarasa, J.-A., 2013. Intensive monitoring suggests population oscillations and migration in wild boar *Sus scrofa* in the Pyrenees. Anim. Biodivers. Conserv. 36, 79–88.

Sastre, N., Francino, O., Ramírez, O., Enseñat, C., Sánchez, A., Altet, L., 2008. Detection of *Leishmania infantum* in captive wolves from Southwestern Europe. Vet. Parasitol. 158, 117–120. https://doi.org/10.1016/j.vetpar.2008.08.008

Sastre, N., Vilà, C., Salinas, M., Bologov, V. V., Urios, V., Sánchez, A., Francino, O., Ramírez, O., 2011. Signatures of demographic bottlenecks in European wolf populations. Conserv. Genet. 12, 701–712. https://doi.org/10.1007/s10592-010-0177-6

Sebastián-González, E., Moleón, M., Gibert, J.P., Botella, F., Mateo-Tomás, P., Olea, P.P., Guimarães Jr., P.R., Sánchez-Zapata, J., 2015. Nested species-rich networks of scavenging vertebrates support high levels of interspecific competition. Ecology 97, 95–105. https://doi.org/10.1890/15-0212.1

Sebastián-González, E., Sánchez-Zapata, J.A., Donázar, J.A., Selva, N., Cortés-Avizanda, A., Hiraldo, F., Blázquez, M., Botella, F., Moleón, M., 2013. Interactive effects of obligate scavengers and scavenger community richness on lagomorph carcass consumption patterns. Ibis (Lond. 1859). 155, 881–885. https://doi.org/10.1111/ibi.12079

Segura, A., Acevedo, P., Rodríguez, O., Naves, J., Obeso, J.R., 2014. Biotic and abiotic factors modulating wild boar relative abundance in Atlantic Spain. Eur. J. Wildl. Res. 60, 469–476.

Seoane, J., Carrascal, L.M., 2008. Interspecific differences in population trends of Spanish birds are related to habitat and climatic preferences. Glob. Ecol. Biogeogr. 17, 111–121. https://doi.org/10.1111/j.1466-8238.2007.00351.x

Seoane, J., Viñuela, J., Díaz-Delgado, R., Bustamante, J., 2003. The effects of land use and climate on red kite distribution in the Iberian peninsula. Biol. Conserv. 111, 401–414. https://doi.org/10.1016/S0006-3207(02)00309-9

Sergio, F., Blas, J., Baos, R., Forero, M.G., Donázar, J.A., Hiraldo, F., 2009. Short- and long-term consequences of individual and territory quality in a long-lived bird. Oecologia 160, 507–514. https://doi.org/10.1007/s00442-009-1314-0

Sergio, F., Blas, J., Forero, M., Fernández, N., Donázar, J.A., Hiraldo, F., 2005. Preservation of wide-ranging top predators by site-protection: Black and red kites in Doñana National Park. Biol. Conserv. 125, 11–21. https://doi.org/10.1016/j.biocon.2005.03.002

Sergio, F., Tavecchia, G., Tanferna, A., López Jiménez, L., Blas, J., De Stephanis, R., Marchant, T.A., Kumar, N., Hiraldo, F., 2015. No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. J. Appl. Ecol. 52, 1665–1675. https://doi.org/10.1111/1365-2664.12520

Skoglund, P., Götherström, A., Jakobsson, M., 2011. Estimation of population divergence times from non-overlapping genomic sequences: Examples from dogs and wolves. Mol. Biol. Evol. 28, 1505–1517. https://doi.org/10.1093/molbev/msq342

Sobrino, R., Acevedo, P., Escudero, M.A., Marco, J., Gortázar, C., 2009. Carnivore population trends in Spanish agrosystems after the reduction in food availability due to rabbit decline by rabbit haemorrhagic disease and improved waste management. Eur. J. Wildl. Res. 55, 161–165. https://doi.org/10.1007/s10344-008-0230-7

Sobrino, R., Arnal, M.C., Luco, D.F., Gortázar, C., 2008a. Prevalence of antibodies against canine distemper virus and canine parvovirus among foxes and wolves from Spain. Vet. Microbiol. 126, 251–256. https://doi.org/10.1016/j.vetmic.2007.06.014

Sobrino, R., Dubey, J.P., Pabón, M., Linarez, N., Kwok, O.C., Millán, J., Arnal, M.C., Luco, D.F., López-Gatius, F., Thulliez, P., Gortázar, C., Almería, S., 2008b. *Neospora caninum* antibodies in wild carnivores from Spain. Vet. Parasitol. 155, 190–197. https://doi.org/10.1016/j.vetpar.2008.05.009

Sobrino, R., Ferroglio, E., Oleaga, A., Romano, A., Millan, J., Revilla, M., Arnal, M.C., Trisciuoglio, A., Gortázar, C., 2008c. Characterization of widespread canine leishmaniasis among wild carnivores from Spain. Vet. Parasitol. 155, 198–203. https://doi.org/10.1016/j.vetpar.2008.05.003

Sobrino, R., Millán, J., Oleaga, Á., Gortázar, C., de la Fuente, J., Ruiz-Fons, F., 2012. Ecological preferences of exophilic and endophilic ticks (Acari: Ixodidae) parasitizing wild carnivores in the Iberian Peninsula. Vet. Parasitol. 184, 248–257. https://doi.org/10.1016/j.vetpar.2011.09.003

Soutullo, A., Cadahía, L., Urios, V., Ferrer, M., Negro, J.J., 2007. Accuracy of lightweight satellite telemetry: a case study in the Iberian peninsula. J. Wildl. Manage. 71, 1010–1015. https://doi.org/10.2193/2006-042

Suárez-Esteban, A., Delibes, M., Fedriani, J.M., 2013. Unpaved road verges as hotspots of fleshy-fruited shrub recruitment and establishment. Biol. Conserv. 167, 50–56. https://doi.org/10.1016/j.biocon.2013.07.022

Sunyer, P., Muñoz, A., Bonal, R., Espelta, J.M., 2013. The ecology of seed dispersal by small rodents: a role for predator and conspecific scents. Funct. Ecol. 27, 1313–1321. https://doi.org/10.1111/1365-2435.12143

Tanferna, A., López-Jiménez, L., Blas, J., Hiraldo, F., Sergio, F., 2013. Habitat selection by Black kite breeders and floaters: Implications for conservation management of raptor floaters. Biol. Conserv. 160, 1–9. https://doi.org/10.1016/j.biocon.2012.12.031

Tapia, L., Domínguez, J., Rodríguez, L., 2009. Using probability of occurrence to assess potential interaction between wind farms and a residual population of golden eagle *Aquila chrysaetos* in NW Spain. Biodivers. Conserv. 18, 2033–2041. https://doi.org/10.1007/s10531-008-9571-5

Tapia, L., Domínguez, J., Rodríguez, L., 2007. Modelling habitat use and distribution of golden eagles *Aquila chrysaetos* in a low-density area of the Iberian Peninsula. Biodivers. Conserv. 16, 3559–3574. https://doi.org/10.1007/s10531-006-9093-y

Tauler, H., Real, J., Hernández-Matías, A., Aymerich, P., Baucells, J., Martorell, C., Santandreu, J., 2015. Identifying key demographic parameters for the viability of a growing population of the endangered Egyptian Vulture Neophron percnopterus. Bird Conserv. Int. 1–14. https://doi.org/10.1017/S0959270914000392

Tavecchia, G., Adrover, J., Navarro, A.M., Pradel, R., 2012. Modelling mortality causes in longitudinal data in the presence of tag loss: application to raptor poisoning and electrocution. J. Appl. Ecol. 49, 297–305. https://doi.org/10.1111/j.1365-2664.2011.02074.x

Tellería, J.L., 2009a. Overlap between wind power plants and Griffon Vultures *Gyps fulvus* in Spain. Bird Study 56, 268–271. https://doi.org/10.1080/00063650902792056doi.org/10.1080/00063650902792056

Tellería, J.L., 2009b. Wind power plants and the conservation of birds and bats in Spain: A geographical assessment. Biodivers. Conserv. 18, 1781–1791. https://doi.org/10.1007/s10531-008-9558-2

Tintó, A., Real, J., Mañosa, S., 2010. Predicting and Correcting Electrocution of Birds in Mediterranean Areas. J. Wildl. Manage. 74, 1852–1862. https://doi.org/10.2193/2009-521

Torres-Porras, J., Fernández-Llario, P., Carranza, J., Mateos, C., 2015. Conifer plantations negatively affect density of wild boars in a mediterranean ecosystem. Folia Zool. 64, 25–31.

Torres, J., Miquel, J., Casanova, J.C., Ribas, A., Feliu, C., Morand, S., 2006. Endoparasite species richness of Iberian carnivores: influences of host density and range distribution. Biodivers. Conserv. 15, 4619–4632. https://doi.org/10.1007/s10531-005-5824-8

Traveset, A., Riera, N., Mas, R.E., 2001. Ecology of fruit-colour polymorphism in Myrtus communis and differential effects of birds and mammals on seed germination and seedling growth. J. Ecol. 89, 749–760.

Urios, V., Soutullo, A., López-López, P., Cadahía, L., Limiñana, R., Ferrer, M., 2007. The first case of successful breeding of a Golden Eagle *Aquila chrysaetos* tracked from birth by satellite telemetry. Acta Ornitho 42, 205–209.

Valdiosera, C.E., Garcia-Garitagoitia, J.L., Garcia, N., Doadrio, I., Thomas, M.G., Hanni, C., Arsuaga, J.-L., Barnes, I., Hofreiter, M., Orlando, L., Gotherstrom, A., 2008. Surprising migration and population size dynamics in ancient Iberian brown bears (*Ursus arctos*). Proc. Natl. Acad. Sci. 105, 5123–5128. https://doi.org/10.1073/pnas.0712223105

Valenzuela, A., Alcover, J.A., 2015. The chronology of the introduction of two species of *Martes* (Carnivora, Mustelidae) on the Western Mediterranean Islands: first direct radiocarbon evidence. Biol. Invasions 17, 3093–3100. https://doi.org/10.1007/s10530-015-0947-7

Valero, E., Picos, J., Álvarez, X., 2015. Road and traffic factors correlated to wildlife-vehicle collisions in Galicia (Spain). Wildl. Res. 42, 25–34. https://doi.org/10.1071/WR14060

Veličković, N., Ferreira, E., Djan, M., Ernst, M., Obreht Vidaković, D., Monaco, A., Fonseca, C., 2016. Demographic history, current expansion and future management challenges of wild boar populations in the Balkans and Europe. Heredity (Edinb). 1. https://doi.org/10.1038/hdy.2016.53

Vicente-Rubiano, M., Martínez-López, B., Sánchez-Vizcaíno, F., Sánchez-Vizcaíno, J.M., 2014. A new approach for rapidly assessing the risk of aujeszky's disease reintroduction into a disease-free spanish territory by analysing the movement of live pigs and potential contacts with wild boar. Transbound. Emerg. Dis. 61, 350–361. https://doi.org/10.1111/tbed.12041

Vicente, J., Barasona, J.A., Acevedo, P., Ruiz-Fons, J.F., Boadella, M., Diez-Delgado, I., Beltran-Beck, B., González-Barrio, D., Queirós, J., Montoro, V., de la Fuente, J., Gortazar, C., 2013. Temporal trend of tuberculosis in wild ungulates from mediterranean Spain. Transbound. Emerg. Dis. 60, 92–103. https://doi.org/10.1111/tbed.12167

Vicente, J., Höfle, U., Garrido, J.M., Fernádez-De-Mera, I.G., Acevedo, P., Juste, R., Barral, M., Gortazar, C., 2007. Risk factors associated with the prevalence of tuberculosis-like lesions in fenced wild boar and red deer in south central Spain. Vet. Res. 38, 451–464. https://doi.org/10.1051/vetres:2007002

Vicente, J., Höfle, U., Garrido, J.M., Fernández-De-Mera, I.G., Juste, R., Barral, M., Gortazar, C., 2006. Wild boar and red deer display high prevalences of tuberculosis-like lesions in Spain. Vet. Res. 37, 107–119. https://doi.org/10.1051/vetres:2005044

Vidal, D., Naranjo, V., Mateo, R., Gortazar, C., De La Fuente, J., 2006. Analysis of serum biochemical parameters in relation to *Mycobacterium bovis* infection of European wild boars (*Sus scrofa*) in Spain. Eur. J. Wildl. Res. 52, 301–304. https://doi.org/10.1007/s10344-006-0062-2

Vilardell, A., Capalleras, X., Budó, J., Molist, F., Pons, P., 2008. Test of the efficacy of two chemical repellents in the control of Hermann's tortoise nest predation. Eur. J. Wildl. Res. 54, 745–748. https://doi.org/10.1007/s10344-008-0176-9

Vilardell, A., Capalleras, X., Budó, J., Pons, P., 2012. Predator identification and effects of habitat management and fencing on depredation rates of simulated nests of an endangered population of Hermann's tortoises. Eur. J. Wildl. Res. 58, 707–713. https://doi.org/10.1007/s10344-012-0620-8

Virgós, E., 2002a. Are habitat generalists affected by forest fragmentation? A test with Eurasian badgers (*Meles meles*) in coarse-grained fragmented landscapes of central Spain. J. Zool. 258, 313–318. https://doi.org/10.1017/S0952836902001449

Virgós, E., 2002b. Factors affecting wild boar (*Sus scrofa*) occurrence in highly fragmented Mediterranean landscapes. Can. J. Zool. 80, 430–435. https://doi.org/10.1139/z02-028

Virgós, E., 2001a. Relative value of riparian woodlands in landscapes with different forest cover for medium-sized Iberian carnivores. Biodivers. Conserv. 10, 1039–1049. https://doi.org/10.1023/A:1016684428664

Virgós, E., 2001b. Role of isolation and habitat quality in shaping species abundance: a test with badgers (*Meles meles* L.) in a gradient of forest fragmentation. J. Biogeogr. 28, 381–389. https://doi.org/10.1046/j.1365-2699.2001.00552.x

Virgós, E., Cabezas-Díaz, S., Mangas, J.G., Lozano, J., 2010. Spatial distribution models in a frugivorous carnivore, the stone marten (*Martes foina*): Is the fleshy-fruit availability a useful predictor? Anim. Biol. 60, 423–436. https://doi.org/10.1163/157075610X523297

Virgós, E., García, F.J., 2002. Patch occupancy by stone martens *Martes foina* in fragmented landscapes of central Spain: The role of fragment size, isolation and habitat structure. Acta Oecologica 23, 231–237. https://doi.org/10.1016/S1146-609X(02)01142-6

Virgós, E., Tellería, J.L., Santos, T., 2002. A comparison on the response to forest fragmentation by medium-sized Iberian carnivores in central Spain. Biodivers. Conserv. 11, 1063–1079.

Virgós, E., Travaini, A., 2005. Relationship between small-game hunting and carnivore diversity in central Spain. Biodivers. Conserv. 14, 3475–3486. https://doi.org/10.1007/s10531-004-0823-8

Wiegand, T., Naves, J., Martín, G., Fernández, N., 2008. Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. Ecol. Monogr. 78, 87–103.

Zamora, M.J., Alvarez, M., Olmedo, J., Blanco, M.C., Pozio, E., 2015. *Trichinella* *pseudospiralis* in the Iberian peninsula. Vet. Parasitol. 210, 255–259. https://doi.org/10.1016/j.vetpar.2015.04.004

Zorrilla, I., Martinez, R., Taggart, M.A., Richards, N., 2015. Suspected flunixin poisoning of a wild Eurasian Griffon Vulture from Spain. Conserv. Biol. 29, 587–592. https://doi.org/10.1111/cobi.12417

Zuberogoitia, I., del Real, J., Torres, J.J., Rodríguez, L., Alonso, M., de Alba, V., Azahara, C., Zabala, J., 2015. Testing pole barriers as feasible mitigation measure to avoid bird vehicle collisions (BVC). Ecol. Eng. 83, 144–151. https://doi.org/10.1016/j.ecoleng.2015.06.026

Zuberogoitia, I., Del Real, J., Torres, J.J., Rodríguez, L., Alonso, M., Zabala, J., 2014a. Ungulate vehicle collisions in a peri-urban environment: Consequences of transportation infrastructures planned assuming the absence of ungulates. PLoS One 9. https://doi.org/10.1371/journal.pone.0107713

Zuberogoitia, I., González-Oreja, J.A., Martínez, J.E., Zabala, J., Gómez, I., López-López, P., 2013. Foraging movements of Eurasian griffon vultures (*Gyps fulvus*): Implications for supplementary feeding management. Eur. J. Wildl. Res. 59, 421–429. https://doi.org/10.1007/s10344-012-0687-2

Zuberogoitia, I., Martínez, J.E., Zabala, J., Belamendia, G., Calvo, J.F., 2012. Solitary hunters sharing an abundant trophic resource: simultaneous hunting by raptors at a brambling winter roost. J. Raptor Res. 46, 318–322. https://doi.org/10.3356/JRR-11-74.1

Zuberogoitia, I., Zabala, J., Martínez, J.A., Martínez, J.E., Azkona, A., 2008. Effect of human activities on Egyptian vulture breeding success. Anim. Conserv. 11, 313–320. https://doi.org/10.1111/j.1469-1795.2008.00184.x

Zuberogoitia, I., Zabala, J., Martínez, J.E., González-Oreja, J.A., López-López, P., 2014b. Effective conservation measures to mitigate the impact of human disturbances on the endangered Egyptian vulture. Anim. Conserv. 17, 410–418. https://doi.org/10.1111/acv.12107

APPENDIX C.
DETAILED DESCRIPTION OF THE CALCULATION OF INDICATORS AND INDICES

An index was created for each source of information by species: photography, wildlife-based tourism, outreach magazines, the GBIF, scientific articles and Google Trends. The indices were created transforming the indicators measured. The 12 indicators were scaled between 0 and 1. Assigning value 1 to the species with greater value for the indicator and pondering the value for the rest of the species. For those source of information for which more than one indicator was measured (i.e. photography, wildlife-based tourism, outreach magazines and the GBIF; Table 1), we summed up the scaled indicators which constitute them, giving a value comprising between 0-3 for those sources of information with 3 indicators (photography and outreach magazines), and giving a value comprising between 0-2 for the sources of information with 2 indicators (wildlife-based tourism and the GBIF). Then, the resulting sum was scaled between 0 and 1, assigning value 1 to the species with greater value for the sum of indicators and pondering the rest.

Case with 3 indicators (I) measured by source of information:

$I_A+I_B+I_C = 0\text{-}3 \rightarrow \text{Index } 0\text{-}1$

Case with 2 indicators (I) measured by source of information:

$I_A+I_B = 0\text{-}2 \rightarrow \text{Index } 0\text{-}1$

Figure C1. Graphical description of the index's calculation.

APPENDIX D.
SUPPLEMENTARY TABLES

Table D1. List of scavenger species included in this study and traits used as explanatory variables in the canonical correspondence analysis.

Common name	Scientific name	Taxonomic group	Conservation status	Body mass	Foraging activity	Home range	Fecundity	Diel activity
Bearded vulture	*Gypaetus barbatus*	vultures	1	1.95	0	4	1.1	diurnal
Griffon vulture	*Gyps fulvus*	vultures	0	2.25	1	4	0.69	diurnal
Egyptian vulture	*Neophron percnopterus*	vultures	1	1.1	0	4	1.1	diurnal
Cinereous vulture	*Aegypius monachus*	vultures	1	2.38	1	4	0.69	diurnal
Golden eagle	*Aquila chrysaetos*	other raptors	0	1.61	0	2	1.39	diurnal
Spanish imperial eagle	*Aquila adalberti*	other raptors	1	1.39	0	2	1.61	diurnal
Black kite	*Milvus migrans*	other raptors	0	0.56	1	1	1.61	diurnal
Red kite	*Milvus milvus*	other raptors	1	0.69	1	1	1.61	diurnal
Common buzzard	*Buteo buteo*	other raptors	0	0.55	0	1	1.79	diurnal
Western marsh harrier	*Circus aeruginosus*	other raptors	0	0.47	0	1	2.08	diurnal
Raven	*Corvus corax*	corvids	0	1.1	1	1	2.2	diurnal
Carrion crow	*Corvus corone*	corvids	0	0.47	1	1	2.08	diurnal
Magpie	*Pica pica*	corvids	0	0.22	1	1	2.3	diurnal
Gray wolf	*Canis lupus*	mammals	0	3.43	1	3	2.4	nocturnal
Brown bear	*Ursus arctos*	mammals	1	4.94	0	3	0.92	both
Red fox	*Vulpes vulpes*	mammals	0	1.95	0	2	2.56	both
Stone marten	*Martes foina*	mammals	0	0.79	0	2	2.2	nocturnal
Pine marten	*Martes martes*	mammals	0	1.06	0	2	2.2	nocturnal
Common genet	*Genetta genetta*	mammals	0	1.06	0	1	1.61	nocturnal
Eurasian badger	*Meles meles*	mammals	0	2.12	0	2	1.79	nocturnal
Egyptian mongoose	*Herpestes ichneumon*	mammals	0	1.45	0	1	1.61	diurnal
Wild boar	*Sus scrofa*	mammals	0	3.99	1	2	2.3	nocturnal

Species detected in the monitoring of the consumption of carcasses using cameras traps. See García-Heras et al., (2011), Mateo-Tomás et al., (2015), Sebastián-González et al., (2016) for a more detailed description of the monitoring and the study areas. Based on Morales-Reyes et al., (2018). Conservation status (1 = threatened species: i.e., listed as 'Critically Endangered', 'Endangered' or 'Vulnerable'; 0 = non-threatened species: i.e., listed as 'Near Threatened' or 'Least Concern') according to IUCN (2017). See Table D.2 for a detailed description of functional traits.

REFERENCES

García-Heras, M.S., Cortés-Avizanda, A. & Donázar, J.A. 2013. Who are we feeding? Asymmetric individual use of surplus food resources in an insular population of the endangered Egyptian vulture Neophron percnopterus. PLoS One 8, e80523.

IUCN. 2017. The IUCN red list of threatened species. Version 2017-3. Available at: http://www.iucnredlist.org/.

Mateo-Tomás, P., Olea, P.P., Moleón, M., Vicente, J., Botella, F., Selva, N., Viñuela, J. & Sánchez-Zapata, J.A. 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Divers. Distrib. 21, 913–924.

Morales-Reyes, Z., Martín-López, B., Moleón, M., Mateo-Tomás, P., Botella, F., Margalida, A., Donázar, J.A., Blanco, G., Pérez, I., Sánchez-Zapata, J.A., 2018. Farmer Perceptions of the Ecosystem Services Provided by Scavengers: What, Who, and to Whom. Conserv. Lett. 11, e12392.

Sebastián-González, E., Moleón, M., Gibert, J.P., Botella, F., Mateo-Tomás, P., Olea, P.P., Guimarães, P.R. & Sánchez-Zapata, J.A. 2016. Nested species-rich networks of scavenging vertebrates support high levels of interspecific competition. Ecology 97, 95–105.

Table D2. List of functional traits for which data were collected on the scavenger species. Based on Luck *et al.*, (2012).

Characteristics	Description
Body mass	Average adult (female and male) weight, in kg. Ln (x+1) transformation was applied to avoid heteroskedasticity
Foraging activity	Foraging in large groups, i.e., social (*1*); foraging alone or in pairs, i.e., solitary (*0*)
Home range	Adult home range normally <10 km^2 (*1*); 10-100 km^2 (*2*); 100-1000 km^2 (*3*); >1000 km^2 (*4*)
Fecundity	Maximum number of offspring per female and year. Ln (x+1) transformation was applied to avoid heteroskedasticity
Diel activity	Mostly nocturnal (*nocturnal*); mostly diurnal (*diurnal*); both nocturnal and diurnal (*both*)

REFERENCES

del Hoyo, J., Elliott, A., Sargatal, J. 1996. Handbook of the Birds of the World. Hoatzin to Auks. Vol. 3. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A., Christie, D.A. 2009. Handbook of the Birds of the World. Bush-shrikes to Old World Sparrows. Vol. 14. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A., Sargatal, J. 1994. Handbook of the Birds of the World. New World Vultures to Guineafowl. Vol. 2. Lynx Edicions, Barcelona.

Luck, G.W., Lavorel, S., McIntyre, S., Lumb, K. 2012. Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. J. Anim. Ecol. 81, 1065–1076.

Wilson, D.E., Mittermeier, R.A. 2009. Handbook of the Mammals of the World. Carnivores. Vol. 1. Lynx Edicions, Barcelona.

Wilson, D.E., Mittermeier, R.A. 2011. Handbook of the Mammals of the World. Hoofed Mammals. Vol. 2. Lynx Edicions, Barcelona

Table D3. Summary statistics and results of the canonical correspondence analysis (CCA) showing the associations between the indices representing non-material nature's contributions to people (NCP) provided by scavenger species and the ecological variables (i.e. conservation status, taxonomic group, and functional traits).

	Axis 1	**Axis 2**	**Axis 3**
Indices of non-material NCP			
Outreach magazines	**-0.635**	-0.383	0.067
Photography	**0.230**	-0.052	-0.150
Wildlife-based tourism	**-0.320**	-0.150	0.111
Google Trends	-0.817	**0.998**	0.125
The GBIF	**0.617**	0.072	0.341
Scientific articles	0.090	0.173	**-0.254**
Conservation status			
Threatened	**-0.205**	**-0.214**	-0.019
Taxonomic group			
Vultures	-0.027	**-0.140**	0.041
Raptors	0.037	-0.079	0.017
Corvids	**0.177**	0.034	0.074
Mammals	-0.111	**0.167**	**-0.092**
Functional traits			
Body mass	**-0.299**	0.085	0.000
Foraging act-social	-0.007	**0.144**	**0.144**
Range	**-0.230**	-0.092	0.039
Fecundity	0.011	**0.212**	-0.027
Diel act-both	-0.048	-0.060	-0.019
Diel act-diurnal	0.125	**-0.161**	0.076
Diel act-nocturnal	-0.101	**0.212**	-0.069
Species			
Aegypius monachus	-0.202	**-0.273**	0.165
Gypaetus barbatus	-0.300	**-0.331**	-0.166
Gyps fulvus	**0.301**	-0.079	**0.307**
Neophron percnopterus	-0.179	**-0.440**	-0.097
Aquila adalberti	**-0.560**	-0.349	-0.060
Aquila chrysaetos	-0.037	-0.167	0.073

Table D3. (Cont.)

	Axis 1	**Axis 2**	**Axis 3**
Circus aeruginosus	**0.330**	0.012	-0.132
Buteo buteo	**0.412**	-0.054	-0.112
Milvus migrans	**0.496**	0.010	0.232
Milvus milvus	-0.007	**-0.184**	0.090
Corvus corax	**0.497**	0.173	0.197
Corvus corone	**0.625**	0.060	0.259
Pica pica	**0.590**	0.085	0.260
Canis lupus	**-0.672**	0.411	0.145
Ursus arctos	**-0.550**	-0.374	-0.050
Vulpes vulpes	**0.260**	0.026	-0.057
Martes foina	0.166	0.053	**-0.188**
Martes martes	0.128	0.088	**-0.210**
Genetta genetta	**0.744**	0.078	-0.394
Meles meles	0.109	0.117	**-0.260**
Herpestes ichneumon	0.428	0.194	**-0.516**
Sus scrofa	-0.294	**0.602**	-0.128
CCA statistics			
Explained variation (%)	56.167	25.624	11.952
Cumulative explained variation (%)	56.167	81.791	93.743

Factor score of response (i.e., indices of non-material NCP), explanatory variables (i.e., conservation status, taxonomic group, and functional traits) and species are shown in the first three axes. Bold font indicates the highest squared cosines (>0.4) for the response variables and the significant regression coefficients for the explanatory variables. The eigenvalues for the first three CCA axes were significant (Monte Carlo permutation test with 500 iterations; $P < 0.0001$). Additional information of response and explanatory variables are shown in Tables 1 and D.1 in Appendix D. Graphical representation of results in Figure 3.

SUPPLEMENTARY MATERIAL FOR: MAPPING THE LARGE-SCALE NON-MATERIAL CONTRIBUTIONS OF SCAVENGERS REVEALS THE IMPORTANCE OF PROTECTED AREAS

THIS MATERIAL INCLUDES:

Table S1. List of Spanish scavenger species included in this study.

Table S2. Search string for webs offering wildlife watching tours in Google.

Table S3. Selected generalized linear models (GLMs).

Table S1. List of Spanish scavenger species included in this study. Species detected consuming carcasses monitored by cameras traps (see García-Heras et al. 2011, Mateo-Tomás et al. 2015, Sebastián-González et al. 2016 for a more detailed description of the monitoring methodology and the study areas). Based on Morales-Reyes *et al.*, 2018.

Common name	Scientific name	Taxonomic group
Bearded vulture	*Gypaetus barbatus*	vultures
Griffon vulture	*Gyps fulvus*	vultures
Egyptian vulture	*Neophron percnopterus*	vultures
Cinereous vulture	*Aegypius monachus*	vultures
Golden eagle	*Aquila chrysaetos*	other raptors
Spanish imperial eagle	*Aquila adalberti*	other raptors
Black kite	*Milvus migrans*	other raptors
Red kite	*Milvus milvus*	other raptors
Common buzzard	*Buteo buteo*	other raptors
Western marsh harrier	*Circus aeruginosus*	other raptors
Raven	*Corvus corax*	non-raptor birds
Carrion crow	*Corvus corone*	non-raptor birds
Magpie	*Pica pica*	non-raptor birds
Gray wolf	*Canis lupus*	mammals
Brown bear	*Ursus arctos*	mammals
Red fox	*Vulpes vulpes*	mammals
Stone marten	*Martes foina*	mammals
Pine marten	*Martes martes*	mammals
Common genet	*Genetta genetta*	mammals
Eurasian badger	*Meles meles*	mammals
Egyptian mongoose	*Herpestes ichneumon*	mammals
Wild boar	*Sus scrofa*	mammals

Table S2. Search string for webs offering wildlife watching tours in Google.

Species	**Search string**
Aegypius monachus	”black vulture” OR “cinereous vulture” OR “Aegypius monachus” AND “wildlife watching” AND “Spain”
Gypaetus barbatus	“bearded vulture” OR ”lammergeier” OR “Gypaetus barbatus” AND ”wildlife watching” AND “Spain”
Gyps fulvus	”griffon vulture” OR “Gyps fulvus” AND “wildlife watching” AND “Spain”
Neophron percnopterus	”egyptian vulture” OR “Neophron percnopterus” AND “wildlife watching” AND “Spain”
Aquila adalberti	“imperial eagle” OR Adalbert’s eagle” OR “Aquila adalberti” AND “wildlife watching” AND “Spain”
Aquila chrysaetos	“golden eagle” OR “Aquila chrysaetos” AND “wildlife watching” AND “Spain”
Milvus migrans	“black kite” OR “Milvus migrans” AND “wildlife watching” AND “Spain”
Milvus milvus	“red kite” OR “Milvus milvus” AND “wildlife watching” AND “Spain”
Buteo buteo	“common buzzard” OR eurasian buzzard” OR “Buteo buteo” AND “wildlife watching” AND “Spain”
Circus aeruginosus	“marsh harrier” OR “Circus aeruginosus” AND “wildlife watching” AND “Spain”
Corvus corax	“raven” OR “Corvus corax” AND wildlife watching” AND “Spain”
Corvus corone	“carrion crow” OR “Corvus corone” AND “wildlife watching” AND “Spain”
Pica pica	“magpie” OR “Pica pica” AND “wildlife watching” AND “Spain”
Canis lupus	“gray wolf” OR “wolf” OR “Canis lupus” AND “wildlife watching” AND “Spain”
Ursus arctos	“brown bear” OR “Ursus arctos” AND “wildlife watching” AND “Spain”
Vulpes vulpes	“red fox” OR fox” OR “Vulpes vulpes” AND “wildlife watching” AND “Spain”
Martes foina	“stone marten” OR “beech marten” OR “Martes foina” AND “wildlife watching” AND “Spain”
Martes martes	“pine marten” OR “Martes martes” AND “wildlife watching” AND “Spain”

Table S2. **(Cont.)**

Species	**Search string**
Genetta genetta	“common genet” OR “Genetta genetta” AND “wildlife watching” AND “Spain”
Meles meles	“eurasian badger” OR badger” OR “Meles meles” AND “wildlife watching” AND “Spain”
Herpestes ichneumon	“egyptian mongoose” OR “Herpestes ichneumon” AND “wildlife watching” AND “Spain”
Sus scrofa	“wild boar” OR “Sus scrofa” AND “wildlife watching” AND “Spain”

Table S3. Selected generalized linear models (GLMs) showing the effects of protected areas (PA), human footprint (HF) and scavenger species richness (Richness) on photography, photography hotspot, tourism, tourism hotspot, observation, observation hotspot and total non-material NCP hotspots. The estimate of the parameters (including the sign), the standard error of the parameters (SE) and the degrees of freedom (df) are shown.

Response variable	Model	Parameter	Estimate	SE	df
Photography	PA + HF + Richness	Intercept	-5.3920	0.2622	5
		PA	0.9289	0.1410	
		HF	0.0564	0.0081	
		Richness	0.2826	0.0224	
Photography hotspot	PA + HF + Richness	Intercept	-6.1845	0.3379	4
		PA	0.6689	0.1586	
		HF	0.0105	0.0109	
		Richness	0.2748	0.0269	
Observation	PA + HF + Richness	Intercept	-3.0867	0.1803	5
		PA	1.5912	0.1178	
		HF	0.0874	0.0064	
		Richness	0.2212	0.0164	
Observation hotspot	PA + HF + Richness	Intercept	-5.6730	0.2780	4
		PA	1.5902	0.1409	
		HF	0.0643	0.0075	
		Richness	0.1288	0.0224	
Tourism	PA + HF + Richness	Intercept	-3.0990	0.1732	5
		PA	1.5422	0.0968	
		HF	-0.0176	0.0065	
		Richness	0.1608	0.0153	
Tourism hotspot	PA + HF + Richness	Intercept	-4.2555	0.2182	4
		PA	1.4878	0.1081	
		HF	-0.0428	0.0089	
		Richness	0.1984	0.0181	
Non-material NCP hotspot	PA + HF + Richness	Intercept	-4.6528	0.2076	4
		PA	1.4231	0.1010	
		HF	-0.0029	0.0071	
		Richness	0.2162	0.0171	

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Photo by Pilar Oliva Vidal.
Black vulture (*Aegypius monachus*) in Pre-Pyrenees of Lleida.

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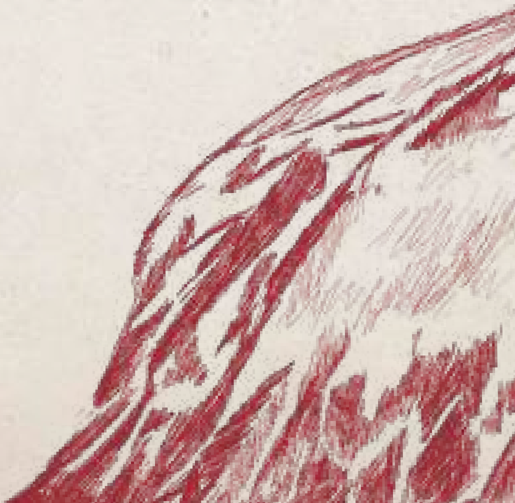

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