UNIVERSITAT DE BARCELONA

SPATIAL ECOLOGY OF THE ENDANGERED EGYPTIAN VULTURE

From Distribution and Movement to Biological Conservation

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Catuxa Cerecedo Iglesias

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Spatial Ecology of the Endangered Egyptian Vulture

From Distribution and Movement to Biological Conservation

Memoria presentada por Catuxa Cerecedo Iglesias para optar al Grado de Doctora por la Universitat de Barcelona

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"*Vale más caer entre las patas de los buitres que entre las manos de los aduladores, porque aquéllos causan daño a los difuntos, y éstos devoran a los vivos*"

Antístenes

Abstract

The current rampant loss of biodiversity is known to be affecting human well-being the world over. Sustainability has become the global go-to solution to ensure the balance between economic growth, social well-being and environmental care is maintained. This concept implies the need for a reduction in human environmental impact if wildlife species are to be preserved and the adequate functioning of ecosystems is to be guaranteed. Obligate avian scavengers, one of the most globally threatened of all groups of vertebrates, play a vital role in the nature-ecosystem services-human well-being dynamic. However, the pursuit of sustainable development can negatively impact vulture conservation and all that it entails. In this thesis, we explore the conservation challenges facing the Egyptian vulture *Neophron percnopterus,* a globally threatened migrant species, within the current context of sustainability. Specifically, we assess the impact of human-driven transformations, changes in food availability and on-going conservation measures on the spatial ecology of this species of great conservation concern. By using novel technologies such as GPS and information generated by classical long-term monitoring schemes, we aimed to increase the knowledge of the environmental factors that have shaped the spatial distribution and movement patterns of this species up to the present day and asses the spatial coverage of the main conservation tool, the Protected Areas (PAs), committed to safeguarding this species. To do so, we focused on the populations of continental and NE of Spain. First, we found that the breeding population of Egyptian vultures in continental Spain has been stable since 2000 but that its abundance is distributed heterogeneously across the whole region. The availability of food sources such as the presence of livestock and supplementary feeding stations and the abundance of griffon vultures were found to be the main factors aggregating breeding pairs and increased local densities in certain areas. By contrast, the increasing number of wind farms correlated with low-density Egyptian vulture areas. However, some of these environmental factors were only significant at specific spatial scales, a significant finding that has practical implications. Second, we found that predictable food sources such as landfills influence the foraging behaviour and movement patterns of tagged vultures in Catalonia (N=16). Whilst the feeding strategy of non-breeding individuals is centred on predictable sources such as landfills, breeders have a more diversified approach and incorporate less predictable food sources such as extensive farms. Additionally, the novel spatial network analysis used in this thesis proves to be a valuable tool for understanding the behavioural dynamics of vultures and this approach highlights the vulnerability of this species to the loss of predictable food sources. The potential closure of landfills will foreseeably prompt behavioural shifts towards other less predictable food sources such as extensive livestock, with non-breeding individuals being particularly affected. Third, an assessment of the coverage of PAs reveals the need to adequately protect key areas of the Egyptian vulture population in Catalonia, especially those linked to feeding areas that are currently unprotected. During PA planning, criteria should be based on ecological and behavioural aspects of breeding and non-breeding vultures rather than on purely administrative factors if the entire population is to be conserved efficiently. This thesis presents new methods for studying the spatial ecology of vultures and provides a greater understanding of the distributions and movements of these long-lived mobile species, thereby contributing to a more complete explanation of these spatial patterns. Finally, it sheds light on the detrimental effects of possible future sustainable actions on vulture populations –keystone species in ecosystems and providers of services at zero cost– and provides essential knowledge that will help inform future guidelines and conservation efforts.

Resumen

La actual pérdida de biodiversidad está afectando al bienestar humano en todo el mundo. La sostenibilidad se ha convertido en la solución mundial para garantizar el equilibrio entre el crecimiento económico, el bienestar social y el cuidado del medio ambiente. Este concepto incluye la necesidad de reducir el impacto ambiental humano si se quiere preservar las especies silvestres y garantizar el funcionamiento adecuado de los ecosistemas. Las aves carroñeras obligadas, uno de los grupos de vertebrados más amenazados a escala mundial, desempeñan un papel vital en la dinámica naturaleza-servicios ecosistémicos-bienestar humano. Sin embargo, la búsqueda del desarrollo sostenible puede repercutir negativamente en la conservación de los buitres y todo lo que ello conlleva. En esta tesis, exploramos los retos de conservación a los que se enfrenta el alimoche común *Neophron percnopterus,* una especie migratoria globalmente amenazada, en el contexto actual de la sostenibilidad. En concreto, evaluamos el impacto de las transformaciones provocadas por el hombre, los cambios en la disponibilidad de alimento y las medidas de conservación en curso sobre la ecología espacial de esta especie de gran interés para la conservación. Mediante el uso de tecnologías novedosas como el GPS y la información generada por métodos tradicionales de seguimiento a largo plazo, pretendemos aumentar el conocimiento de los factores ambientales que han configurado la distribución espacial y los patrones de movimiento de esta especie hasta la actualidad, así como evaluar la cobertura espacial de la principal herramienta de conservación, las Áreas Protegidas (APs), comprometidas con la salvaguarda de esta especie. Para ello, nos centramos en las poblaciones de la España continental y el NE de la Península Ibérica. En primer lugar, encontramos que la población reproductora de alimoches en España continental se ha mantenido estable desde 2000, pero que su abundancia se distribuye de forma heterogénea por toda la región. La disponibilidad de fuentes de alimento, como la presencia de ganado y comederos suplementarios, y la abundancia de buitres leonados resultaron ser los principales factores de agregación de parejas reproductoras y de aumento de las densidades locales en determinadas zonas. Por el contrario, el creciente número de parques eólicos se correlacionó con zonas de baja densidad de alimoches. Sin embargo, algunos de estos factores ambientales sólo fueron significativos a escalas espaciales concretas, un hallazgo importante que tiene implicaciones prácticas. En segundo lugar, encontramos que fuentes de alimento predecibles como los vertederos influyen en el comportamiento de búsqueda de alimento y en los patrones de movimiento de los buitres marcados en Cataluña (N=16). Mientras que la estrategia de alimentación de los individuos no reproductores se centra en fuentes predecibles como los vertederos, los reproductores tienen una estrategia más diversificada e incorporan fuentes de alimento menos predecibles como las granjas extensivas. Además, el novedoso análisis de redes espaciales utilizado en esta tesis constituye una valiosa herramienta para comprender la dinámica del comportamiento de los buitres y pone de manifiesto la vulnerabilidad de esta especie ante la pérdida de fuentes de alimento predecibles. El posible cierre de los vertederos provocará cambios de comportamiento hacia otras fuentes de alimento menos predecibles, como la ganadería extensiva, y los individuos no reproductores se verán especialmente afectados. En tercer lugar, la evaluación de la cobertura de las APs pone de manifiesto la necesidad de proteger adecuadamente áreas clave para la población de alimoche común en Cataluña, especialmente aquellas vinculadas a zonas de alimentación que actualmente se encuentran desprotegidas. Durante la planificación de las APs, los criterios deberían basarse en aspectos ecológicos y de comportamiento de los buitres reproductores y no reproductores en lugar de en factores puramente administrativos si se quiere conservar toda la población de forma eficiente. Esta tesis presenta nuevos métodos para estudiar la ecología espacial de los buitres y proporciona una mayor comprensión de las distribuciones y movimientos de esta especie móvil y longeva, contribuyendo así a un entendimiento más completo de estos patrones espaciales. Por último, arrojamos luz sobre los efectos perjudiciales de posibles futuras actuaciones sostenibles sobre las poblaciones de buitres –especies clave en los ecosistemas y proveedoras de servicios a coste cero– y aportamos conocimientos esenciales que ayudarán a fundamentar directrices y esfuerzos de conservación.

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GENERAL INTRODUCTION

Crisis in the interconnection between human society and biodiversity

Humans and biodiversity are deeply interconnected in a delicate balance in which humans depend intensely on biodiversity for their livelihoods. Humans receive what are known as 'ecosystem services' –nature's contribution to people's lives– at zero cost in the form of provisioning, regulation, maintenance and cultural services (Cardinale et al., 2012; Marselle et al., 2021). Many societies depend on the richness of local ecosystems for their traditions, cultural identities and spiritual practices (Pretty et al., 2009; Clark et al., 2014). However, humans, motivated by the pursuit of so-called 'prosperity', have over the centuries transformed and destroyed habitats and exploited resources unsustainably.

This rampant humanisation and destruction of the environment has led to the disruption of biogeochemical cycles and favoured the spread of alien/invasive species, as well as provoking a host of other reactions that are causing the current global biodiversity crisis (Brondizio et al., 2019). In fact, it is said that we are now experiencing the Sixth Extinction in what has been termed the 'Anthropocene era' (Ceballos et al., 2015; Johnson et al., 2017). We are having to face up to highly significant challenges such as the rapid extinction of species, the degradation of ecosystems and the loss of resilience in both aquatic and terrestrial natural systems due to global change. In this context, sustainable development has emerged as a unified social and environmental framework for preserving life on our planet (Griggs et al., 2023).

Sustainable development and its role in halting the biodiversity crisis

The concept of sustainable development was first formally introduced in the seminal report *Our Common Future*, published by the United Nations World Commission on Environment and Development in 1987, and commonly referred to as the *Brundtland Report* (Purvis et al., 2019). This document defined sustainable development as "development that meets the needs of the present without compromising the ability of future generations to meet their own needs". It postulates that achieving harmonious and lasting progress requires the integration of three fundamental dimensions –economy, society and environment (Emas, 2015; Purvis et al., 2019)– as we seek to avoid further depletion of natural resources and/or irreparable damage to the environment (Purvis et al., 2019). This approach emphasises the need for a change in our lifestyles aimed at reducing our environmental impact while still effectively meeting human needs.

In the race towards sustainability, Europe included in its 2030 Agenda 17 Sustainable Development Goals (SDGs) covering a diverse set of thematic areas including, for example, poverty eradication (SDG 1), health (SDG3), education (SDG 4), gender equality (SDG 5) and climate action (SDG 13), among others. However, the most relevant aims for this thesis are the commitment to work for the conservation of oceanic (SDG 14) and terrestrial (SDG 15) wildlife, which are closely linked to targets and actions designed to preserve biodiversity (UN, 2018). Since their adoption, the SDGs have become widely accepted and are now a key aspect guiding planning and the other actions promoted by various stakeholders including governments, the private sector and the world's citizens.

However, the rapid loss of biodiversity that is apparent may ultimately hinder the fulfilment of many of the SDG targets. This is because this loss affects the ability of ecosystems to provide vital services to human society. In addition, paradoxically, certain conflicts have emerged between SDGs and biodiversity (Blicharska et al., 2019): for example, investment in reducing greenhouse gas emissions can positively affect biodiversity and sustainable development but may also have unintended negative consequences (Neri et al., 2019; see below). On the other hand, integrating biodiversity conservation into the economic sustainable development of local communities in protected areas can help stem the loss of ecosystem integrity (Ma et al., 2009). Thus, sustainable development is currently triggering new conservation challenges.

Overall, within this sustainable development framework, biodiversity conservation has become a key element due to its relevance to human well-being (Sachs et al., 2009). As well as being the cornerstone of life-supporting ecosystems (United Nations, 1992), our biodiversity engenders a range of benefits that create economic value and generate indispensable ecosystem services that are essential for the proper development of human societies (Naeem et al., 2016). Hence, the recognition of ecosystem services has become a key tenet worldwide in the development and implementation of sustainable development.

Avian scavengers as providers of ecosystem services

Not all species have the same relevance and importance when it comes to providing services for the well-being of human society. In recent decades, vultures have attracted considerable attention due to the significance of their role in ecosystems (Ogada et al., 2012a; Moleón et al., 2014; DeVault et al., 2016). The crux lies in their role as obligate carrion consumers, essential for nutrient cycling, infectious disease control and maintaining the balance and functionality of ecosystems, all of which provide invaluable contributions to human well-being (Markandya et al., 2008; Moleón et al., 2014). As obligate scavengers, vultures have specialised adaptations such as soaring flight, an ability that affords them unparalleled efficiency in benefitting from unpredictable pulses of food resources across large areas without spending excessive energy whilst foraging (Ruxton et al., 2004). Additionally, morphological adaptations such as strong hooked beaks enable them to rip and tear the flesh of carcasses.

Vultures also exhibit various behavioural traits such as social foraging strategies that facilitate the search on the wing for unpredictable food sources (Jackson et al., 2008). They can create a focal point for community interactions around carrion, which attract other scavenger animals and organisms, thereby accelerating carrion decomposition (DeVault et al., 2003), a vitally important ecosystem service (Moleón et al., 2014; DeVault et al., 2016). Additionally, vultures also provide many crucial and often overlooked services, ranging from substantial economic gain to roles in cultural and spiritual heritage, that extend beyond their ecology and favour the well-being of human societies (see **BOX 1** for more information).

BOX 1

Additional ecosystem services of vultures

In addition to supporting ecosystem services, i.e. nutrient cycling, infectious disease control and maintaining ecosystem functionality (Moleón et al., 2014; DeVault et al., 2016), vultures provide tangible economic benefits that are often overlooked but are crucial for various sectors. For instance, the impact of rabies on human health associated with the decline of vultures in India resulted in increased health costs at national level (Markandya et al., 2008). Another example occurred in Europe, where strict sanitary regulations

BOX 1

obliged farmers to eliminate their dead cattle by systematic industrial incineration, a measure introduced after the 'mad cow' crisis. Governments, stakeholders and farmers have had to bear the costs of transporting and incinerating dead livestock over the past decade (Donázar et al., 2009a,b), a service that vultures and other scavengers perform at zero cost (Morales-Reyes et al., 2015). Conversely, the recovery of vulture populations has provided economic benefits that exceed the costs associated with their conservation (Becker et al., 2010). Ornithological tourism has increased exponentially in many regions and now represents important direct income for local communities, which are sometimes affected by restrictions imposed on their activities as a means of guaranteeing conservation targets (Macdonald et al., 2017). For example, in the Spanish Pyrenees, the observation of avian scavengers at feeding sites generates an average of $4.9 million of income annually (García-Jiménez et al., 2021), which is not only an important source of revenue for the local population but also constitutes an important cultural service. In addition, ornithological tourism helps policy managers and administrations address socio-economic conflicts that arise after the implementation of conservation initiatives.

Vultures also occupy a prominent place in various societies and cultures where they form an integral part of human history through a relationship that dates back to the Pleistocene epoch. The guild of avian scavengers has benefited humans ever since the first bipedal hominids followed vultures to exploit carrion for food. This competition for carrion resources influenced the development of tools and language, thereby promoting successful competition for carcasses (Bickerton and Szathmáry, 2011; Moleón et al., 2014). In all cultures, vultures have acquired symbolic significance and are evident in numerous myths and legends (Şekercioğlu, 2006). Vultures also have contrasting symbolic interpretations in different cultural contexts: while some cultures associate vultures with bad luck or death, i.e. negative perceptions, others venerate them for their fundamental role in removing mortal remains and performing rituals related to spiritual cleansing (Donázar, 1993).

The European vulture crisis before sustainable development goals

Three hundred years ago, vultures were abundant and extensively spread across most European mountain ranges and were some of the continent's commonest breeding raptors (Donázar et al., 1997). However, various factors including shifts in food availability and changes in human activities precipitated a severe decline in their populations (Cortés-Avizanda et al., 2015a; **Fig. 1**). These birds of prey had evolved to feed on the unpredictable appearance of carcasses of the large wild ungulates that once grazed the open areas of Europe (Donázar, 1993). However, the transformation of hunting groups into agrarian societies during the Neolithic obliged vultures to become dependent on livestock carcasses linked to human activities and during this period vultures began to take advantage of dead cattle on farms if not consumed by humans (Moleón et al., 2014).

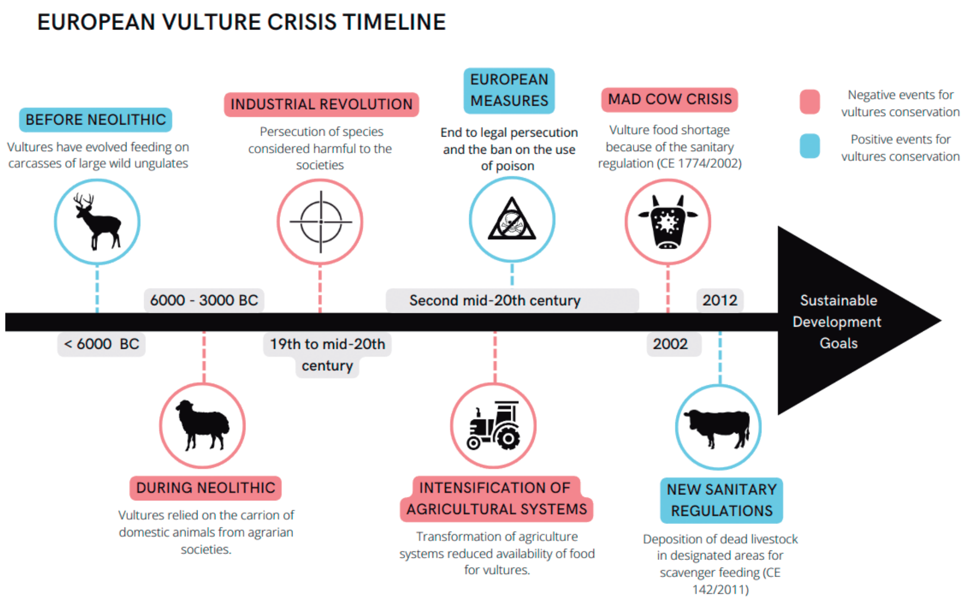

Figure 1. European vulture crisis timeline. This figure illustrates the critical events occurring in Europe that have influenced the vulture crisis. Events detrimental to vulture populations are shown in red (i.e. challenges such as a reduction in food availability and active persecution). Conversely, events beneficial to vulture populations are shown in blue. By highlighting these key events, this timeline provides a comprehensive overview of the factors shaping the status and conservation trajectory of European vulture species.

After the Industrial Revolution the increasing anthropisation of the landscape and rising utilitarian views of nature led to the persecution of certain species –scavengers included– that were considered to be harmful human society (Bijleveld, 1974). This shift culminated in declining vulture populations that were threatened by hunting and other types of persecution throughout Europe. Simultaneously, the Industrial Revolution boosted the transformation of agriculture whereby systems based on pastoralism and traditional grazing were replaced by other more intensive systems, resulting in reduced food availability for scavengers due to a lack of livestock carrion in the field (Grande et al., 2018). Consequently, vultures had to adjust their flight patterns to access alternative food sources (Monsarrat et al., 2013), which increased competition among vultures and other scavengers for the limited predictable resources that were still available (López-López et al., 2014; Cortés-Avizanda et al., 2012).

Subsequently, shifts in European sanitary policies in 2002 have had a serious impact on scavenger populations. The outbreak of a new variant of Creutzfeldt-Jakob disease in humans caused by the consumption of cattle infected with bovine spongiform encephalopathy (BSE, commonly known as the 'mad cow' crisis) led European sanitary authorities to enact legislation (Regulation CE 1774/2002) preventing the disposal of livestock in nature that obliged farmers to incinerate animal carcasses in authorised facilities (Schiermeier, 2001; Donázar et al., 2009a). This legal shift provoked a chain reaction: a substantial reduction in available food for scavengers (Camiña and Montelío, 2006), followed by declines in reproductive rates (Margalida et al., 2014) and elevated mortality rates among young vultures (Donázar et al., 2009b). This situation generated tension between vultures and farmers given that the availability of food for vultures fell drastically; as a consequence, some vulture species presumably killed livestock for food leading to economic losses for certain stakeholders (Oliva-Vidal et al., 2022). This conflict was seized upon by the media who stirred up societal rejection of these scavengers (Donázar et al., 2009b) and provoked a negative perception that probably motivated further pursuit of vultures wherever conflicts were latent (e.g. using poison to kill facultative and obligate scavengers; Margalida et al., 2010).

The deliberate poisoning of carnivores has historically been the most widespread cause of vulture deaths in both Europe and the rest of the world (Ogada, 2014; see **BOX 2**). Vultures are exceptionally vulnerable to exposure to contaminants due to their feeding habits. The fact that they eat in aggregates (e.g. >100 individuals/carrion) means that numerous birds are exposed simultaneously to the same toxins (DeVault et al., 2016). Although the poisoning of carnivores is still a widespread practice, it causes fewer vulture deaths than other anthropogenic threats such as wind farms (see below). In Europe, poisons are used to eliminate animals that compete with game species since, it is said, they decrease the number of trophies available for hunters. Furthermore, farmers also use poison to prevent carnivores attacking livestock. Toxins including veterinary anti-inflammatory drugs such as diclofenac are now being used in Europe and have caused the deaths of thousands of vultures (Ogada et al., 2016). Despite this alarming trend, the use of this drug has been legalised in some European countries such as Spain without any previous adequate assessment of its potential impact on vulture populations. That said, risk assessment studies indicate that the measures implemented to prevent the inappropriate use of diclofenac are effective, although ongoing surveillance is recommended to mitigate any potential risks (Moreno-Opo et al., 2021).

In this rapidly changing world where humans have a significant impact on the planet, it is a challenge to quantify the threats that vultures are currently having to confront, which include disturbance at nesting sites (Zuberogoitia et al., 2014), collision with human infrastructures such as power lines (Donázar et al., 2002), habitat alteration and changes in trophic resources due to climate change (Donázar et al., 2016), all of which contribute to the so-called ‘vulture crisis’. To reverse this negative trend and preserve healthy vulture populations, it is essential to take these factors into account and implement appropriate measures.

BOX 2

Vultures in other regions of the world

Vultures have experienced severe population declines in many regions of the world and are one of the most threatened of all groups of animals (Ogada et al., 2016; McClure et al., 2018). The 23 vulture species, including condors, are grouped into two main families: Old World vultures (family *Accipitridae*) and New World vultures (family *Cathartidae*). Among Old World vultures, 14 out of 16 species are globally Endangered or Near Threatened, while among New World vultures, two out of seven species are currently Endangered (Ogada et al., 2012b). The reasons for the decline in vulture populations are highly diverse.

BOX 2

The most significant decline has been in southern Asia, where veterinary anti-inflammatory drugs such as diclofenac have caused a drastic reduction in vulture populations. In India, for example, more than 90% of the vultures belonging to the genus *Gyps* (long-billed vulture *Gyps indicus*, slender-billed vulture *Gyps tenuirostris* and oriental white-backed vulture *Gyps bengalensis*) have disappeared (Green et al., 2004; Chaudhary et al., 2012). Unfortunately, the use of diclofenac in domestic livestock, which goes unnoticed in carrion (Oaks et al., 2004), has spread to Europe and Africa, and has caused the deaths of thousands of vultures (Donázar, 1993; Ogada et al., 2016). In addition, other toxic veterinary products such as pesticides (Hernández and Margalida 2008; Ogada, 2014) and rodenticides (Plaza et al., 2019) used in intensive agriculture have also contributed significantly to the worldwide decline of these scavengers. Similarly, lead ingestion, stemming from abandoned carcasses containing residual lead shot used by hunters, has emerged as another significant threat, mainly in North America. This has caused poisoning and death in scavengers (Cade, 2007; Hernández and Margalida, 2009a) and other raptors (Pain et al., 2019). In some regions of Africa, however, the primary cause of vulture decline was and is active persecution encouraged by the trade in vulture body parts since some cultures believe in their medicinal properties, all of which further exacerbates the threats to these populations (Mckean et al., 2013; Saidu and Buij, 2013; Buij et al., 2016).

In addition to the well-studied causes described above, i.e. increasingly humanised landscapes due to expanding human infrastructures and the progress of global change, new threats are arising that today are still threatening vulture populations (Boshoff et al., 2011; Janss 2000; Angelov et al., 2013; Ogada et al., 2016).

Main achievements in Europe: recovering vulture populations and sustainable development

Fortunately, the global biodiversity crisis has promoted greater understanding of the importance of vultures for human well-being. At the end of the twentieth and beginning of the twenty-first centuries, coordinated efforts by various stakeholders including governments, NGOs, conservation groups, scientists and local action groups including captive breeding and reintroduction programs, research and monitoring, as well as public education and awareness campaigns, were being undertaken to address the threat to vulture populations (e.g. Schaub et al., 2009; Moreno-Opo and Margalida, 2014; Badia-Boher et al., 2019). These efforts are today backed by international conservation agreements and greater social awareness of the problem. The first steps in the recovery of European vulture populations were the end to legal persecution and the ban on the use of poison, which were first implemented at the end of the twentieth century (Margalida et al., 2010; **Fig. 1**).

Protected Areas (PAs) are essential in fulfilling the abovementioned SDGs. Above all, SDGs 14 and 15, which deal with, respectively, preserving life below water and on land, are recognised as crucial for preserving biodiversity. Even before the establishment of the SDGs, PAs were widely used to conserve biodiversity and are still the most fundamental tool in this process (Geldmann et al., 2013; UNEP-WCMC and IUCN, 2016). In this context, avian scavengers are no exception to these conservation efforts. For instance, in 2012 the European Parliament approved a new directive that reversed previous regulations regarding the 'mad cow' crisis (see above) that permitted the deposition of dead livestock for scavenger feeding in designated areas after sanitary screening to ensure vulture safety (CE 322/2003, CE 830/2005, CE 142/2011). These designated areas, termed *Protected Areas for the Feeding of Necrophagous species of European interest*, were included in the Natura 2000 network –Europe's largest network of PAs– and are specifically earmarked for the development of conservation plans to ensure ample food resources for these species. These regulatory and sanitary policy actions have contributed significantly to the recovery of vulture populations and to the mitigating of greenhouse gas emissions. The original mandatory removal of livestock carcasses from the field –the transportation of dead extensive livestock resulted in the emission of more than 77,000 metric tons of CO_2 in Spain alone (Morales-Reyes et al., 2015)– led to an increase in greenhouse gas emissions in contradiction of SDG 13 (Climate Action), which seeks to reduce emissions worldwide. This means that today, after many changes in sanitary legislation (see above), the adequate management of 'more naturalised' sources of carrion has reduced its impact on climate change. However, despite these efforts to establish natural PAs, there are still many places outside PAs where thousands of vultures perish due to the causes described above (Santangeli et al., 2019). Thus, PAs may in fact be insufficient for ensuring effective vulture conservation and, consequently, SDGs.

The promotion of the other SDGs may have a positive impact on vulture conservation. For instance, research has shown that traditional grazing and extensive livestock farming can serve as a conservation strategy for vulture populations by naturally increasing the availability of carrion in the wild (Olea and Mateo-Tomás, 2009; Delgado-Gonzalez et al., 2022; Arrondo et al., 2023). This strategy alleviates the need for artificial feeding points, which can adversely affect avian scavengers (see Cortés-avizanda et al., 2016). Indeed, this agropastoral approach is coherent with several other SDGs, including SDG 2 (Food Security), SDG 13 (Climate Action) and SDG 15 (Life on Land). Therefore, promoting sustainable development by conserving traditional grazing can act as an effective strategy in vulture conservation.

Vultures and uncertainty in the face of new sustainable scenario

The European decline in vulture populations is not attributable to a single cause but, rather, to a combination of factors whose effects are cumulative. However, it is worth highlighting the fact that, in addition to the abovementioned well-documented causes, vultures live and move in areas that are increasingly being affected by human activities and are subject to global change. As a result, they are now more likely to encounter new threats posing additional conservation challenges. One such challenge is, precisely, sustainable development, whose impact on biodiversity and, in particular, on vultures is still uncertain. Specifically, to address SDG 13 (Climate Action), the expansion of renewable energy sources (mainly wind farms and solar panels) has undoubtedly become a crucial way of mitigating climate change by avoiding the use of fossil fuels and reducing greenhouse gas emissions (Fawzy et al., 2020). However, these infrastructures occupy large tracts of land (**Fig. 2**), some of which are close to breeding colonies/territories, feeding grounds and/or the edge of protected areas (Boshoff et al., 2011; Janss, 2000; Angelov et al., 2013; Ogada et al., 2016; Kati et al., 2021). In particular, Oppel et al., (2021) argue that the accomplishment of certain SDGs may inadvertently jeopardise vulture populations in East Africa. Specifically, these authors criticise SDG 7 (Affordable and Clean Energy), which aims to achieve universal access to electricity. Global moves towards the adoption of renewable energy sources, albeit commendable, poses inherent risks to biodiversity (Santangeli et al., 2016) since, for instance, the proliferation of wind farms has been associated

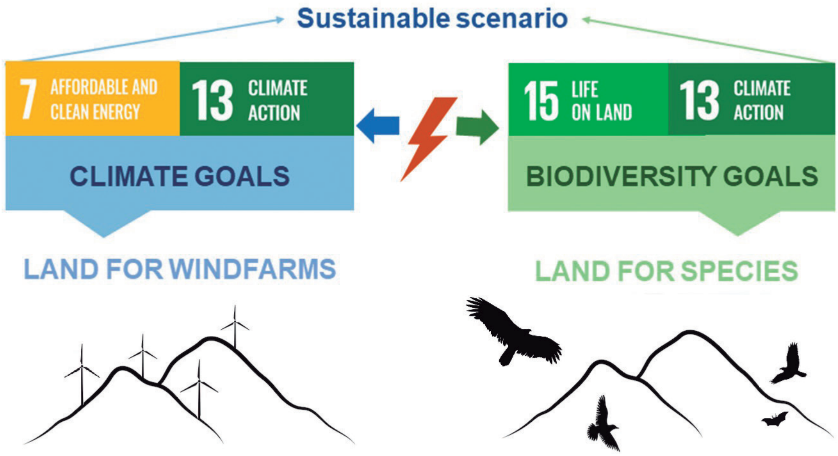

Figure 2. Conflict for land demand within the framework of the Sustainable Development Goals: the case of wind energy. SDGs 7 and 13 to mitigate climate change by reducing greenhouse gas emissions require habitat alteration, which contradicts SDG 15 to protect wildlife. Adapted from Kati et al., 2021.

with significant damage to wildlife given that collisions with these structures increase mortality rates, especially amongst birds of prey (Watson et al., 2018). Furthermore, if not meticulously planned and designed, expanding evacuation infrastructures such as power lines for the generated renewable energy can lead to electrocutions and fatal collisions, thereby exacerbating the current conflict between renewable energies and biodiversity conservation. While developed regions, particularly Europe, currently host a substantial proportion of existing renewable energy infrastructure, an immediate future concentration is projected for developing regions such as India, Southeast Asia, South America and Africa that harbour great biodiversity (Rehbein et al., 2020), which will magnify this potential emerging threat on a global scale.

Furthermore, in line with SDG 12 (Sustainable Production and Consumption), several nations advocate transitioning toward a circular economy, which emphasises the economic dimension of sustainability. The circular economy model aims to extend the life cycles of products, materials and resources to reduce energy costs and waste generation (Rodriguez-Anton et al., 2019). However, the impact of the transition to a circular economy on biodiversity has not yet been sufficiently studied (Buchmann-Duck and Beazley, 2020). Although the circular economy advocates strategies that aim to safeguard biodiversity, its establishment does not uniformly translate into less impact (Ruokamo et al., 2023). For example, advocating the closure of landfills poses a challenge that requires scientific research and quality data as a means of predicting species' response to these measures. Landfills, in addition to being sources of greenhouse gases (El-Fadel and Massoud, 2000), also cause contamination (e.g. waterproofing membranes can contaminate groundwater if they are damaged; Iravanian and Ravari, 2020) and disrupt wildlife migration and feeding patterns (Plaza and Lambertucci, 2017). In relation to food, reducing the amount of waste implies a reduction in both inorganic material and organic waste, food sources for several animal groups including mammals such as bears (Peirce and Van Daele, 2006), birds such as white storks (Gilbert et al., 2016), condors and vultures (Houston et al., 2007; Tauler-Ametller et al., 2019), and even reptiles such as lizards (Uyeda et al., 2015). Consequently, altering waste disposal systems within the framework of a circular economy can have significant ecological implications for diverse animal populations that depend on organic material in landfills as a food source (Arévalo-Ayala et al., 2023).

Sustainable development is a challenge that puts biodiversity conservation efforts to the test. Therefore, assessing the current conservation status of threatened avian scavengers and exploring its spatial ecology within the context of sustainable development is necessary. It should be investigated the potential impacts of landscape alterations, changes in food availability and the rapid implementation of novel sustainable European policies on vultures. Through this, we could gain valuable insights into how we can balance the demands of sustainable development with environmental conservation and the protection of threatened species.

Methodology and advanced analytical techniques in Spatial Ecology: opportunities for future vulture conservation

In this thesis, novel methodologies are evaluated to explore further the distribution and movement changes occurring in these birds. These techniques are incorporated into the Spatial Ecology framework, a dynamic field that requires the use of cutting-edge technology to explore the effects of space on individuals, populations, communities and biodiversity, and the role of space in the overall ecosystem functioning (Fletcher and Fortin, 2018). We employ two subdisciplines within Spatial Ecology related to (i) spatial patterns including species distributions and (ii) animal movement.

In terms of spatial patterns, our focus is on Species Distribution Models (SDMs), which unravel the mechanisms shaping geographic spatial occupancy and abundance based on surrounding environmental features (Elith and Leathwick, 2009). This knowledge can greatly assist in determining the most appropriate geographical areas for endangered species conservation (e.g., Villero et al., 2017), identifying priority areas for protection (e.g. Buechley et al., 2022), guiding species recovery efforts (e.g., Anoop et al., 2020) and predicting the future impact of climate or other environmental changes (e.g. Mateo-Tomás and Olea, 2015). In this regard, technological advancements in remote sensing and Geographical Information Systems (GIS) have facilitated the acquisition of large-scale environmental data and allow them to be mapped on geographical space (Jetz et al., 2012), thereby providing invaluable information for future conservation efforts (Guisan et al., 2013; Villero et al., 2017).

A key issue is that SDMs often only capture information about species-environment interactions at a specific moment –a snapshot– without taking into account the fact that these interactions will vary over time (Zurell et al., 2009). For instance, when dealing with invasive species, the SDMs used to determine their distribution in their native range may not necessarily apply to their interactions with their new environments (Broennimann et al., 2007). Additionally, SDMs have limitations related to spatial scales since at broad spatial scales (i.e. coarse grains and large extents) biotic interactions (e.g. competitions with other species) are hypothesised to have minimal effects on distribution, and abiotic factors (e.g. climatic information), above all, are thought to determine species distribution (Sax and Gaines, 2003). Consequently, researchers must carefully select the predictor variables that best explain species distributions in terms of the spatial scale at which they are working (Porfirio et al., 2014). In this thesis, we tackle these two major constraints on species distribution modelling by incorporating specific temporal and spatial terms into the SDMs. In the temporal term we assume that the variability in distribution could be explained by previous distributions as a proxy for habitat quality, while for the spatial term we consider geographical space as a predictor for avoiding false correlations between species distribution and the environment (Legendre and Fortin, 1989). This approach enables us to gain a better understanding of the factors that influence the distribution of species and provides valuable insights for conservation and management practices.

Telemetric technology has played a pivotal role in advancing our understanding of how, where and when animals move (Kays et al., 2015). Traditionally, tracking methods relied on antennas to gather limited animal locations, which required substantial sampling efforts for data collection (e.g. conventional VHF and Argos). Consequently, these methodologies only produced rudimentary movement patterns (Bridge et al., 2011). However, in recent years, tracking technology (e.g. GPS-GSM devices) has advanced significantly and now provides continuous high-definition data on animal movements (Kays et al., 2015). This technology allows researchers to evaluate the responses of animals to different anthropogenic perturbations and their development of behavioural changes throughout their lifespans (Cooke et al., 2004; Tomkiewicz et al., 2010). It also helps conservation managers and policymakers implement targeted conservation strategies to ensure the survival of endangered species (Katzner and Arlettaz, 2020); for instance, knowledge of the movement patterns of endangered species is crucial for defining PAs or increasing the extension of currently PAs (Buechley et al., 2022).

Vultures have played a key role in developing telemetry and, given their large body sizes, are important models for animal-attached devices (Cooke et al., 2004). Although most research focusses strictly on ecological issues such as home-range size, decision-making or the transmission of information (see review by Alarcón and Lambertucci, 2018), particular attention has also been paid to studying vulture movement patterns during their foraging phases. This is because vultures have increasingly become dependent on resources managed or produced by humans, which has affected their movement patterns and introduced new challenges that need to be addressed to ensure the survival of these endangered species (Monsarrat et al., 2013; López-López et al., 2014; Margalida et al., 2016). Additionally, the data gathered through this technology have revealed a rise in accidents involving collisions with human infrastructures such as power lines and wind farms (Sheppard et al., 2015). Although this threat has existed for a number of decades, telemetry now provides a far more accurate analysis of its occurrence.

Several analytical methodologies have been developed to study movement patterns based on telemetric information. This is a challenge given the large volume of data generated and the close correlation between data points (Urbano et al., 2010). For instance, GPS data is not spatial-temporally independent as each GPS point depends on the previous one, which contradicts a key statistical assumption (i.e. independence assumption). The conventional method for studying and analysing animal movement typically employs kernel density estimators, which do not consider the temporal dependency of GPS data (Fleming et al., 2015). In this thesis, we employ complex statistical methods, specifically Dynamic Brownian Bridge Models (dBBMMs), which estimate spatial-use likelihood by accounting for the temporal dependency of GPS data (Horne et al., 2007; Kranstauber et al., 2012).

In addition, we adopt a network approach to comprehend how vultures navigate and connect within the landscape (Fortuna et al., 2006; Jacoby et al., 2012). Network analysis uses graph theory (Urban and Keitt, 2001) to represent complex biological systems in terms of nodes (i.e. the space used by individuals) and links (i.e. the flightpaths that connect the landscape). The analysis of these networks has a significant advantage because each network has unique features that can be interpreted in biological terms (Jacoby et al., 2012). By simulating perturbations and observing how these perturbations change network features, we can predict future behavioural responses in vultures resulting from human activities.

The Egyptian vulture as a case of study under a new scenario: research opportunities based on conventional monitoring and new technologies

We selected the Egyptian vulture *Neophron percnopterus*, one of the most endangered vulture species worldwide, as the study species. This species is characterised by several distinct ecological traits: it has a long lifespan, often extending for decades, and a monogamous mating system that lasts a lifetime (Donázar, 1993). Despite being a scavenger that typically feeds on medium-to-small-sized carrion, it is also an opportunistic predator. It can adapt to prey upon small prey items such as immature or sick mammals. In general it has a number of diverse feeding strategies and will obtain food from various sources including livestock and wild animal carcasses, and will occasionally scavenge in anthropogenic environments such as landfills (Hidalgo et al., 2005; Margalida et al., 2012; Tauler-Ametller et al., 2019). The Egyptian vulture begins to breed at an average age of seven years (Sanz-Aguilar et al., 2017) in territories that it tends to maintain over the years (Donázar, 1993). Both members of the breeding pair engage in nesting activities during the spring and summer months and both are strongly territorial (Mateo and Olea, 2007, Cortés-Avizanda et al., 2009a). After the breeding season, pairs migrate to wintering grounds in Africa (García-Ripollés et al., 2010, Meyburg et al., 2004; Efrat et al., 2023). Non-breeding individuals (or immatures) are not attached to any territory and aggregate in communal areas or roosts until they migrate (Donázar et al., 1997). These roosting sites are generally associated with predictable food sources and serve as gathering points where these nomadic individuals can exchange information and socialise (Margalida and Boudet, 2003).

This thesis employs two study areas, one in continental Spain and the other in the north-east of the Iberian Peninsula (central and eastern Catalonia). The Spanish Egyptian vulture population is at the western limit of its global distribution in Africa, Asia and Europe and accounts for a substantial proportion (~12-43%) of its total population, estimated at 12,400-36,000 mature individuals worldwide (BirdLife International, 2021). However, thanks to systematic monitoring efforts across several regions in Spain, the latest Egyptian vulture breeding census carried out in 2018 estimated a population size of 1,490-1,569 pairs, the highest count since the first national census in 1998 (Del Moral and Molina, 2018a). It is worth mentioning that the Spanish population underwent a severe population decline (~25%) at the end of the twentieth century (Del Moral and Martí, 2002; Donázar, 2004) and has historically always been threatened by factors linked to habitat alteration, human pressure and inherent behaviour (BirdLife International, 2021; Carrete et al., 2007). In addition, it was affected by the policies implemented in response to the European 'mad cow' crisis (Donázar et al., 2010). Although the impact of all these factors has tended to decrease, several thousand vultures still perish annually from collisions with wind turbines and electrocution on power lines (Sanz-Aguilar et al., 2015). Over the past two decades, the Spanish population has stabilised and the size of its breeding population remains unaltered (Del Moral and Molina, 2018a). Despite the stable trend observed in the overall Spanish population, regional variations do occur. For instance, a population decline has been noted in regions such as Andalucia, La Rioja, Castilla y León, Aragón and Navarra (Carrete et al., 2007; Zuberogoitia, 2008; Del Moral, 2009), while in regions such as the Basque Country, Asturias, Canary Islands, Valencia and Catalonia, there has been an increase in the number of breeding pairs (Zuberogoitia et al., 2009; Tauler et al., 2015; Del Moral and Martí, 2018; Badia-Boher et al., 2019).

In Catalonia, the second study area of this thesis, the number of breeding pairs has tripled since the 1980s and currently stands at 85 (Franch et al., 2021), a substantial increase on the 25 pairs recorded in the 1980s (Muntaner et al., 1983). This increasing population offers valuable lessons for conservation efforts elsewhere. The study of successful populations helps identify the pivotal factors that ensure their success, which include resource availability, effective management strategies and less human impact. This knowledge is vital for conservation practices in areas where species are struggling, and can help replicate successful outcomes and improve overall conservation effectiveness. The demographic models that analyse this upsurge in Catalonia indicate that there are potentially two main contributing factors: first, the increase can be attributed to greater survival rates in adults, mainly due to successful measures to control the environmental use of poisoned baits (Tauler et al., 2015); and, second, there appears to have been a significant influx of immigrant vultures from neighbouring populations (Tauler et al., 2015). This population increase has gone hand-in-hand with an expansion of breeding territories in Catalonia, with pairs of vultures colonising previously unoccupied areas. This growth is closely linked to the availability of anthropogenic feeding sites in the region, i.e. landfills (Tauler-Ametller et al., 2017), a habitual food source for this population, and to extensive and intensive livestock rearing (Tauler-Ametller et al., 2019).

Finally, this thesis uses data from two different sources. The first, corresponding to continental Spain, is based on a national breeding census data carried out by SEO/Birdlife (Del Moral and Martí, 2002; Del Moral, 2009; Del Moral and Molina, 2018a) and performed using a standardised protocol for all Spanish autonomous communities in 2000, 2008 and 2018. The second source, corresponding to central and eastern Catalonia, uses data from fieldwork conducted within the framework of this thesis derived from 22 Egyptian vultures tagged with GPS-GSM devices to track their movements. However, during this thesis, we only make use of data corresponding to 16 individuals as the remaining six birds all suffered some kind of accident relating die to human activities. This information, together with monitoring data for the breeding population, is central to the understanding of how emerging conservation challenges influence the behaviour and, consequently, the conservation of Egyptian vultures.

OBJECTIVES AND THESIS STRUCTURE

This thesis examines urgent conservation issues derived from sustainability, such as human-driven transformations, circular economy, changes in agricultural systems and the current conservation measures confronting a globally endangered migratory bird, the Egyptian vulture (*Neophron percnopterus*). Specifically, our major interest is to expand existing knowledge of the spatial ecology of this vulture in the current context of sustainable development. Within these general objectives, we address the following specific objectives:

1) Identify the factors that shape the current distribution and movement patterns.
2) Understand how changes in habitat features and shifts in food availability derived from human action affect these spatial patterns.
3) Assess the spatial coverage of Protected Areas (PAs) committed to safeguarding this species of great conservation significance.

To achieve our goals, we divided this thesis into three chapters **(Fig. 3**). In **Chapter 1**, we fulfil specific objectives 1 and 2. Here, we address the environmental factors that influence temporal and spatial variation in the distribution and abundance of the Egyptian vulture in continental Spain over the past two decades. To do so, we employ an approach based on monitoring data from breeding censuses and the Species Distribution Models (SDMs) to analyse spatial changes at two scales: at regional level (i.e. continental Spain) and at local level defined by spatial autocorrelation analysis. We also analyse temporal changes in abundance patterns and identify significant environmental factors, some of which derive from the sustainable policies that have caused the population regression of this avian scavenger. In **Chapter 2**, we also fulfil specific objectives 1 and 2. Here, we use telemetric data from 16 individuals tagged with GPS devices in Catalonia to measure how a particular European sustainable measure has affected the movements of vultures via a novel approach based on network analysis. In this chapter, we investigate what would happen if some predictable food sources (e.g. landfills) for vultures were to disappear. In particular, through simulations, we analyse which other sources would be exploited and which are most important for the conservation of this species. Finally, in **Chapter 3**, we fulfil specific objective 3. We focus on the role of PAs as the primary conservation tool to preserve Egyptian vulture populations in central and eastern Catalonia under a sustainable scenario. Our analysis uses both traditional monitoring and telemetric technology to specifically assess whether the Natura 2000 (regional) and ZPAEN (local) networks successfully embrace the most crucial areas for vulture survival. Few studies have ever assessed how these PAs coincide with this species' vital areas (e.g. feeding grounds); indeed, even fewer have ever considered the non-breeding part of the population, which is generally overlooked when conservation measures are being implemented.

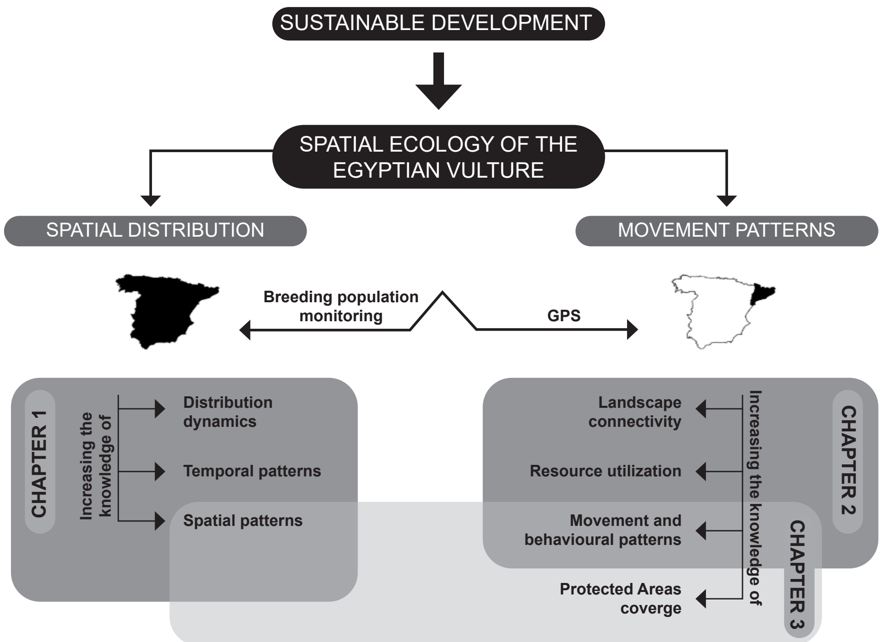

Figure 1. Conceptual framework of methodological part of this thesis.

We tackle a series of questions and methodologies throughout the thesis that provide a cross-sectional view of important aspects of the spatial ecology of threatened vultures. Additionally, the diversity of methods used and developed can be extrapolated to other regions and even to other species that share ecological characteristics with vultures. Finally, the questions raised here are of special ecological and behavioural interest and have great application for conservation.

SUPERVISOR'S REPORT

Joan Real Ortí, Joan Ll. Pretus Real and Ainara Cortés-Avizanda, co-directors of the doctoral thesis titled "Spatial Ecology of the Endangered Egyptian Vulture: from Distribution and Movement to Biological Conservation" by Catuxa Cerecedo Iglesias, certify that the candidate has carried out the research described in this thesis. The thesis comprises three scientific works in scientific article format, two of which have already been published in international scientific journals, including the Science Citation Index (SCI), and another is under review. The references of these articles are detailed below, along with the candidates' contributions to each of them and the impact factor of each journal. Furthermore, we certify that no co-author of these articles or other works presented in this doctoral thesis has implicitly or explicitly used these works as part of other theses.

Chapter 1. Cerecedo-Iglesias, C., Pretus, J.L., Hernández-Matías, A., Cortés-Avizanda, A., Real, J., 2023. Key factors behind the dynamic stability of pairs of egyptian vultures in continental Spain. Animals 13, 2775. https://doi.org/10.3390/ani13172775.

- Contribution of the candidate: Design and development of analytical methods, interpretation of the results, leading of manuscript writing.
- About the journal: *Animals* was evaluated at Journal Citation Reports (JRC) with an Impact Factor of 3.0 (2022). The Impact Factor of the journal was listed as number 13 out of 143 in the field of veterinary science (Q1), and as number 12 out of 62 in agriculture, dairy and animal science (Q1).

Chapter 2. Cerecedo-Iglesias, C., Bartumeus, F., Cortés-Avizanda, A., Pretus J.L., Hernández-Matías, A., Real, J. 2023. Resource predictability modulates spatial-use networks in an endangered scavenger species. Mov. Ecol. 11, 22. https://doi.org/10.1186/s40462-023-00383-4.

- Contribution of the candidate: Data collection, design and development of analytical methods, interpretation of the results, leading of manuscript writing.
- About the journal: *Movement Ecology* was evaluated at Journal Citation Reports (JRC) with an Impact Factor of 5.25 (2021). The Impact Factor of the journal was listed as number 35 out of 173 in the field of ecology (Q1).

Chapter 3. Cerecedo-Iglesias, C., Cortés-Avizanda, A., Pretus, J.L., Hernández-Matías, A., Real, J. Assessing protected areas for avian scavengers: Insights for the conservation of an endangered long-lived and mobile species. Under review in Ibis.

- Contribution of the candidate: Data collection, design and development of analytical methods, interpretation of the results, leading of manuscript writing.
- About the journal: *Ibis* was evaluated at Journal Citation Reports (JRC) with an Impact Factor of 2.1 (2022). The Impact Factor of the journal was listed as number 5 out of 29 in the field of ornithology (Q1).

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CHAPTERS

CHAPTER 1

Key factors behind the dynamic stability of pairs of Egyptian vultures in continental Spain

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ABSTRACT

Conservation science aims to identify the factors influencing the distribution of threatened species, thereby permitting the implementation of effective management strategies. This is key for long-lived species that require long-term monitoring such as the worldwide endangered Egyptian vulture (*Neophron percnopterus*). We studied temporal and spatial variations in the distribution of breeding pairs and examined the intrinsic and anthropic factors that may be influencing the abundance of breeding territories in continental Spain. Based on the census data of breeding pairs from 2000, 2008, and 2018, we used Rank Occupancy-Abundance Profiles to assess the temporal stability of the population and identified the spatial heterogeneity through a Local Index of Spatial Autocorrelation analysis. The GLMs showed that the abundance distribution was mainly influenced by the abundance of griffon vultures (*Gyps fulvus*) and cattle at a regional scale. Nonparametric comparisons showed that the presence of wind farms had a significant negative effect on local breeding pairs abundance, but that supplementary feeding stations and food resource-related variables had a positive impact. In light of these findings, we recommend a hierarchical approach in future conservation programs involving actions promoting regional-scale food resource availability and highlight the need to address the negative impact of wind farms at local levels.

Keywords: abundance distribution; Egyptian vultures; LISA; ROAPs; spatial autocorrelation; trophic resources; supplementary feeding stations; vulture conservation; wind farms.

INTRODUCTION

The species-environment relationships determining the current distribution of endangered species within their geographic range are a key ecological process; therefore, examining and understanding these species-environment relationships may be essential for the development of effective conservation strategies devoted to recovering endangered species (Lindenmayer and Burgman, 2004; Sutherland et al., 2004; Groom, et al., 2006). However, the study of the distribution patterns of large long-lived species presents exceptional challenges, as it requires the integration of spatial and temporal shifts in abundances (Soberón, 2007; Pearman et al., 2008). Furthermore, species-environment relationships depend greatly on the scale at which they are studied (Sax and Gaines, 2003; Whittingham et al., 2007; Boyd et al., 2008), and the neglect of appropriate spatial and temporal considerations can lead to inaccuracies in forecasts of species distribution (Lee-Yaw et al., 2022). Species distribution is a dynamic phenomenon, characterized by spatial contractions and expansions over time, that is influenced by the interplay of biological, ecological, and biogeographic factors. In this context, the application of species distribution models (SDMs; see review Elith and Leathwick, 2009) has been widely used to study species occupancy and abundance patterns.

SDMs empirically examine species occupancy or abundance using grid-cells and the species-environment relationship in terms of intrinsic and extrinsic factors. Despite the advantages of using such methods (e.g., identifying important areas for species conservation; Margules and Pressey, 2000), the consideration of variability in the temporal dimension is rarely addressed. The incorporation of the continuous temporal dimension (i.e., neither a static nor specific time interval; Elith and Leathwick, 2009; El-Gabbas et al., 2021) is a novel approach that allows us to use distinct ecological processes and time-dependent factors governing fluctuations in occupancy and abundance (Bateman et al., 2012; Fernandez et al., 2017; Milanesi et al., 2020). In addition, since species distribution patterns are also sensitive to factors operating in the local environment such as microclimate or food availability (Willis and Whittaker, 2002) that differ greatly from those at work at larger scales (Sax and Gaines, 2003), SDMs require a specific spatial scale or scales under scrutiny. Additionally, landscape heterogeneity in terms of the availability of suitable breeding sites may also influence occupancy and abundance patterns (Pearson et al., 1996), thereby promoting spatial aggregation and uneven distribution across a landscape (Condit et al., 2000; Lichstein et al., 2002).

Studying the occupancy and abundance distribution of large long-lived vertebrate species presents numerous challenges due to their wide range of different behaviors that require large interconnected habitats (Gibb et al., 2017; Buechley et al., 2021; Gantchoff et al., 2022). In this context, vultures are no exception, and their spatial and temporal distribution is often influenced by multiple, often environmental (Oppel et al., 2017) and human-related (Zuberogoitia et al., 2014; Oliva-Vidal et al., 2022) factors whose impact varies depending on scale. As long-lived birds, they exhibit late maturity and low reproductive rates, which leads to slow natural changes in population numbers over time (Donázar, 1993).

Here, we use a novel approach to analyze the factors that influence temporal and spatial variation in the abundance distribution of breeding pairs of the long-lived Egyptian vulture (*Neophron percnopterus*), a species threatened worldwide at different local (i.e., specific 100 km^2 areas within a landscape) and regional (i.e., larger geographic regions such as countries) spatial scales. Despite the crucial role that Egyptian vultures play in ecosystem health, they face threats such as habitat loss, persecution, electrocution, and poisoning (BirdLife International, 2021). In Spain, human activities have resulted in local extinctions (Carrete et al., 2007) but, interestingly, in some regions the number of breeding territories is now increasing (Tauler et al., 2015; Franch et al., 2021). We used long-term Egyptian vulture monitoring information in one of this vulture's main breeding areas. We aimed (1) to test whether or not Egyptian vulture occupancy and abundance has changed over time in continental Spain; (2) to determine the spatial patterns, i.e., the spatial heterogeneity, of the abundance of breeding territories in the study region; (3) to identify the factors contributing to spatial variation at the local scale; and (4) to investigate the factors responsible for changes in abundance over both time and space at the regional scale. Based on the hypothesis that both temporal and spatial factors influence species distribution, we predicted that the abundance of breeding pairs of Egyptian vultures would vary over time (i.e., a non-stationary distribution) and space (i.e., an aggregated distribution). Furthermore, we anticipated that the factors driving this species' distribution would differ depending on the spatial scale employed (Sax and Gaines, 2003). The findings of this study will help develop targeted conservation plans for declining vulture populations and facilitate efforts to increase the occupancy rate of their breeding populations.

MATERIALS AND METHODS

Study Species

The Egyptian vulture is a long-lived migratory scavenger that is globally "Endangered" (BirdLife International, 2021). During the breeding period (March-August), it establishes territories in southern Europe, the Middle East, and central and southern Asia, but spends the winter in various parts of Africa. The Spanish population, which represents 12% of the world's total (BirdLife International, 2021) and 27% of the European total, suffered a serious decline in 1987-2000 (Donázar, 2004) due to multiple causes, including poisoning (Hernández and Margalida, 2009), disturbance at breeding territories (Zuberogoitia et al., 2014), electrocution (Donázar et al., 2002), collision with human infrastructures such as power lines and wind turbines (Carrete et al., 2009), and reduced food availability (Donázar et al., 2010). Here, we used data from the last three censuses (2000, 2008, and 2018) from continental Spain (493,719 km^2, **Fig. 1**), but excluded data from the Canary and Balearic Archipelagos where this vulture is a resident species (Donázar et al., 2002). Censuses were conducted using a standardized methodology in which territorial breeding pairs in potential breeding areas were searched for (Del Moral and Martí, 2002; Del Moral, 2009; Del Moral and Molina, 2018a). For each breeding territory, the location and status (occupied vs. unoccupied) was recorded. To obtain the abundance data for each census year, these locations were incorporated into a spatial Universal Transversal Mercator (UTM) grid with a resolution of 10 x 10 km and the abundance of each cell was calculated by summing the locations of confirmed breeding territories. During the analysis, we only took into account cells where the species was present in at least one year in the period 2000-2018 ($n = 1033$).

Analytical Procedure

Analyzing the Temporal Variation in Distribution

The Rank Occupancy-Abundance Profiles (ROAPs; Collins et al., 2009) approach was used to test the null expectation that the regional population of Egyptian vulture can be considered stable over the years or, conversely, that significant changes have occurred (either increase or decrease) in both abundance and occupancy patterns. ROAPs are a graphical procedure based on the position of cells in a rank according to their occupancy and abundance

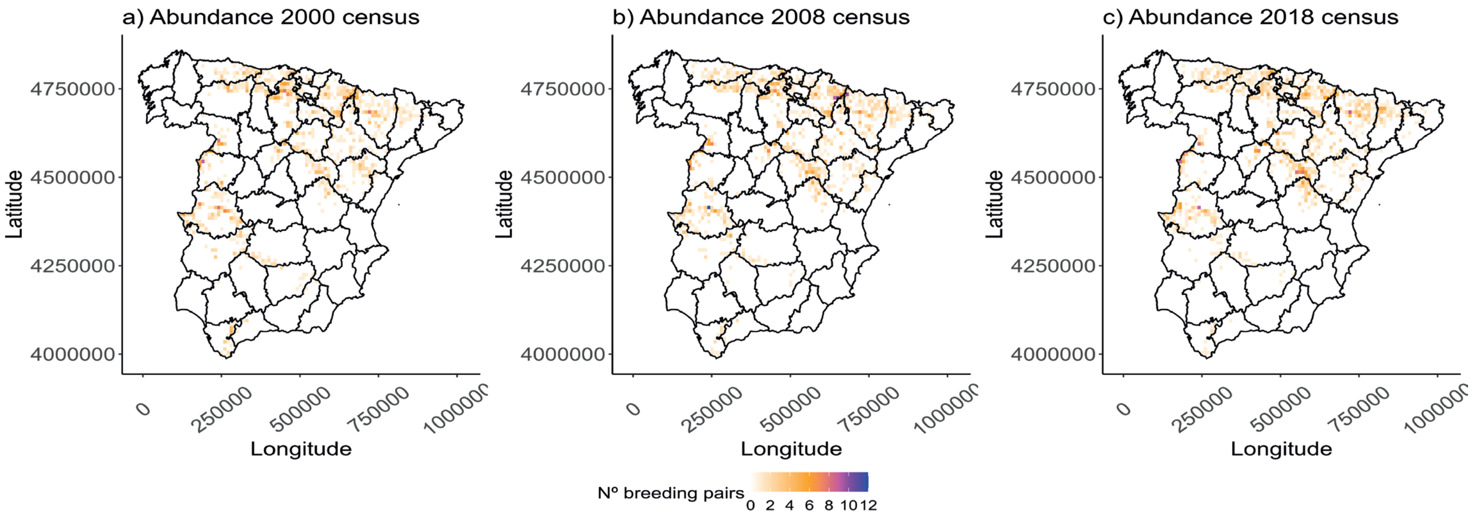

Figure 1. The distribution of Egyptian vulture breeding pairs in three different years: (**a**) 2000, (**b**) 2008, and (**c**) 2018. Each 100 km^2 grid shows the number of occupied territories during the breeding period.

that is similar to a classical ranking of species within communities (see Collins et al., 2009). They consist of scatterplots in which the X-axis (values range from 0 to 1) corresponds to the relative ranks of grid-cells based on their occupancy, and the Y-axis corresponds to the absolute abundance of pairs per grid-cell. To obtain the relative ranks, we assigned the rank position 1 to the highest abundance and divided each rank by the total number of cells (n = 1033). Three profiles were built separately from the abundance of pairs data for each 10 x 10 km cell (2000, 2008, and 2018).

Additionally, to test for differences in the occupancy and abundance distribution between the three censuses, we followed the procedure described by Collins et al. (2009), which consists of pooling the abundance data of the three censuses and randomly assigning a year. We iterated this routine 100 times and calculated the D* statistic (the area under the curve of abundances of each year) for each run to obtain a reference random distribution. Furthermore, we compared the observed statistic D* with the random distribution and tested to see whether or not it could be considered within the scope of randomized distribution at a significance level of $\boldsymbol{\alpha} = 0.05$.

Analyzing the Spatial Heterogeneity

To investigate the spatial variation in abundance, i.e., the spatial heterogeneity, we first identified the cells exhibiting aggregation patterns. To do so, we first checked for the existence of spatial autocorrelation by using the global Moran's I test (Moran, 1950), a preliminary procedure for detecting at which scales a significant spatial positive dependency occurs. We further identified the cells with spatially aggregated patterns using the procedure known as the Local Index of Spatial Autocorrelation (LISA; Anselin, 1995). For this two-step analysis, we analyzed the 2018, 2008, and 2000 censuses separately. Moran's I Index reflects the degree of similarity or dissimilarity between abundance values based on the distances between the central points of the cells. The values in this index range between –1 (regular distribution, negative autocorrelation) and +1 (aggregated distribution, positive autocorrelation), zero being the reference random distribution. This index was calculated using the distance matrix between the central points of the cells that had been occupied at least once during the census (n = 1033). Then, we used a Monte Carlo simulation and 999 permutations to obtain the significance of the spatial autocorrelation at a regional level. Once we had detected the spatial autocorrelation of the abundance data, we used the LISA to detect spatial aggregation areas in which the number of breeding pairs was greater or lower than in nearby areas. The LISA measures allow us to distinguish between spatial aggregation units and non-aggregation units using the scatterplot resulting from Moran's I Index and by dividing it into four quadrants with the abundance values plotted against spatial distances (Nelson and Boots, 2008; Martínez Batlle and Van der Hoek, 2018). These values are classified according to the quadrant in which they are located on the scatterplot: High-High (high surrounded by high), Low-Low (low surrounded by low), High-Low (high surrounded by low), and Low-High (low surrounded by high). Then, we combined classified the High-High and High-Low cells as High cells, and Low-Low and Low-High cells as Low cells. High cells represent the clusters where the number of breeding pairs is significantly higher than in neighboring cells (spatial aggregation), while Low cells represent clusters in which abundances are significantly lower than the abundances in neighboring cells (spatial non-aggregation).

Analyzing the Factors That Shape Recent Abundances at Local and Regional Scales

At local scale, once we had identified the cells with aggregated patterns, we then analyzed the factors driving this aggregation. To do so, we used a nonparametric Kruskal-Wallis test to compare each of the 16 variables relating to habitat, food availability, human pressure, and heterospecific attraction that explain the differences in abundance between the High and Low cells (**Table 1**). The significance level was adjusted using the Bonferroni correction.

To determine the factors that shaped the abundance distribution of Egyptian vultures in the 2018 census in continental Spain at a large scale, we performed generalized linear models (GLM; negative binomial distribution and log link function; Zuur et al., 2009). The challenge of limited fine environmental data is a common issue in studies analyzing diverse environmental and anthropic variables across lengthy time spans. Our study encountered this limitation, with a temporal mismatch between the explanatory variable data and species abundance data collected in 2000, 2008, and 2018. Notably, data for explanatory variables were available only after 2008, such as 2009 census data for livestock and 2018 data for wind turbines and landfills. To address this, we focused our analysis on the year 2018, postulating that this later data would yield stronger models for associating Egyptian vulture distribution compared to earlier years. Additionally, we considered only explanatory variables with significant differences between High and Low cells and used the abundance of breeding pairs per cell as a dependent variable to analyze whether or not the same factors drive the abundance distribution at different scales. Moreover, in our analyses, we considered two key assumptions regarding the relationship between Egyptian vulture abundance and environmental factors. Firstly, we assumed that most of the variability in abundances observed in 2018 could be explained by the abundances registered during the previous census and therefore we considered the abundance of the previous census to be a proxy for habitat quality, based on the findings of Serrano et al. (2021). Secondly, we incorporated a temporal term into our statistical model to account for changes in abundance distribution over time. We assumed that any independent variable (e.g., food availability) that was found to have a significant effect on abundance distribution after accounting for temporal changes was a potential driver of abundance changes between censuses. Therefore, apart from variables with differences between High and Low cells, we also considered spatial and temporal terms. The spatial term was the third-degree polynomial derived from coordinates, longitude (x), and latitude (y) of the central point of the 10 x 10 km cells in order to, on the one hand, avoid the false correlation between species and its environment and, on the other hand, to identify if there were spatial patterns in the abundance data that could not be accounted for or explained by the environmental variables (Legendre and Fortin, 1989). The temporal terms corresponded to the abundance of breeding pairs of Egyptian vultures according to data from the 2000 (hereafter, NP00) and 2008 (hereafter, NP08) Egyptian vulture censuses. These two temporal terms were included separately in two different models.

We developed the analysis in the R environment (R Core Team, 2021) using the “adespatial” (Dray et al., 2023), “MASS” (Venables and Ripley, 2002), and “MuMIn” packages (Barton, 2009). To select the best models, we used the Corrected Akaike Selection Criterion (AICc; Sugiura, 1978).

Table 1. Explanatory variables used to describe the spatial aggregation patterns and the regional distribution model of the Egyptian vulture in continental Spain. All variables were obtained at a resolution of 10 x 10 km cells (more information in **Supplementary Material A**).

Acronym	Definition	Source of Information
(1) Habitat		
ALT	Altitude (meters above sea level)	Digital Elevation Model (DEM)
NIC	Cover (%) of non-irrigated crops (e.g., regular annual crops, cereals, leguminous crops)	CORINE Land Cover
IRR	Cover (%) of irrigated crops (e.g., arable, crops, rice fields, non-permanent grass)	CORINE Land Cover
TREE	Cover (%) of permanent crops (e.g., olive groves, orchids, vineyards, fruit trees)	CORINE Land Cover
DEH	Cover (%) of agroforest systems (named dehesas in Spain)	CORINE Land Cover
ROC	Cover (%) of bare rocks (e.g., stable rocks with limestone pavements)	CORINE Land Cover
FOR	Cover (%) of forests (e.g., broad-leaved, coniferous, and mixed forests)	CORINE Land Cover
PAS	Cover (%) of pasturelands (e.g., permanent grasslands)	CORINE Land Cover
(2) Food availability		
COW	Number of cows surveyed on national census	National Institute of Statistics (INE)
SHEEP	Number of sheep surveyed on national census	National Institute of Statistics (INE)
LAND	Number of landfills	MAPAMA
SFS	Number of supplementary feeding stations	MAPAMA

Table 1 *Cont.*

Acronym	Definition	Source of Information
(3) Human pressure		
URB	Cover (%) of urban areas (e.g., residential and commercial/ industrial buildings, parking lots, small squares)	CORINE Land Cover
WTG	Number of wind turbines	*Asociación Empresarial Eólica* (AEE)
POIS	Number of poison-related mortality events of wild fauna	WWF and SEO/Birdlife (De la Bodega et al., 2020)
(4) Heterospecific relationship		
GF	Number of breeding pairs of griffon vultures	SEO/Birdlife (Del Moral and Molina, 2018b)

Explanatory Variables

Grid cells were characterized by 16 variables relating to habitat, food availability, human pressure, and heterospecific relationships to determine the factors potentially shaping the abundance distribution. Habitat was represented by land-use coverage in several different categories (see **Table 1**). In addition, we included elevation as a habitat-related variable since it is associated with the reproductive habitat of breeding pairs such as cliffs (Donázar, 1993). We used the number of cows and sheep per 10 x 10 km cell as a proxy for potential food resources following Margalida et al. (2007). We also considered the locations of landfills and supplementary feeding stations (specific places where carcasses are deposited to feed avian scavengers to increase the availability of food resources as a vulture conservation measure; see review Cortés-Avizanda et al., 2016) as predictable anthropogenic food sources (Tauler-Ametller et al., 2017). Human pressure was evaluated using various sources of information, including the location of wind farms, the number of poison-related mortality events (De la Bodega et al., 2020), and the coverage of urban areas, all of which have been shown to be relevant factors in the breeding distribution of Egyptian vultures (Sarà and Di Vittorio, 2003). Finally, we used the number of breeding pairs of the dominant species in the scavenger guild, the griffon vulture (*Gyps fulvus*), as a proxy for controlling heterospecific effects (Cortés-Avizanda et al., 2010; Cortés-Avizanda et al., 2012). These variables were chosen to comprehensively represent the factors potentially shaping the abundance distribution of the scavenger guild in the study area. A summary of the specific variables and their sources can be found in **Table 1** (see **Supplementary Material A** for details of data preparation). All units of food availability, human pressure (except urban areas) and heterospecific relationship-related explanatory variables refer to densities, i.e., the quantity or concentration of some abiotic or biotic factor within a given 100 km^2 grid-cell.

RESULTS

Temporal Variation on Distribution

From year 2000 onwards, censuses (every 8-10 years) showed a slight increase in the total number of breeding pairs of Egyptian vultures in continental Spain, with a total of 1270, 1364, and 1372 pairs in 2000, 2008, and 2018, respectively. Occupancy also increased over the years, with a total of 700, 725, and 731 occupied cells in 2000, 2008, and 2018, respectively. Visual inspection of ROAPs, in combination with the D* statistic, showed an almost exact profile of the three different censuses, indicating that the overall abundance and the frequency of abundances are statistically indistinguishable over the years (**Table 2; Fig. 2**). In addition, the abundance maps for the Egyptian vulture showed a temporal variation in cells despite a similar occupancy and abundance distribution across the study area (see **Fig. 1**).

Table 2. Egyptian vulture breeding pairs abundance and occupancy changes in Spain in 2000, 2008, and 2018. The D* statistics represent the area under the curve of the ROAPs. *P* is the *p*-value. The abundance change is calculated by subtracting the absolute abundances between years, while the occupancy change is calculated by subtracting the total number of occupied grid cells between years.

Years	D*	P	Abundance Change	Occupancy Change
2018-2008	0.992	0.648	8	6
2008-2000	0.970	0.615	94	25
2018-2000	0.918	0.640	102	31

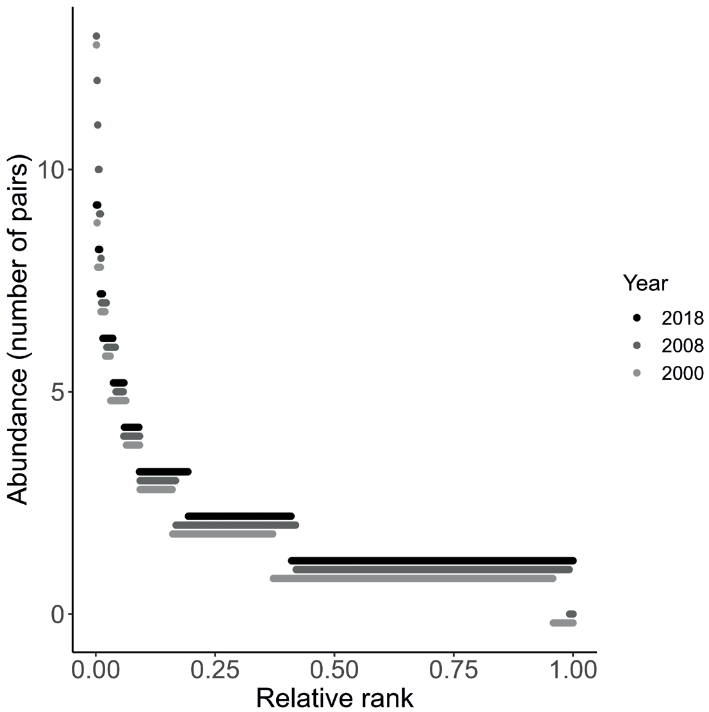

Figure 2. Rank Occupancy-Abundance Profiles (ROAPs) of Spanish national census data of Egyptian vultures in three different years. Local abundance was measured as the number of breeding territories on a 100 km^2 grid. Relative rank was calculated by dividing the rank descending order of cells by the total number of grid cells in which species has been present at least once during the study period (N = 1033). Grid cells where species were not present in any census.

Spatial Variation on Distribution

The autocorrelation analysis showed a strong spatial correlation in the distribution of abundances of the Egyptian vulture. Furthermore, the spatial autocorrelation structure of the abundance distribution remained consistent over the years (see **Supplementary Material B**). Moran's test was statistically significant (Moran's I = 0.075; P = 0.001) and the correlogram showed a diminishing positive autocorrelation with increasing distances (**Fig. 3a**). The LISA index of the abundances of breeding pairs in 2018 showed that 57 cells were classified as High-cells, with a mean abundance (± SE) of 5.37 (±0.22) breeding pairs per cell, while 31 cells were classified as

Low-cells, with a mean abundance of 0.65 (±0.09) pairs per cell. Meanwhile, the remaining 945 cells were not spatially associated with their neighboring cells in terms of abundance. In addition, the High cells represented 22.3% of the abundance (306 breeding pairs) and occupied 18.12% (5700 km^2) of the distribution area. The aggregation abundance patterns rarely occurred in isolated cells but were usually a set of two or more cells (**Fig. 3b**).

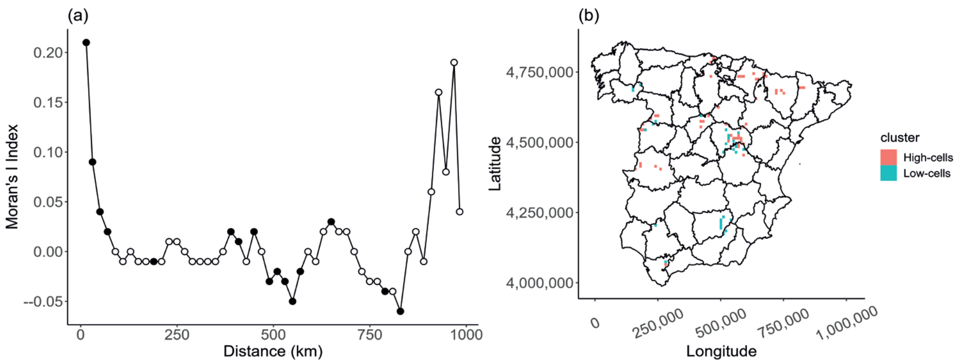

Figure 3. Spatial autocorrelation of the abundance distribution of reproductive pairs of Egyptian vultures in continental Spain in 2018. (**a**) Moran's I correlogram shows the distance lag between abundances in which spatial autocorrelation is significant (black-filled circles). (**b**) High (red) and Low (blue) cells detected by LISA analysis. High cells represent cells with significantly high abundances compared to neighboring cells, while Low cells represent cells with significantly low abundances compared to neighboring cells.

Local Drivers of Abundance Patterns at Different Spatial Scales

The Kruskal-Wallis comparison between High and Low cells revealed that the densities of cows (ca. heads/100 km^2), *dehesas* (wood pasture; %), supplementary feeding stations (units/100 km^2), and griffon vultures (ca. number of breeding pairs/100 km^2) were significantly higher in High than in Low cells. Conversely, the number of wind turbines (ca. units/100 km^2) was significantly lower in the High than in the Low cells, this number being almost seven times higher in the Low cell areas (**Fig. 4**). The remaining variables showed no significant differences (see **Supplementary Material C**).

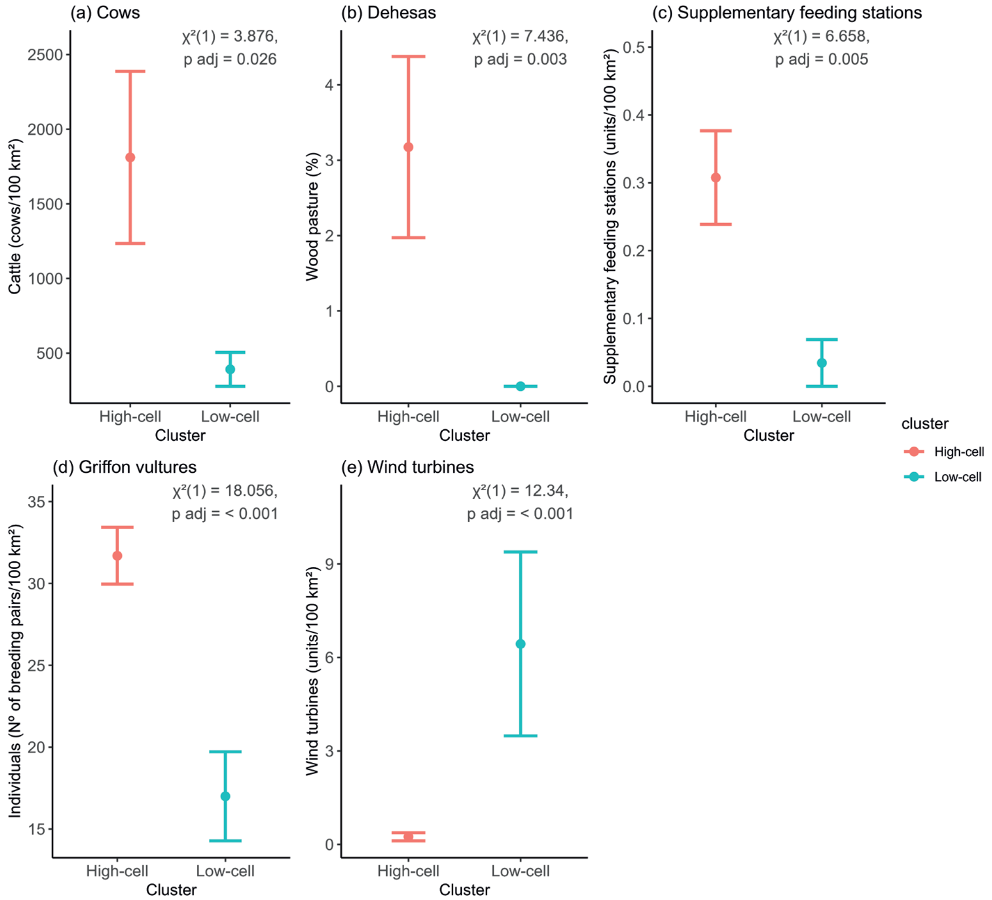

Figure 4. Plots of variables with significant differences between High (H) and Low (L) cells. High cells are areas where environmental features drive a local increase in abundance, while Low cells are areas where environmental features drive a local decrease in abundance. Each variable represents the density of that variable in each 10 x 10 km grid. Plots show mean values of each variable and 95% CIs. We only plotted the variables with significant differences between High and Low cells.

By contrast, both GLMs conducted at the regional scale revealed the range of factors affecting the vulture distribution (**Table 3**). The average models showed statistically positive associations between the abundance of breeding pairs of Egyptian vultures and the abundance of griffon vultures, as well as a weaker association with the number of cows (see the average model with a ΔAIC threshold of <2 in **Supplementary Material D**). The model, which included the Egyptian vulture abundance in 2008 as an independent variable, exhibited a better goodness-of-ft (Model 1; pseudo-R^2 = 0.315) compared to the model that used the abundance in 2000 (Model 2; pseudo-R^2 = 0.245). Our GLM analysis indicated that the abundance of breeding pairs is primarily explained by previous census variables, while the variation not accounted for by the previous census data is influenced by the abundance of griffon vultures and cows. These latter variables are identified as the principal drivers of changes in Egyptian vulture abundance.

Table 3. Top 10 competing models for GLM from abundance distribution of Egyptian vultures in continental Spain. The abundance of 2008 (NP08) was included as an independent variable in Model 1 and the abundance of 2000 (NP00) was included as an independent variable in Model 2. Y- and X-related variables correspond to the third-polynomial spatial terms of the model.

Model	Variables	df	Loglik	AICc	Delta	Weight
1.1.	COW + GF + NP08 + Y + Y^2	7	−1365.67	2745.44	0.000	0.0046
1.2	COW + GF + NP08 + Y + Y^3	7	−1365.69	2745.50	0.058	0.0045
1.3.	COW + GF + NP08 + Y^2 + Y^3	7	−1365.73	2745.57	0.127	0.0043
1.4	COW + GF + SFS + NP08 + Y + Y^2	8	−1365.04	2746.22	0.785	0.0031
1.5	COW + GF + SFS + NP08 + Y + Y^3	8	−1365.07	2746.27	0.834	0.0030
1.6	COW + GF + SFS + NP08 + Y^2 + Y^3	8	−1365.10	2746.33	0.895	0.0029
1.7	COW + GF + NP08 + X + X^2Y + XY + XY^2	9	−1364.14	2746.46	1.023	0.0028
1.8	COW + DEH + GF + NP08 + Y + Y^2	8	−1365.17	2746.48	1.039	0.0027
1.9	COW + GF + NP08 + WTG + Y + Y^2	8	−1365.19	2746.52	1.080	0.0027
1.10	COW + GF + NP08 + X + X^2 + XY + XY^2	9	−1364.18	2746.54	1.099	0.0027
2.1	COW + GF + NP00 + Y + Y^2	7	−1415.04	2844.19	0.000	0.004
2.2	COW + GF + NP00 + Y + Y^3	7	−1415.08	2844.27	0.076	0.004
2.3	COW + GF + NP00 + Y^2 + Y^3	7	−1415.13	2844.36	0.168	0.004
2.4	COW + GF + NP00 + WTG + Y + Y^2	8	−1414.27	2844.67	0.479	0.003
2.5	COW + GF + NP00 + WTG + Y + Y^3	8	−1414.29	2844.72	0.527	0.003
2.6	COW + GF + NP00 + WTG + Y^2 + Y^3	8	−1414.32	2844.78	0.589	0.003
2.7	COW + DEH + GF + NP00 + Y + Y^2	8	−1414.41	2844.97	0.773	0.003
2.8	COW + DEH + GF + NP00 + Y + Y^3	8	−1414.48	2845.10	0.903	0.003
2.9	COW + DEH + GF + NP00 + Y^2 + Y^3	8	−1414.55	2845.25	1.052	0.002
2.10	COW + DEH + GF + NP00 + WTG + Y + Y^2	9	−1413.57	2845.33	1.132	0.002

DISCUSSION

This study presents an analysis of the temporal and spatial variation, as well as the distribution patterns at different scales, of breeding pairs of the endangered Egyptian vulture in one of its global strongholds. Our findings revealed stability in its breeding population in continental Spain after years of continuous decline (Donázar, 2004; Del Moral, 2009). However, despite this regional stability, significant spatiotemporal variation occurred. The distribution of Egyptian vultures exhibited an aggregated pattern, with the highest abundances concentrated in locations with specific environmental characteristics. This aggregation is a result of scale-dependent factors that shape the population trend. In addition, we identified a hierarchical structure of factors affecting the distribution patterns at two different local and regional scales.

Contrary to our initial expectations, we only found limited significant changes in the regional distribution of the species over time. Both the occupancy and abundance distribution patterns, assessed using ROAPs and D* statistics, exhibited a relatively stable trend during the study period. This stability can be attributed to the intrinsic and consistent fidelity of Egyptian vultures to their breeding territories (López-López et al., 2014), a characteristic observed in other raptors (Bosch et al., 2010), which ensures that individuals remain in their territories for many years regardless of environmental changes. Moreover, the combination of territorial fidelity and the conspecific attraction of raptor species (Margalida et al., 2008), resulting in the selection of territories near successful conspecific settlements (see *habitat-copying hypothesis* in Danchin et al., 2004), probably confers great population stability at a regional scale. However, despite this regional stability, we did detect temporal variability expressed as a large number of cells with low abundance values (e.g., with only one breeding pair) with discontinuous occupancy over time (**Fig. 1**). This observed variability in temporal abundance can be explained by human-related factors (e.g., illegal poisoning; Grande et al., 2009; Hernández and Margalida, 2009) or by demographic stochasticity (i.e., if there are few individuals, the grid cell is more likely to empty).

Additionally, the shape of the ROAP suggested a spatial aggregation of breeding territories. The steep curves indicated that breeding pairs tend to cluster in specific areas, which was confirmed by the LISA analysis that identified cells with a large number of breeding pairs. We observed more cells with low abundances (one breeding pair per cell) than cells with high abundances (five or more breeding pairs per cell), resulting in a heterogeneous distribution pattern. Moreover, this heterogeneity was also supported by our autocorrelation analyses, which revealed clear spatial autocorrelation in the census data over short distances (i.e., 20 km), consistent with patterns observed in other populations (e.g., in Turkey, Katzenberger et al., 2019) and other raptors (e.g., lesser kestrel; De Frutos et al., 2007). The observed spatial aggregation was found to be a result of scale-dependent factors that shape the abundance distribution. Certain local-level factors such as the presence of wind turbines were associated with lower values of abundance, suggesting they acted as drivers of these patterns. The higher cover of *dehesas* and presence of supplementary feeding stations were associated with more breeding territories, which indicates that these factors favor the study species. However, it is worth noting that these factors only act in specific marginal areas and not throughout continental Spain. For instance, an Egyptian vulture population in southern Spain was affected by wind farm-related mortality during the breeding (Carrete et al., 2009) and migration (Sanz-Aguilar et al., 2015) periods. Additionally, the *dehesas* and agroforestry areas located only in western Spain serve as important foraging habitats for other vulture species due to the higher availability of food compared to other agricultural systems or landscapes (Carrete and Donázar, 2005; Martin-Díaz et al., 2020) and support a high relative abundance of livestock grazing and other species (e.g., rabbits) that scavenging birds can exploit. The authors of Grande (2006) reported that supplementary feeding stations used as a conservation measure help both the maintenance of the closest breeding territories and breeding success. Nevertheless, these supplementary feeding sites that act as local attractors for high densities of vultures and other scavengers may have detrimental consequences. For instance, supplementary feeding stations can adversely affect the productivity of Pyrenean Bearded vultures (*Gypaetus barbatus*) due to the congregation of non-breeding individuals, leading to a decline in the quality of the reproductive habitat (Carrete et al., 2006).

The main factors associated with changes in abundance at the regional scale over both time and space were griffon vulture and cattle abundances. On the one hand, our results suggest that cattle are one of the main food sources of carrion and feces at local and regional levels for the Egyptian vultures breeding in continental Spain, and play an important role in its distribution (Mateo-Tomás and Olea, 2015; Tauler-Ametller et al., 2017). In addition, the coprophagous behavior of this species also explains its close association with cows. Egyptian vultures consume cow dung to obtain lutein, a yellow carotenoid responsible for its facial coloration (Negro and Galván, 2018) that also plays an important role in its immunological system as an antioxidant (Tauler-Ametller et al., 2019). On the other hand, the positive correlation between breeding Egyptian and griffon vultures suggests a heterospecific interaction between these two species that positively impacts the number of Egyptian vulture breeding pairs. Nevertheless, in other studies, the presence of griffon vultures was not associated with the territory occupancy rate of Egyptian vultures as observed in the Balkan Peninsula (Oppel et al., 2017). In addition, both vulture species probably respond in a similar fashion to specific environmental characteristics, which means that the abundance of griffon vultures will be an indicator of the most suitable habitat for breeding pairs of Egyptian vulture (Margalida et al., 2007; Van Beest et al., 2008). Due to the spatial overlap between these two species, some authors define this interaction as commensalism (Carlon, 1998) because (i) both species have similar ecological requirements (e.g., they are both cliff-nesting; Donázar, 1993) and (ii) given that breeding individuals, regardless of the species, are linked to a breeding area, the abundance of breeding griffon vultures may not only indicate a suitable breeding habitat but also a habitat with food availability (Carlon, 1998; Margalida et al., 2007).

Despite the fact that our main aim was to assess the likely causes of changes in the abundance distribution of breeding Egyptian vultures at different spatial scales, other factors relating to human pressure that probably also play an important role in their distribution should not be neglected in future research (e.g., electrocution and/or collision against power lines; Donázar et al., 2002; Carrete et al., 2009). Indeed, our results underscore the importance of considering both temporal and spatial variability during the process of generating distribution models. On the one hand, we used temporal population dynamics (i.e., changes between censuses) to capture how the abundance distribution can enhance the subsequent abundance distribution in such a way that the model revealed the suitability of a breeding territory. On the other hand, we took into account spatial autocorrelation in the modelling process because ignoring spatial constraints can lead to inaccurate conclusions (see Lee-Yaw et al., 2022). To fully understand the changes in endangered species distribution, more research is needed using other approaches, such as Bayesian INLA models, that consider the spatiotemporal variation in species abundance (Bakka et al., 2018).

Conservation Implications

Our findings reveal the scale-dependent factors that influence the Egyptian vulture breeding population in continental Spain. At the regional level, these factors require the implementation of global conservation strategies to ensure the species is protected across large areas and to serve as guidelines for developing conservation synergies between neighboring areas. At the local scale, the factors affecting populations or even individuals require specific actions related to the main threats affecting each population. Therefore, it is important to highlight the impact of hierarchical approaches on environmental policies. Thus, successful conservation programs aimed at preserving large vertebrate species over large areas should incorporate efficient local management actions (Whittingham et al., 2007; McAlpine et al., 2008). Based on our results, we advocate the development of a national strategy promoting, at the regional level, extensive livestock farming and the abandoning of healthy carcasses (with sanitary control) as an important and unpredictable food source for not only Egyptian vultures but the whole vulture guild (Blanco et al., 2019). Although this approach is partially implemented through the ZPAEN network (Protection Zones for the Feeding of Necrophagous Species of Community Interest), local administrations use different criteria to establish these zones, which leads to a lack of coordination at the regional scale (see Morales-Reyes et al., 2018). Additionally, some local actions should be taken to counteract the negative effect of the blades of wind turbines with which certain soaring birds including vultures are prone to collide (Carrete et al., 2012; Marques et al., 2014; personal data). Some studies have shown that the strategic placement of wind turbines and appropriate mitigation measures could help minimize the potential negative effects of wind farms on soaring birds while still allowing for the generation of renewable energy (Palacín et al., 2023). Finally, we believe it is important to underline the importance of grids with a single or few breeding pairs, since the potential for recovery and growth of endangered populations lies in these low-density areas. Conserving small populations allows them to reproduce and expand gradually, and to serve as future sources for repopulating larger areas.

CONCLUSIONS

The breeding Egyptian vulture pairs in continental Spain are generally stable but exhibit spatial variability in their distribution, thereby indicating a hierarchical structure of drivers affecting abundance patterns at different scales. Our data indicate that local-level factors such as the presence of supplementary feeding stations play an important role in the aggregation of breeding pairs. However, the overall stability of the population is mainly driven by the availability of natural food sources, particularly from livestock. Based on the scale-dependent factors influencing the distribution patterns of Egyptian vultures, we recommend the development of a national strategy promoting extensive livestock farming and encouraging the abandoning of healthy carcasses in the field as an important food source for these vultures. In addition, it is important to consider the potential local negative impacts of wind farms and other infrastructures on these species and the need for their strategic placement. Our findings highlight the importance of adopting a holistic approach to conservation efforts that takes into account over time both local –and regional– level factors.

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SUPPLEMENTARY MATERIAL

Key factors behind the dynamic stability of pairs of Egyptian vultures in continental Spain

Supplementary Material A

Supplementary Material B

Supplementary Material C

Supplementary Material D

Supplementary Material A

A.1. Digital Elevation Model

The elevation data were obtained from the 25 m resolution Digital Elevation Model provided by the National Institute of Geography (www.ign.es, accessed on 19 December 2019). To align the resolution with our 100 km^2 abundance data, we resampled the raster by applying a grid with fewer pixels. To do so, we used the *resample*() function of the raster R package and a bilinear interpolation method that uses the distance-weighted average of the four nearest pixel values to estimate a fresh pixel value.

A.2. CORINE Land Cover Maps

We used the 2018 CORINE land cover maps from Copernicus (www.land.copernicus.eu, accessed on 16 October 2019) to obtain seven variables relating to habitat and one variable relating to human pressure. The CORINE maps include 44 land-cover classes, which we reclassified into 8 different cover classes: non-irrigated crops, irrigated crops, tree crops, agroforest systems known as *dehesas*, bare rock, forests, pasturelands, and urban areas. **Table A1** shows the reassigned land-cover classes. Next, we calculated the percentage of the land cover by converting each reclassified land-cover class into polygon shapefiles, extracting the portion of the land cover in each cell, and finally rasterizing the layer with the proportion of land cover of each cell using the elevation layer as the raster base.

Table A1. Reclassifcation of CORINE land covers (CLC) with the new categories URB: urban areas; NIC: non-irrigated crops; IRR: irrigated crops; TREE: permanent crops; PAS: pasturelands; DEH: agroforestal systems (*dehesas*), and FOR: forests. Some categories of CORINE Land Cover were not reassigned to a new category. Modifed table CORINE Land Use Covers 2018 legend (land.copernicus.eu, access on 16 October 2019).

CLC Level 1	CLC Level 2	CLC Level 3	New Code
Artificial surfaces	Urban fabric	Continuous urban fabric	URB
		Discontinuous urban fabric	URB
	Industrial, commercial, and transport units	Industrial or commercial units	URB
		Road and rail networks and associated land	URB
		Port area	URB
		Airports	URB
	Mine, dump, and construction sites	Mineral extraction sites	URB
		Dump sites	URB
		Construction sites	URB
	Artificial, non-agricultural vegetated areas	Green urban areas	URB
		Sport and leisure facilities	URB
Agricultural areas	Arable land	Non-irrigated arable land	NIC
		Permanently irrigated land	IRR
		Rice fields	IRR
	Permanent crops	Vineyards	TREE
		Fruit trees and berry plantations	TREE
		Olive groves	TREE
	Pastures	Pastures	PAS
	Heterogeneous agricultural areas	Annual crops associated with permanent crops	NIC
		Complex cultivation patterns	NIC
		Land principally occupied by agriculture, with significant areas of natural vegetation	NIC
		Agroforestal areas	DEH

Table A1 *Cont.*

CLC Level 1	CLC Level 2	CLC Level 3	New Code
Forest and semi natural areas	Forest	Broad-leaf forest	FOR
		Coniferous forest	FOR
		Mixed forest	FOR
	Scrub and/ or herbaceous vegetation associations	Natural grasslands	PAS
		Moors and heathland	–
		Sclerophyllous vegetation	–
		Transitional woodland–shrub	–
	Open spaces with little or no vegetation	Beaches, dunes, sands	ROC
		Bare rocks	ROC
		Sparsely vegetated areas	ROC
		Burnt areas	–
		Glaciers and perpetual snow	–
Wetlands	Inland wetlands	Inland marshes	–
		Peat bogs	–
		Salt marshes	–
	Maritime wetlands	Salines	–
		Intertidal flats	–
Water bodies	Inland waters	Water courses	–
		Water bodies	–
		Coastal lagoons	–
	Marine waters	Estuaries	–
		Sea and ocean	–

A.3. INE

Food availability information (i.e., cows and sheep) was obtained from the agricultural census of Spain (www.ine.es, accessed on 16 December 2019), which calculates the number of different domestic animals in each municipality. We translated the density of domestic animals from each municipality into spatial information. Then, we rasterized the spatial information using a bilinear interpolation (see above) using the elevation raster as a base layer.

A.4. MAPAMA

Data on landfills and supplementary feeding stations, also used as food resources by Egyptian vultures, were obtained from the Ministry of Agriculture, Fisheries, Food and Environment (MAPAMA; www.mapa.god.es, accessed on 10 October 2019). Landfill locations were used to create a raster of landfill density. As data on landfills in Catalonia and Valencia were not available from MAPAMA, we obtained this information from the Catalan Waste Agency (www.residus.gencat.cat, accessed on 22 October 2019) and the Environment Department of the Generalitat Valenciana (www.agroambient.gva, accessed on 22 October 2019), respectively. We also obtained the geographic locations of all supplementary feeding stations and verified their operational status in 2000-2018. Information on active supplementary feeding stations was included in the data using the same procedure as for landfills.

A.5. Asociación Empresarial Eólica (AEE)

We obtained the number of wind turbines per 10 x 10 km cell from the locations of national wind farms and their corresponding number of wind turbines (available at www.aeeolica.org, accessed on 14 October 2019). We first obtained the geographic locations of all wind turbines and then created a raster by rasterizing the information on the density of wind turbines in each cell using the elevation layer as a base map.

A.6. The Poison-Related Mortality Event Database from SEO/Birdlife and WWF

The number of poison-related mortality events was calculated using the “El veneno en España“ database (De la Bodega et al., 2020). We considered a poison-related mortality event to be the use of any chemical substance that causes the death of wildlife after ingestion. We assumed that several dead wild animals found at the same location within a 15-day period represented the same poison-related mortality event. We obtained the location of each poison-related mortality event and calculated the number of poison-related mortality events per 10 x 10 km cell.

A.7. Griffon Vulture National Census

We used the same procedure as for the Egyptian vulture to obtain the number of breeding pairs of griffon vultures (*Gyps fulvus*). For each communal breeding area or colony, we recorded the location and status (occupied vs. unoccupied). To obtain the abundance distribution, we incorporated these locations into a 10 x 10 km grid-cell and calculated the abundance in each cell by summing the locations of the confirmed communal breeding areas.

Supplementary Material B

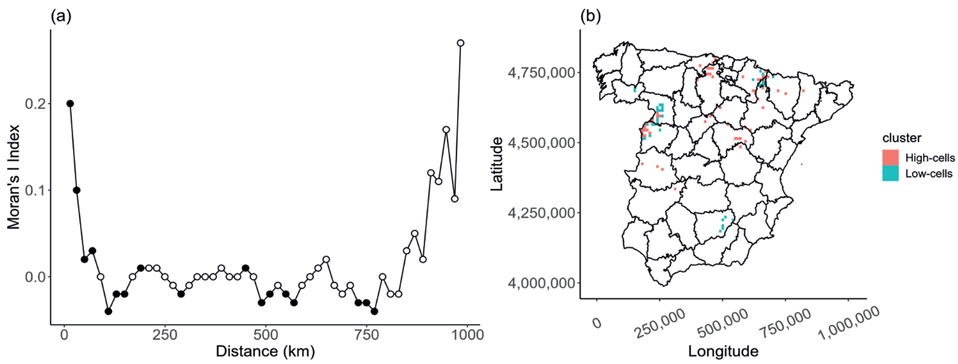

Figure A1. Spatial autocorrelation of the abundance distribution of reproductive pairs of Egyptian vultures in continental Spain in 2008. (**a**) Moran's I correlogram shows the distance lag between abundances in which spatial autocorrelation is significant (black-filled circles). (**b**) High (red) and Low (blue) cells detected by LISA analysis. High cells represent cells with significantly high abundances compared to neighboring cells, while Low cells represent cells with significantly low abundances compared to neighboring cells.

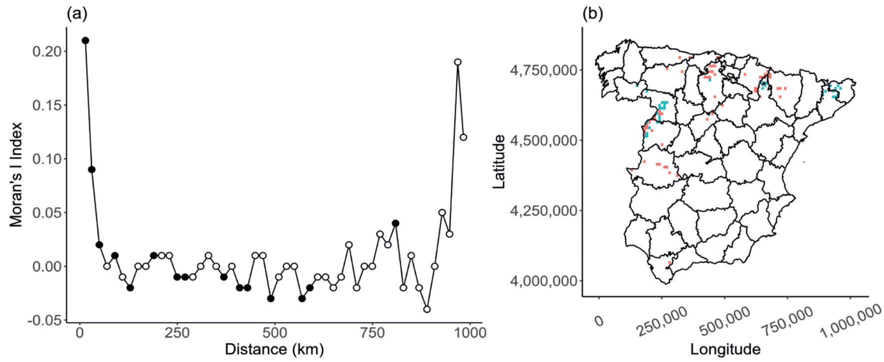

Figure A2. Spatial autocorrelation of the abundance distribution of reproductive pairs of Egyptian vultures in continental Spain in 2000. (**a**) Moran's I correlogram shows the distance lag between abundances in which spatial autocorrelation is significant (black-filled circles). (**b**) High (red) and Low (blue) cells detected by LISA analysis. High cells represent cells with significantly high abundances compared to neighboring cells, while Low cells represent cells with significantly low abundances compared to neighboring cells.

Supplementary Material C

Table A2. Kruskal-Wallis test of no significant differences between High cells and Low cells. *P* is the *p*-value. *P adj* is the *p*-value adjusted using the Bonferroni correction.

Variables	H	df	*P*	*Padj*
(1) Habitat				
ALT	0.069	1	0.792	0.3958
NIC	16.748	1	0.650	0.325
IRR	2.654	1	0.103	0.052
TREE	0.842	1	0.359	0.179
ROC	62.978	1	0.903	0.451
FOR	93.876	1	0.761	0.381
PAS	0.400	1	0.527	0.264
(2) Food availability				
SHEEP	1.444	1	0.230	0.115
LAND	3.648	1	0.581	0.291
(3) Human pressure				
URB	2.018	1	0.155	0.078
POIS	2.449	1	0.118	0.059

Supplementary Material D

Tabla A3. Estimates for average GLM (selection based on those with the lowest AICc scores, with a ΔAIC threshold of <2) describing abundance distribution of Egyptian vultures in continental Spain. Two models are specified: Model 1 incorporates the 2008 Egyptian vulture abundances (NP08) as a predictor variable and Model 2 incorporates the 2000 abundances (NP00). *P* is the *p*-value. Significant *p*-values < 0.05 are **in bold**.

	Variables	E	SE	Adj SE	Z	*P*
Model-1	Intercept	−36.790	74.020	74.080	0.497	0.619
	NP08	0.196	0.012	0.012	16.185	**<0.001**
	COW	1.647×10^{-5}	6.569×10^{-6}	1.647×10^{-5}	2.504	**0.012**
	GF	0.141	0.020	0.020	6.931	**<0.001**
	MUL	−0.042	0.037	0.037	1.116	0.264
	DEH	−0.003	0.003	0.003	0.981	0.327
	WTG	−0.002	0.002	0.002	1.059	0.290
	y	2.86×10^{-5}	6.46×10^{-5}	6.47×10^{-5}	0.442	0.658
	y^2	-1.91×10^{-12}	1.48×10^{-11}	1.48×10^{-11}	0.129	0.898
	y^3	-1.96×10^{-19}	1.19×10^{-18}	1.19×10^{-18}	0.164	0.869
	x	-2.19×10^{-4}	5.90×10^{-5}	5.91×10^{-5}	3.707	**<0.001**
	x^2y	-2.76×10^{-19}	1.85×10^{-19}	1.86×10^{-19}	1.488	0.137
	xy	9.56×10^{-11}	2.55×10^{-11}	2.56×10^{-11}	3.741	**<0.001**
	xy^2	-1.04×10^{-17}	2.76×10^{-18}	2.76×10^{-18}	3.762	**<0.001**
	x^2	-1.30×10^{-12}	8.80×10^{-13}	8.81×10^{-13}	1.472	0.141
	x^3	-4.23×10^{-19}	5.32×10^{-19}	5.33×10^{-19}	0.795	0.427
Model-2	Intercept	−68.530	56.810	56.850	1.205	0.228
	NP00	0.166	0.015	0.015	10.936	**<0.001**
	COW	0.000	0.000	0.000	2.492	**0.013**
	GF	0.182	0.020	0.020	9.097	**<0.001**
	MUL	−0.026	0.035	0.035	0.726	0.468

Table A3 *Cont.*

	Variables	E	SE	Adj SE	Z	*P*
Model-2	DEH	−0.004	0.003	0.003	1.348	0.178
	WTG	−0.003	0.002	0.002	1.214	0.22 5
	y	3.46×10^{-5}	4.03×10^{-5}	4.03×10^{-5}	0.859	0.390
	y^2	-7.19×10^{-13}	9.99×10^{-12}	1.00×10^{-11}	0.072	0.943
	y^3	-4.71×10^{-19}	7.20×10^{-19}	7.21×10^{-19}	0.653	0.514
	x	-4.36×10^{-5}	1.06×10^{-4}	1.06×10^{-4}	0.412	0.681
	x^2y	1.89×10^{-11}	4.61×10^{-11}	4.61×10^{-11}	0.410	0.682
	xy	-2.07×10^{-18}	5.00×10^{-18}	5.00×10^{-18}	0.414	0.679
	xy^2	-1.50×10^{-13}	1.67×10^{-13}	1.67×10^{-13}	0.896	0.371
	x^2	-3.10×10^{-20}	3.58×10^{-20}	3.58×10^{-20}	0.867	0.386
	x^3	-1.34×10^{-19}	1.85×10^{-19}	1.85×10^{-19}	0.726	0.468

CHAPTER 2

Resource predictability modulates spatial-use networks in an endangered scavenger species

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ABSTRACT

Background Changes in human-induced resource availability can alter the behaviour of free-living species and affect their foraging strategies. The future European *Landfill Waste Directive* and *Circular Economy Action Plan* will reduce the number of predictable anthropogenic food subsidies (PAFS), above all, by closing landfills to preclude negative effects on human health. Obligate avian scavengers, the most threatened group of birds worldwide, are the most likely group of species that will be forced to change their behaviour and use of space in response to landfill site closures. Here, we examine the possible consequences of these management decisions on the foraging patterns of Egyptian vultures (*Neophron percnopterus*) in an expanding population in the Iberian Peninsula.

Methods We tracked 16 individuals in 2018–2021, including breeders and non-breeders, and, using a combination of spatial-use and spatial-network modelling, assessed landscape connectivity between key resources based on movement patterns. We then carried out simulations of future scenarios based on the loss of PAFS to predict likely changes in the movement patterns of both non-breeders and breeders.

Results Our results show that foraging strategies in non-breeders and breeders differ significantly: non-breeders performed more dispersal movements than breeding birds across a spatial-use network. Non-breeding and breeding networks were found to be vulnerable to the removal of central foraging areas containing landfill sites, a highly predictable resource, while perturbation analysis showed dissimilar foraging responses to the gradual reduction of other predictable resources. Under a context of the non-availability of landfills for breeders and non-breeders, vultures will increase their use of extensive livestock as a trophic resource.

Conclusions Future environmental policies should thus extend the areas used by scavengers in which livestock carcasses are allowed to remain in the wild, a strategy that will also mitigate the lack of food caused by any reduction in available waste if landfills close. In general, our results emphasize the

capabilities of a spatial network approaches to address questions on movement ecology. They can be used to infer the behavioural response of animal species and, also demonstrate the importance of applying such approaches to endangered species conservation within a context of changing humanized scenarios.

Keywords Egyptian vulture, Foraging movements, Landfills, Predictable anthropogenic food subsidies (PAFS), Spatial networks, Space use, Spatial connectivity

INTRODUCTION

Many human activities result in modifications in both the spatial distribution and availability of trophic resources, thereby altering the behaviour of wildlife species (Didham et al., 2007; Margalida et al., 2010; Zuluaga et al., 2022). Alterations of spatial-use strategies by individuals when exploiting resources (e.g. foraging; Webb et al., 2011; Gilbert et al., 2015) may ultimately determine the survival and reproductive performance of wildlife populations worldwide (Van Moorter et al., 2013). A better understanding of how species respond to human-induced changes in the availability of food resources is needed to (1) assess the expected effect of environmental policies on their food resources and (2) design conservation actions to counterbalance the negative effects of human-altered environments (see review Riotte-Lambert and Matthiopoulos, 2020). Resource exploitation patterns in humanized environments are particularly worrying in the case of avian scavengers, for which available evidence indicates that predictable anthropogenic food subsidies (PAFS) may influence their use of space and movement patterns (Monsarrat et al., 2013; Oro et al., 2013; Van Overveld et al., 2018). This avian guild includes vultures, one of the most world's most endangered group of birds (Buechley and Şekercioğlu, 2016) and thus their conservation management is critical (Delgado-González et al., 2022; Fernández-Gómez et al., 2022).

The term PAFS refers to resources of anthropic origin whose appearance is predictable over space and/or time (Oro et al., 2013). The most common example of PAFS are the landfills that have become an important predictable –and unlimited– source of food for many scavenger species, and the predominant food resource for many of them (Houston et al., 2007; Bino et al., 2010; Gilbert et al., 2015; Tauler-Ametller et al., 2018; Langley et al., 2021). Other example of PAFS are supplementary feeding stations, also known as 'vulture restaurants', where humans intentionally offer resources to wild scavengers as part of specific conservation measures or leisure activities (e.g., Margalida et al., 2017; Mateo-Tomás et al., 2019). The relative costs and benefits of PAFS use by scavengers are controversial because, while positive effects have been described in terms of breeding success (Plaza and Lambertucci, 2017; Langley et al., 2021), the increase in the number of scavenger individuals in places with great food abundance can cause a density-dependent depression of productivity parameters (Carrete et al., 2006). In this paradoxical context, although vultures as obligate avian scavengers have evolved to depend on ephemeral and unpredictable carrion resources (Ruxton and Houston, 2004; Cortés-Avizanda et al., 2014; Kendall et al., 2014), the intensification of livestock farming practices and the increase in the number of PAFS may have led them to adapt their foraging strategies (Cortés-Avizanda et al., 2010; Tauler-Ametller et al., 2017), especially when their main food resources originate from landfills (Houston et al., 2007). In Europe the availability of human waste as a feeding resource is expected to decrease drastically owing to the future *Landfill Waste Directive* (2008/98/EC) and the *Circular Economy Action Plan* (European Commission, 2015), which contemplate the closure of landfills as a health-improving measure. Therefore, the study of the movement behaviour of vulture species in relation to trophic resources in European systems is an excellent scenario for understanding how birds exploit PAFS, as well as the effects they have on feeding resources due to the implementation of waste-management measures. In addition, more detailed research on how avian scavengers respond to this reduction in food availability is urgently required to shed light on management designed to preserve populations of some of the continent's most endangered avian species.

Several approaches have been developed to study movement behaviour including state-of-the-art animal tracking by telemetry that can explore movements by wild animals (Cooke et al., 2004; Nathan et al., 2008; Kays et al., 2015). The traditional approach to studying and analyzing animal movement with telemetry data uses kernel density estimators (Kie et al., 2010), which measure the intensity with which animals use different areas in their home ranges. A network approach has been used in ecological studies, above all to characterize food webs (e.g. Ings et al., 2009) and interactions between species (e.g., Fortuna et al., 2009). Yet, little attention has been paid to spatial ecology

(Fortuna et al., 2006; Jacoby et al., 2012), which focuses on the relationship between the environment and network topology. The spatial network approach using graph theory (see Urban and Keitt, 2001) provides a graphic description of complex biological systems (e.g. composed of individuals) based on a set of nodes (i.e. areas with resources) interconnected by links (e.g. movement paths). Spatial networks can provide new insights into how animals interconnect in key areas (i.e. nodes) by movements (i.e. links between nodes) at landscape scale. In addition, using a novel network approach we can determine how the availability of PAFS influences vulture movement behaviour and so identify priority areas for conservation due to the strong spatial connectivity between key central areas (Rhodes et al., 2006). In addition, by generating simulations based on variations in topological networks we can plausibly predict changes in spatial use caused by key alterations in spatial features (e.g. removal of well-connected nodes; Urban and Keitt, 2001; Jacoby et al., 2012).

Here, we use spatial network analyses to investigate changes in movement behaviour in free-ranging Egyptian vultures (*Neophron percnopterus*) as responses to food availability. Firstly, we identified the key resources within home ranges and their connectivity at landscape scale (i.e. how animals forage between different food resources). Secondly, we tested the effect of different types of perturbations (i.e. resource-removal simulations) on resource prioritization and infer a population-level response.

The Egyptian vulture, an avian scavenger considered as 'Endangered' worldwide, has one of its strongest populations in the Iberian Peninsula, where its population trend is classified stable or slightly decreasing (BirdLife International, 2021). Here, we study a population in the northern Iberian Peninsula that over the past two decades has increased in size and even colonized new areas of a highly anthropogenically modified region (Tauler et al., 2015; Franch et al., 2021). The individuals from this population exploit a wide range of food resources, ranging from small wild prey to large carcasses originating from extensive and intensive grazing regimes placed in 'vulture restaurants' (Tauler-Ametller et al., 2018), as well as resources obtained in large landfills (Tauler et al., 2015; Tauler-Ametller et al., 2017). These sites exert an important attraction during the exploration and exploitation movements of these vultures (Margalida et al., 2007; López-López et al., 2014; McGrady et al., 2018). Thus, we used a network approach to (1) examine the foraging behaviour and spatial-use patterns of Egyptian vultures in an anthropogenically modified landscape;

and (2) to predict individual foraging responses to the reduction and/or closure of PAFS. In addition, we addressed certain research and conservation measures in light of the future circular economy scenarios. Our initial hypotheses were that focal non-breeders and breeders would have different foraging strategies due to distinct spatial networks, and that the elimination of PAFS nodes would have a differential impact on non-breeders and breeders. We predicted that non-breeders, which are not tied to a particular breeding site, would have larger home ranges with a significant number of nodes of highly predictable feeding sites and would be seriously affected by the closure of PAFS, while breeders, which are tied to a nest site, would be more likely to exploit unpredictable food resources at fewer sites and be less influenced by landfill closures. Consequently, different conservation strategies are required for these two types of vulture populations.

METHODS

Data collection

We tagged 16 breeding Egyptian vultures –six breeding adults (i.e. 5 year-old or older) and 10 non-breeders (1 adult and 9 immatures)– with GPS-GSM devices during the summers of 2018 and 2019. All birds were captured at a landfill site in Osona (Catalonia, Spain). We equipped eight birds with 40-g solar-powered e-Obs satellite transmitters GPS-GSM (www.e-obs.de) and eight birds with Ornitela (www.ornitela.com) digital telemetry devices using a Teflon ribbon harness. Captured birds were aged according to plumage (**Additional file 1: Table S1**; Blasco-Zumeta and Heinze, 2006, pers. data). As we were only interested in studying movements during the summer, we discarded migration locations and winter quarters from the data. We considered the beginning of the breeding period to occur when the rectilinear migration path of individuals from Africa began to show great sinuosity on arrival in the study area, and the end of the period when we began to observe, conversely, a rectilinear southwards path. We were interested in prospecting and feeding behaviour during the day and so to optimize the energy performance of the devices the sleep interval of the e-Obs tags was set as 18 h ON/6 h OFF (6:30–22:30, Coordinated Universal Time) and for the Ornitela tags set in terms of the relative 18° sun angle above or below the horizon. We scheduled the GPS devices to record one location every 30 min and, as we were focused on foraging behaviour, we only selected locations within the daily time intervals between sunrise and sunset where birds were active.

Paired individuals in adult plumage holding a breeding territory were classified as breeders whilst nomadic individuals not linked to a breeding territory were classified as non-breeders (Donázar, 1993).

Spatial-use networks based on landscape features

We built two spatial networks based on the reproductive status of birds (non-breeders vs. breeders) composed of nodes and links to determine how animals interconnect feeding areas along movement paths. The nodes –the areas most used by all individuals– were spatially delimitated as follows. First, we measured the home range of all tagged individuals using the 50% Dynamic Brownian Bridge Movement Model (dBBMM) for each individual and year to represent the core areas in which these birds spent the most time. The dBBMM algorithm allows us to estimate the spatial-use likelihood by taking into account the temporal dependency of GPS data. The outcome of the dBBMM algorithm is a probability layer with a 500-m^2 grid cell known as the Utilization Distribution (UD; Kranstauber et al., 2012), a probability that refers to the likelihood of a specific area being used by an individual or individuals. Then, we calculated UDs at individual-year level by averaging all UDs to obtain a single global home range that clearly defines all the available geographical areas that any of the birds would use (**Additional file 1: Fig. S1**). Second, given that our home range at 50% contour at population level was composed of several polygons, each was considered to be a node. The links were the movement paths (i.e. movements of animals between nodes) that focal vultures performed when connecting a 'departure' node to an 'arrival' node. The frequency of the links between two nodes equated to the strength of the spatial connection. As we found very few movement paths between nodes with a duration of less than half an hour (less than 10% of the trips connecting two nodes), we selected only movement paths lasting one hour or more.

To analyse which environmental factors influenced the movement paths and space used in the networks, we characterized the nodes with nine land-cover categories taken from the CORINE 2018 Land Cover (www.land.copernicus.eu/) program (see **Table 1**) and with three ecological categories: feeding, roosting or breeding territories (the latter only for breeding birds). For feeding, we considered five types of food resources: landfill sites, intensive farms, vulture restaurants, extensive livestock, and other unpredictable resources (ordered by predictability over time and spatial heterogeneity). In addition, we selected the main food resource of each node by overlapping the UD layer of all tagged individuals and the resource location layer using both the CORINE Land Cover layer and satellite images. We assigned one resource type to each node by selecting the food source with the greatest probability of use according to the UD values. Roosting sites and breeding territories are binary features indicating whether or not a roosting site or breeding territory is present within the node (**Additional file 1: Table S2**). Roosting sites are communal roosts where birds socialize. To verify breeding territories, i.e. the areas where breeding individuals build their nests, at least one visit to the breeding territory was made between April and July.

We characterized the network topology using two quantitative metrics at network level (*diameter* and *density*) and two quantitative metrics at node level (*degree* and *betweenness*; see **Table 1** and **Additional file 2**). Metrics at network level describe on average the movement paths of focal birds. To measure the average length of movement paths (i.e. the movement between nodes or links), we calculated the *diameter*, which reflects the speed of movement through a network and scales up as more nodes are used by the focal birds. Therefore, a larger *diameter* implies a greater dispersing capacity in the focal birds, while *density* measures the heterogeneity of the averaged movement paths. The heterogeneity shows how movement paths and space use differ during an individual's movements inside the network. Homogeneous networks (lower *density* values) have the same number (on average) of links per node, whereas heterogeneous networks (greater *density* values) differ in the number of links per node (Newman, 2003). In biological terms, *density* illustrates whether the movement paths of birds are random or non-random (Jacoby et al., 2012). Metrics at node level indicate the relative importance of a node in terms of connectivity and show the core locations to which animals are attracted. Thus, by measuring the number of links of each node in terms of its interaction with neighbourhood nodes, we calculated the *degree* to identify which nodes were most heavily used by individuals. We used *betweenness* to measure the frequency of a node as an intermediate step between the path of two other nodes. Higher values of *betweenness* represent a more central position for nodes with large numbers of links to other nodes (i.e. connectivity; Newman, 2003). The nodes with the highest values of *betweenness* –known as hubs– were considered to have greater relative importance in the foraging movements of individual birds (Jacoby and Freeman, 2016).

Table 1. Description of the metrics of the networks (A) and the features of the nodes (B) for the non-breeders and breeders' Egyptian vultures in the study area.

(A) Network metrics	Level	Description
Diameter	Network	The length (in number of edges) of the longest path through the network from one node to another between any two vertices
Density	Network	The average probability that two nodes that are network neighbours are themselves neighbours of another node
Degree	Nodes	The number of links joining a node to its neighbours
Betweenness	Nodes	The number of shortest paths through the network from one node to another that passes through a given node (the highest values are also called hubs)
(B) Nodes features	**Classes (Acronym)**	
Land-use (Acronym)	Forest (FOR)	Cover (%) of forest per node
	Pastureland (PAS)	Cover (%) of pastureland per node
	Scrubs (SCR)	Cover (%) of scrubs per node
	Irrigated crops (IRR)	Cover (%) of irrigated crops per node (e.g., rice)
	Non-irrigated crops (NIC)	Cover (%) of non-irrigated crops per node (e.g., wheat)
	Permanent crops (TREE)	Cover (%) of permanent crops per node (e.g., olives)
	Bare rock (ROC)	Cover (%) of bare rock per node
	Urban areas (URB)	Cover (%) of urban areas per node
	Others (OTH)	Cover (%) of other typologies of land uses per node
Ecological functions	Resources	Set of food sources (categorized in: landfills, extensive and intensive farms, and vultures' restaurant
	Resting	When a node is used as roosting site
	Breeding territorya	When a node has a known nest

* Only for breeders

Finally, we calculated two sets of parameters: first, the node fidelity was used to understand in detail the effects of node features on the use of space and was defined by (1) the number of revisits that individuals make to a specific node and (2) the accumulated residence time that focal birds spent at each node. Second, the spatial connectivity of non-breeders and breeders was represented by the *degree* and *betweenness*.

Statistical analyses

We used the F-statistic of analysis of variance (ANOVA) to test differences between non-breeders and breeders in the metric parameters of their foraging behaviour at network level. We compared the number of elements (nodes and links) and the network quantitative metrics at network level (*diameter* and *density*) in terms of reproductive status (Quinn and Keough, 2002). We performed linear regressions to identify which features of the nodes determined node fidelity (number of revisits and residence time) and node importance in terms of interconnections along movement paths (*degree* and *betweenness*). To do this, we fitted separate models for each response variable (number of revisits, residence time, *degree* and *betweenness*) and each reproductive status because the spatial-use networks of non-breeders and breeders were completely different (see Results). For each model, we estimated the importance of each explanatory variable (node features described above) by removing it from the model and then performing an F-ratio test to derive P values for the variable of interest (Zuur et al., 2009). In terms of ecological functions, nodes with breeding territories were only considered in the linear model for breeders. In order to avoid collinearity between each category of land cover in the linear regressions, we carried out a Principal Component Analysis (PCAs) to reduce the number of correlated explanatory variables to just a few uncorrelated variables (orthogonal). Each Principal Component (PC) was obtained from the covariance matrix of the original variables (Quinn and Keough, 2002).

Finally, we used a perturbation analysis to assess the foraging responses of individuals under future scenarios linked to the limitation of PAFS by environmental regulations. We simulated different perturbations on the network by removing nodes of different types and computing network robustness and the presence of key nodes according to available food resources. Network robustness refers to the ability of a network to maintain its features regardless of the degradation of the network itself (Jacoby and Freeman, 2016). The structure of spatial-use networks is characterized by their elements and their distribution as any degradation of their structure may modify the movement paths of individuals and reveal the underlying robustness (or vulnerability) of the connection (or disconnection) between key areas (Jacoby and Freeman, 2016). So, we first performed a 'random removal' of nodes and the subsequent measures of *betweenness* at each iteration. We then performed 'targeted removal' by removing nodes with a specific feature (e.g. nodes where landfills are present) until there were no more nodes with a specific feature, and then recalculated the *betweenness* measures for each iteration. In both cases, each iteration refers to the gradual one-by-one removal of nodes. 'Random removal' of nodes allowed us to infer whether the foraging response to the limitation on PAFS is a stochastic process if compared to the 'targeted removal' of nodes, or whether it follows a deterministic process. Therefore, we ran each random and targeted removal iteration 1000 times to generate two different frequency histograms of the *betweenness*. Finally, we compared these histograms resulting from each random and targeted simulation using a paired T-test. In such a way, we identified which node feature drives the robustness of both the non-breeder and breeder spatial-use networks.

All analytical procedures were carried out within the R environment (R Core Team, 2021) using the *recurse* (Bracis et al., 2018), *move* (Kranstauber et al., 2016) and *igraph* packages (Csardi and Nepusz, 2006).

RESULTS

When considering all individuals, i.e. non-breeders and breeders, the spatial-use network included a total of 44 nodes scattered throughout the northeast Iberian Peninsula (Catalonia, Aragón, Navarra, and Castilla y Leon) and southern France (**Additional file 1: Fig. S1**). Nonbreeding and breeding vultures had different patterns of space use, as illustrated by the ANOVA in the topology of the spatial-use network. For example, the number of nodes (mean ± SD; non-breeders 11.7 ± 2.31; breeders 3.5 ± 1.38) and links (mean ± SD; non-breeders 38.3 ± 10.4; breeders 7.17 ± 5.53) were significatively higher in the networks of non-breeders than in breeders (nodes: $F_{4,600} = 61.29$, $P < 0.001$; links: $F_{4,600} = 45.16$, $P < 0.001$). Moreover, comparing the *diameter* and *density* at network level between non-breeders and breeders, we found two completely different patterns of movement. Compared to breeders, non-breeders had more dispersive movement paths (Mean ± SD; non-breeders 5.4 ± 1.65; breeders 2.33 ± 1.03; $F_{4,600} = 16.61$, $P < 0.01$) and made many more random and heterogeneous movements (mean ± SD; non-breeders 0.04 ± 0.01; breeders 0.008 ± 0.006; $F_{4,600} = 45.16$, $P < 0.001$). Nevertheless, for both breeders and non-breeders landfills were central areas during their movements. Nodes in which landfills were present had the highest *betweenness* and acted as hubs connecting the other nodes with different space use and ecological features (**Fig. 1**).

In the non-breeder spatial-use network, multiple linear regression analysis revealed that node fidelity (number of revisits and residence time) was related to the presence of roosting sites, extensive livestock and intensive farms and landfills (revisits: $F_{5,35} = 6.61$, $P < 0.001$, $R^2 = 0.49$; residence time: $F_{6,34} = 10.7$, $P < 0.001$, $R^2 = 0.65$; **Table 2**); however, land-cover classes were not good predictors for explaining node fidelity or the relative importance of nodes within the spatial-use network (**Additional file 3: Table S4**). We selected two PCs in non-breeder regressions that explained a total of 75% variance. We found that PC1 relies positively on forest and negatively on non-irrigated land cover (**Additional file 1: Table S3**). Non-irrigated crops and forest (i.e. PC1; **Additional file 1: Table S3**) were selected to explain residence time but had no significant effect on non-breeders' use of networks. Moreover, the nodes most used by non-breeders were explained by roosting sites and the presence of landfills and extensive livestock (*degree*: $F_{5,35} = 9.29$, $P < 0.001$, $R^2 = 0.57$), both factors having a positive effect on the *degree.* Likewise, the nodes considered as central areas were positively driven by the presence of landfills (*betweenness*: $F_{4,35} = 5.4$, $P > 0.05$, $R^2 = 0.38$). On the other hand, for breeding individuals, node fidelity was positively explained by breeding territory (number of revisits: $F_{5,13} = 5.53$, $P < 0.05$, $R^2 = 0.68$) and extensive livestock (residence time: $F_{4,14} = 4.4$, $P < 0.05$, $R^2 = 0.56$; **Table 3**). However, no significant effect of node features was found to explain *degree* and *betweenness* in the spatial-use networks of breeding birds (see simple ANOVA comparisons in **Additional file 1: Fig. S3** and **S4**).

In general, the perturbation analysis showed that the gradual disappearance of PAFS will significantly alter the movement paths and the degree of relative importance of nodes (connectedness of nodes) and, in turn, modify the foraging strategy of these two subsets of this vulture population (*P* values

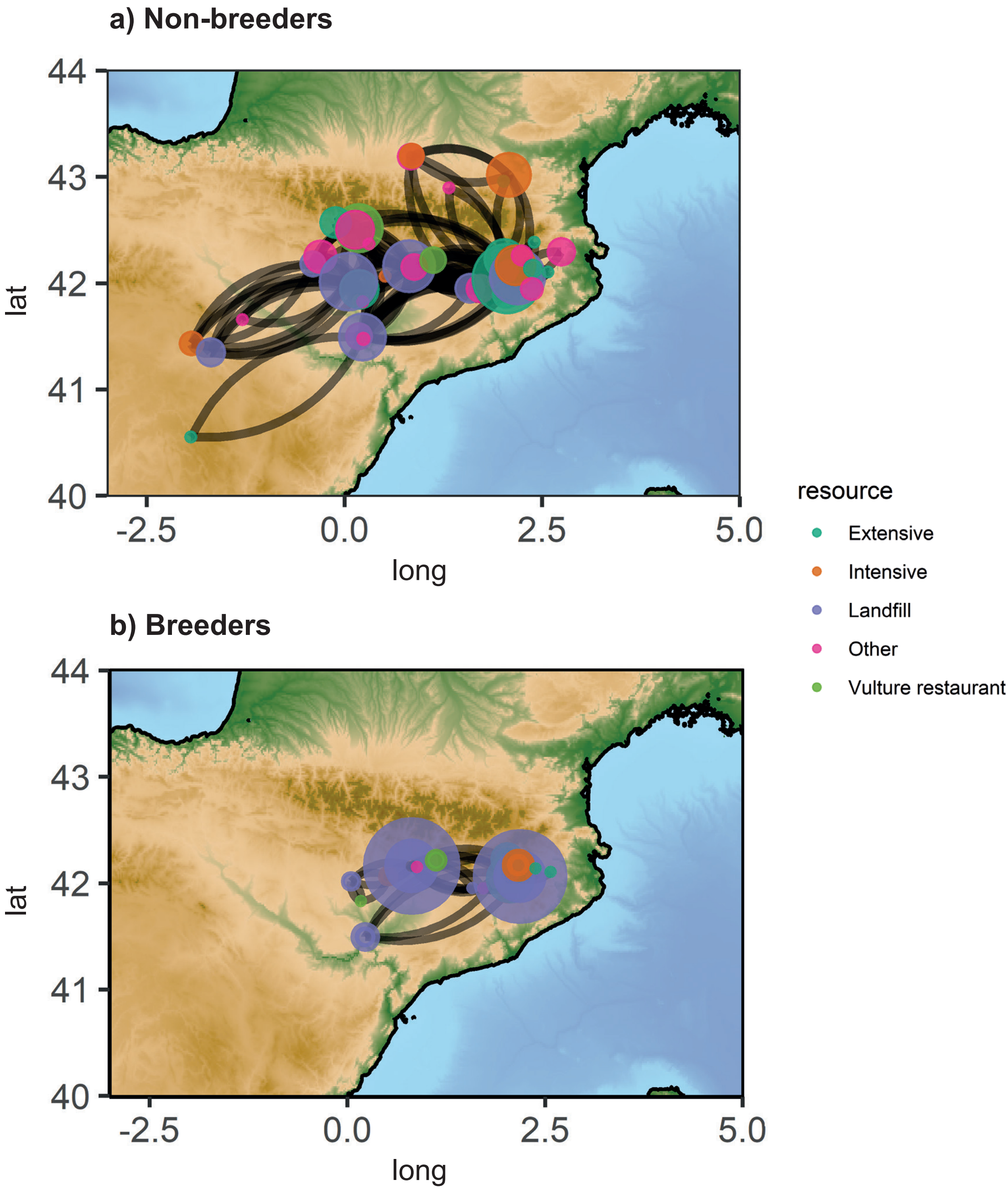

Figure 1. Spatial-use networks of **a**) non-breeding and **b**) breeding Egyptian vulture populations in the study area. At the nodes the type of resources (i.e. landfill, intensive farm, extensive farm, and vulture restaurant and others that act as random or ephemeral resources) are shown. Node sizes are proportional to the *betweenness* value. Links represent the foraging trips connecting nodes. The length of the links depends on the frequency of the movement paths between the two nodes.

Table 2. Multiple linear regressions analysis for site fidelity (number of revisits and residence time) and network connectivity (*degree* and *betweenness*) of non-breeding Egyptian vultures.

	Non-breeders																			
	log(number of revisits)					log(residence time)					log(degree)					Betweenness				
Variables	*E*	*SE*	95%CI		*P*	*E*	*SE*	95%CI		*P*	*E*	*SE*	95%CI		*P*	*E*	*SE*	95%CI		*P*
			LL	*UL*				*LL*	*UL*				*LL*	*UL*				*LL*	*UL*	
(Intercept)	0.84	0.37	0–09	1.59	**0.029**	0.64	0.59	– 0.57	1.84	0.291	1.15	0.17	0.80	1.50	**< 0.001**	29.48	1.43	– 12.50	71.46	0.163
PC1 Resources	–	–	–	–	–	0.18	0.10	– 0.38	0.02	0.082	–	–	–	–	–	–	–	–	–	–
Extensive	0.91	0.44	0.02	1.79	**0.046**	1.48	0.71	0.04	2.92	**0.044**	0.52	0.21	0.09	0.96	**0.020**	14.68	0.43	– 55.28	84.64	0.673
Intensive	1.80	0.55	0.68	2.92	**0.003**	2.01	0.90	0.17	3.84	**0.033**	0.55	0.27	0.00	1.09	**0.052**	48.53	1.15	– 37.50	134.55	0.260
Landfill	2.09	0.51	1.05	3.14	**< 0.001**	2.51	0.87	0.75	4.27	**0.006**	1.01	0.25	0.49	1.52	**< 0.001**	167.98	4.48	91.90	244.07	**< 0.001**
Vulture rest	0.72	0.69	– 0.69	2.13	0.310	1.18	1.14	– 1.13	3.49	0.307	0.35	0.34	– 0.34	1.05	0.312	64.19	1.23	– 41.45	169.83	0.226
Roosting YES	1.59	0.41	0.77	2.42	**< 0.001**	3.87	0.73	2.40	5.35	**< 0.001**	0.73	0.20	0.34	1.13	**< 0.001**	–	–	–	–	–
					$R^2 = .595$					$R^2 = .654$					$R^2 = .570$					$R^2 = .381$

Significant P values < 0.05 are in bold
E estimate, *SE* standard error, *CI* confidence interval, *LL* lower bound at 95% level of confidence, *UL* upper bound at 95% level of confidence, *P* values. R^2 represent the coefficient of determination for each selected model which does not include all explanatory variables.

Table 3. Multiple linear regressions analysis for site fidelity (number of revisits and residence time) breeding Egyptian vultures.

	Breeders																			
	log(number of revisits)					log(residence time)					log(degree)					Betweenness				
Variables	*E*	*SE*	95%CI		*P*	*E*	*SE*	95%CI		*P*	*E*	*SE*	95%CI		*P*	*E*	*SE*	95%CI		*P*
			LL	*UL*				*LL*	*UL*				*LL*	*UL*				*LL*	*UL*	
(Intercept)	1.33	0.60	0.04	2.62	**0.045**	1.93	1.16	− 0.56	4.42	0.119	1.68	0.17	3.21	2.11	**< 0.001**	14.59	5.42	3.21	25.98	**0.015**
Resources																				
Extensive	2.34	1.08	0.00	4.68	0.050	5.98	1.74	2.25	9.71	**0.044**	–	–	–	–	–	–	–	–	–	–
Intensive	− 0.10	1.01	− 2.28	2.09	0.924	1.16	1.90	− 2.91	5.22	0.552	–	–	–	–	–	–	–	–	–	–
Landfill	0.99	0.86	– 0.86	2.85	0.269	3.38	1.64	– 0.14	6.90	0.058	–	–	–	–	–	–	–	–	–	–
Vulture rest	– 1.36	1.19	– 3.93	1.20	0.272	– 1.48	2.17	– 6.13	3.18	0.508	–	–	–	–	–	–	–	–	–	–
Breedeing territory																				
YES	1.86	0.81	0.12	3.61	–	–	–	–	–	**< 0.001**	–	–	–	–	–	–	–	–	–	–
					R^2 = .680					*R^2 = .557*										

Significant *P* values < 0.05 are in bold
E estimate, *SE* standard error, *CI* confidence interval, *LL* lower bound at 95% level of confidence, *UL* upper bound at 95% level of confidence, *P* values. R^2 represent the coefficient of determination for each selected model which does not include all explanatory variables. Models related to spatial connectivity (degree and betweenness) are not significant (null models are shown).

for paired T-tests comparing random and targeted simulation were less than 0.05; **Fig. 2**). The removal of key nodes where landfills exist would have a deterministic effect on foraging movements at population level resulting in an increase in nodes that are poorly connected to the non-breeding and breeding networks, as shown by the significantly lower *betweenness* values of the targeted simulation compared to the random simulation (**Fig. 2a, e**). Moreover, the removal of nodes from the non-breeding network, where intensive or extensive farms are the main food resource, would have a similar impact on foraging strategies as landfill-site removal but at a lower intensity (**Fig. 2b, d**). Thus, the non-breeding network will be slightly more robust in the event of the disappearance of intensive and extensive farms. Compared to the non-breeding network, the breeding network was found to be more resilient to

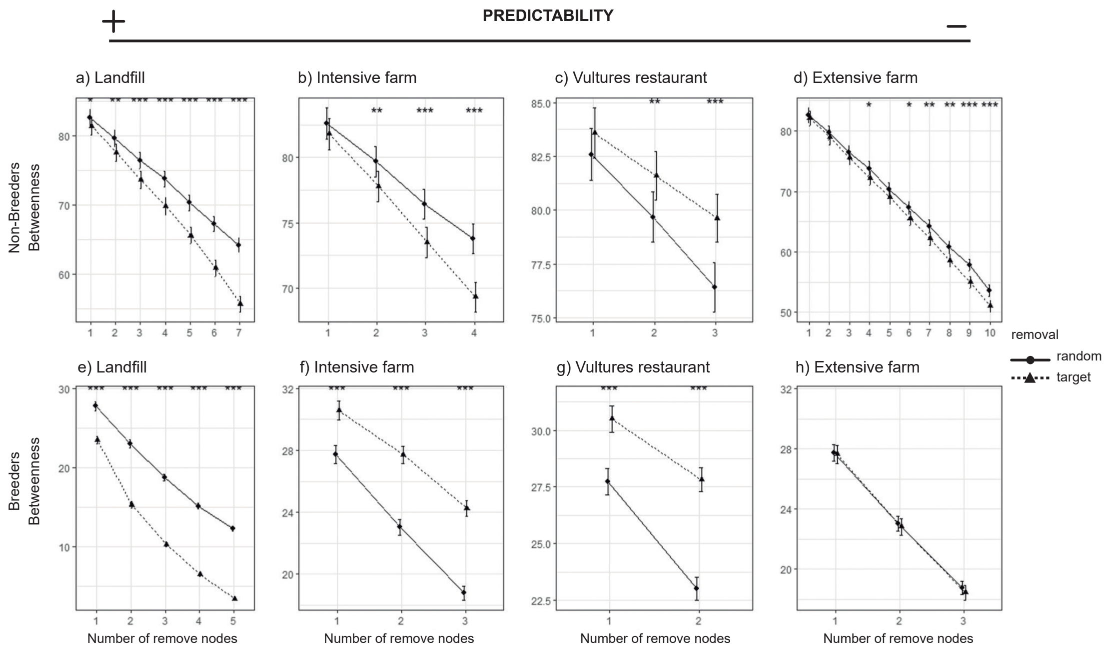

Figure 2. Environmental perturbation analysis. Random and Targeted node removal used to examine the response of non-breeding (**a**-**d**) and breeding (**e**-**h**) Egyptian vultures to future sanitary legislation if implemented. Plots show the mean *betweenness* values and confidence intervals along, respectively, random (circle or thick line) or targeted (triangle or dashed line) node-removal simulations. Coefficient intervals (5-95%) are shown. Aesthetics show significant differences ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$).

intensive farm removal as key nodes would become either more interconnected or there would be an increase in the number of well-connected nodes (**Fig. 2f**). Similar foraging responses in both non-breeding and breeding networks were found when nodes with vulture restaurants were removed (**Fig. 2c, g**). In addition, the perturbation analysis showed that there were no effects on foraging responses when we removed nodes with extensive farms from the breeding network (**Fig. 2h**).

DISCUSSION

It is well-known that transformations of human-mediated ecosystems have the potential to alter animal movement patterns and foraging behaviour (e.g. Bartumeus et al., 2010; Gilbert et al., 2015; Selva et al., 2017; Shaffer et al., 2017). By studying changes in space use and connectivity in an endangered vulture species, the Egyptian vulture, we improved our understanding of how environmental and ecological conditions influence the foraging movements of different fractions of the population (i.e. non-breeders and breeders) in different ways. We show here that landfills are a key environmental factor driving spatial-use patterns and how inferred future scenarios in the event of landfill closure will generate profound changes in movement patterns in terms of connectivity in this endangered vulture's populations.

Non-breeding and breeding vultures have different foraging strategies, as illustrated by the differences in the spatial topology of their networks. Non-breeding individuals disperse more along a spatial-use network that has more nodes and links than the breeding bird networks. This could be related to the larger exploratory capacity of non-breeders as they have no nest attachments or functional constraints imposed by the demands of breeding. It is known that non-breeders have larger home ranges than breeders (López-López et al., 2014; McGrady et al., 2018) and this is probably associated with the greater number of areas they visit and more connections between them (networks with more nodes and links). The exploratory foraging behaviour undertaken by non-breeders may also explain the heterogeneity of movements found in their networks, in which individuals rarely use or connect certain spatial areas and mostly travel through well-used and well-connected areas, the so-called hub-nodes. Such heterogeneous topologies are reminiscent of the limiting case of scale-free network properties (see Barabási and Albert, 1999; **Additional file**

4). This special type of network has been described in other species (e.g. bats; Rhodes et al., 2006) and are known to be robust against random-node removal but susceptible to (hub)-node removal (Watts and Strogatz, 1998). In the foraging networks of non-breeding Egyptian vultures, hub-nodes are represented by landfills and intensive farms. Thus, it is not surprising that the main roosting sites in our study area are near landfills (pers. obs.), which are closely associated with predictable food sources. These roosting sites are both stopovers during migration and temporary settlement areas during the breeding season where individuals socialize and exchange information (Donázar et al., 1996; Margalida and Boudet, 2003; Cortés-Avizanda et al., 2011). As well, landfills may act as highly visible and familiar landmarks or waypoints along movement paths that aid navigation between other nodes, a mechanism that has been reported in Western Gulls (*Larus occidentalis*; Shaffer et al., 2017). Conversely, the territorial behaviour of breeders is characterized by low dispersal and homogeneous movements, and individuals travel between nodes with a similar degree of usability (exploitability) and connectivity. We found a parallel in seabird literature, in which researchers also described generally more specialized foraging behaviour in breeding adult Northern Gannets (*Morus bassanus*) than in non-breeding birds, almost certainly imposed by their central foraging behaviour and habitat use (Votier et al., 2017). The space use and connectivity emerging in breeding individuals is thus potentially vulnerable to random landscape transformation but less sensitive to targeted landscape transformations. This is probably due to the few nodes present in breeders' spatial-use networks, in which the slightest alteration spreads quickly and has a strong effect on network topology, as has been described in other kinds of networks (Albert et al., 2000). Although the increase in our focal population over the past decades is probably linked to the appearance of landfills (Tauler-Ametller et al., 2017), it is known that extensive livestock can also act as one of the main food sources in breeding territories far from landfills (Tauler-Ametller et al., 2018). Accordingly, our results support the idea that breeding birds are currently heavily reliant on extensive livestock (Mateo-Tomás and Olea, 2010; Tauler-Ametller et al., 2018). Overall, our findings agree with past studies regarding the interconnection between space use and reproductive status in vultures (Krüger et al., 2014; Pfeifer et al., 2015; Thompson et al., 2020) despite our use of a novel application of a network approach to shed light on movement patterns during foraging, and use of the connectivity between distinct feeding resources in two subsets of an

Egyptian vulture population. We also demonstrate here that predictable food availability affects large-scale movement behaviour in avian scavengers, as has been recognized in other species (e.g. seabirds, Bartumeus et al., 2010; white storks, Gilbert et al., 2015; brown bears, Selva et al., 2017; gulls, Langley et al., 2021).

Perturbation analysis demonstrates that both non-breeder and breeder foraging strategies are vulnerable to the removal of nodes with highly predictable food sources, especially if landfills are present. Our results show that the systematic removal of landfills (hub-nodes) changes patterns of population movements such that other nodes become key in the use-of-space strategies of focal birds. Therefore, when a node with a landfill is removed, another node with a different food resource becomes the new hub. In line with our prediction, we found that this is especially important for non-breeding birds whose movements mainly target local areas with landfills (see also McGrady et al., 2018). A possible explanation for this foraging pattern could be their lack of experience in prospecting, as well as their lack of dependency on a breeding territory, which favours the exploitation of predictable food sources (see e.g. Monsarrat et al., 2013). By contrast, although we predicted that the disappearance of PAFS would not affect the foraging behaviour of breeding individuals, interestingly our results did show that an important alteration in movement patterns occurred if landfills, intensive farms and vulture restaurants were sequentially removed. The fact that breeders take advantage of less predictable resources such as extensive livestock is most likely due to their location near breeding territories (Tauler-Ametller et al., 2018). Indeed, at population level, our simulations predict that, in the lack of landfill-site scenario, the core behavioural response of birds will be to switch to extensive livestock (see **Fig. 3**), which thus makes extensive livestock a key element in any future conservation strategy.

The studied Egyptian vulture population showed a great dependence on PAFS and our results indicate that the future closure of landfills (see 2008/98/EC; European Commission, 2015) will reconfigure their spatial networks and lead to a shift in home ranges in such a way that landfills will no longer be their central foraging areas. Currently, landfills concentrate large numbers of individuals of different ages and reproductive status from both local and neighbouring populations (e.g. France, Spain; pers. obs.). This makes them key places for information exchange, socialization and roosting, as well as a profitable feeding sites, particularly for non-breeders (e.g. Delgado et al., 2021), and, in turn, for

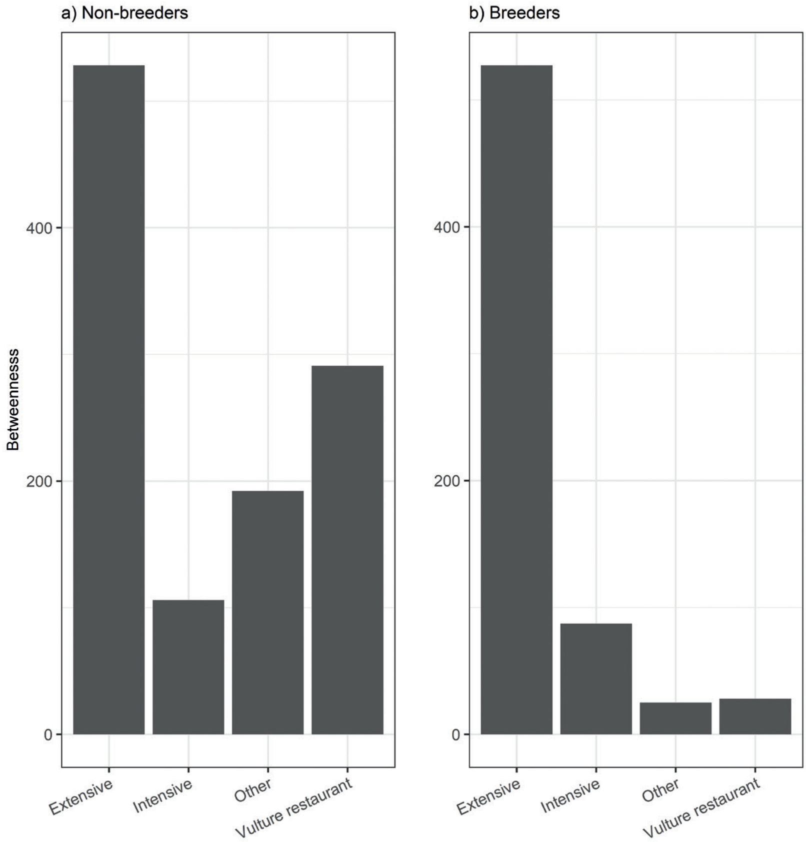

Figure 3. Average *betweenness* of spatial-use networks for **a**) non-breeding and **b**) breeding Egyptian vulture populations in terms of the different sets of resources for all nodes from which landfills were removed.

the recruitment and viability of local and regional populations (Tauler-Ametller et al., 2017; pers. obs.). An option for filling this gap in food provision if landfills close is to favour a natural supply of carrion, if necessary, by maintaining certain supplementary feeding points specifically targeting Egyptian vultures and non-breeder survival (Moreno-Opo et al., 2015; Cortés-Avizanda et al., 2016) and/or guaranteeing the connection between non-breeding and breeding populations that ensures population viability. In fact, some vulture restaurants designed specifically for Egyptian vultures replace the roosting functions that landfills currently perform (Margalida and Boudet, 2003; pers. obs.). In any case, our findings suggest that more research is required into how PAFS affect the non-breeder subset of vultures. It is not clear to what extent landfill closure will affect the performance of breeding birds, although it is known that the occupancy of breeding areas is somehow related to these feeding sites (Tauler-Ametller et al., 2017). Our results reveal that the spatial-use network of breeders is shaped above all by extensive farming and the benefits of this type of animal husbandry for vulture breeding populations have been noted elsewhere (Mateo-Tomás and Olea, 2015; Tauler-Ametller et al., 2018). Thus, future conservation farming policies should promote extensive livestock practices and allow more farmers to freely abandon livestock carcasses in the field. To do so, regional policies should focus on extending the areas in which the abandoning of extensive carcasses is permitted (e.g. in Spain, ZPAEN). Long-term monitoring is key to identifying how population numbers vary over time, and the combination of telemetric information and other tracking methods (e.g. ringing) will allow us to measure vital parameters and evaluate population viabilities under new food availability scenarios. In conclusion, we emphasize how movement ecology and network modelling are highly promising tools and can potentially play a key role in movement research. They allow us to predict the responses of wild species having to face up to environmental changes and landscape transformation (e.g. Rhodes et al., 2006; Fortuna et al., 2009) and so will play a crucial role in the search for the most efficient conservation practices.

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SUPPLEMENTARY MATERIAL

Resource predictability modulates spatial-use networks in an endangered scavenger species

Additional file 1. Data available and exploration analysis

Additional file 2. Topology parameters of spatial networks

Additional file 3. Linear regression models

Additional file 4. Distribution of degree and betweenness define scale-free networks

Additional file 1. Data available and exploration analysis

Table S1. Egyptian vultures tagged with GPS-GMS devices during the summer period between 2018 and 2019 in Catalonia (NE Spain). Note that age (adults, A; immatures, I) was determined by plumage according to Blasco-Zumeta and Jeinze et al., 2006 and breeding status (breeder, B; non-breeder, NB) was determined based on the GPS location and the monitoring of focal species. There were no changes in reproductive status at the individual level during the study period. Nodes visited per year and home rage (dBBMM) are also shown for each bird.

ID	Tag devices	Reproductive status	Age class	Nodes visited				Years tracked	dBBMM (km^2)	
				2019	2020	2021	All years		50%	95%
6977	e-Obs	B	A	-	3	4	4	2	21 (1)	278 (22)
6978	e-Obs	B	A	-	5	6	6	2	73 (11)	735 (1)
6616	e-Obs	B	A	-	3	2	3	2	22 (3)	221 (49)
181648	Ornitela	B	A	-	-	4	4	1	60	503
201397	Ornitela	B	A	-	-	3	3	1	58	576
200666	Ornitela	B	A	-	-	1	1	1	23	226
201395	Ornitela	NB	A	-	-	12	12	1	87	5613
6223	e-Obs	NB	A	-	8	5	8	2	50 (13)	4632 (130)
6979	e-Obs	NB	I	-	14	7	15	2	24 (10)	2952 (267)
6224	e-Obs	NB	I	10	10	-	14	2	137 (4)	3155 (237)
201398	Ornitela	NB	I	-	-	14	14	1	107	9412
6222	e-Obs	NB	I	10	8	10	13	3	151 (91)	5129 (1395)
6615	e-Obs	NB	I	-	10	10	13	2	128 (101)	6857 (985)
181649	Ornitela	NB	I	-	9	7	10	2	68 (7)	2942 (992)
201452	Ornitela	NB	I	-	-	10	10	1	12	1412
201399	Ornitela	NB	I	-	-	9	9	1	174	138835

Numbers inside parentheses are SD.

Table S2. Total of nodes used by non-breeder and breeder Egyptian vultures. The nodes are classified according to the following 3 ecological features: feeding, roosting, and breeding territory. We considered five food resources: landfills, intensive farms, vulture restaurants, extensive livestock, and other unpredictable resources. Roosting and breeding territory are binary features; YES implies that a roosting site or breeding territory is present within the node and viceversa.

Ecological features	Level	N. of nodes used	
		Non-breeders	Breeders
Feeding	Landfill	7	5
	Intensive farm	5	3
	Vultures' restaurant	3	2
	Extensive livestock	10	4
	Other	16	5
Roosting	Yes	29	16
	No	12	3
Breeding territory[a]	Yes	7	6
	No	34	13
Total		41	19

[a]Only for breeders

Table S3. Factor loadings after Principal Component Analysis (PCA) for the nine categories assigned to land uses in the study area.

Land uses	Non-breeders		Breeders	
	PC1	PC2	PC1	PC2
Pasturelands	-0.16	-4.47	0.29	0.13
Forest	11.39	4.68	9.98	1.00
Non-irrigated crops	-9.37	6.42	-3.58	-7.51
Irrigated crops	-0.56	-1.13	-0.79	0.18
Scrublands	-1.17	-4.57	-5.94	6.19
Permanent crops	0.00	-0.01	0.00	0.00
Urban areas	-0.11	-0.53	0.04	0.00
Bare rocks	-0.03	-0.41	-	-
Others	0.01	0.01	-	-
Eigenvalue	2350	1132	2353	1453
Variance (%)	0.51	0.24	0.54	0.35

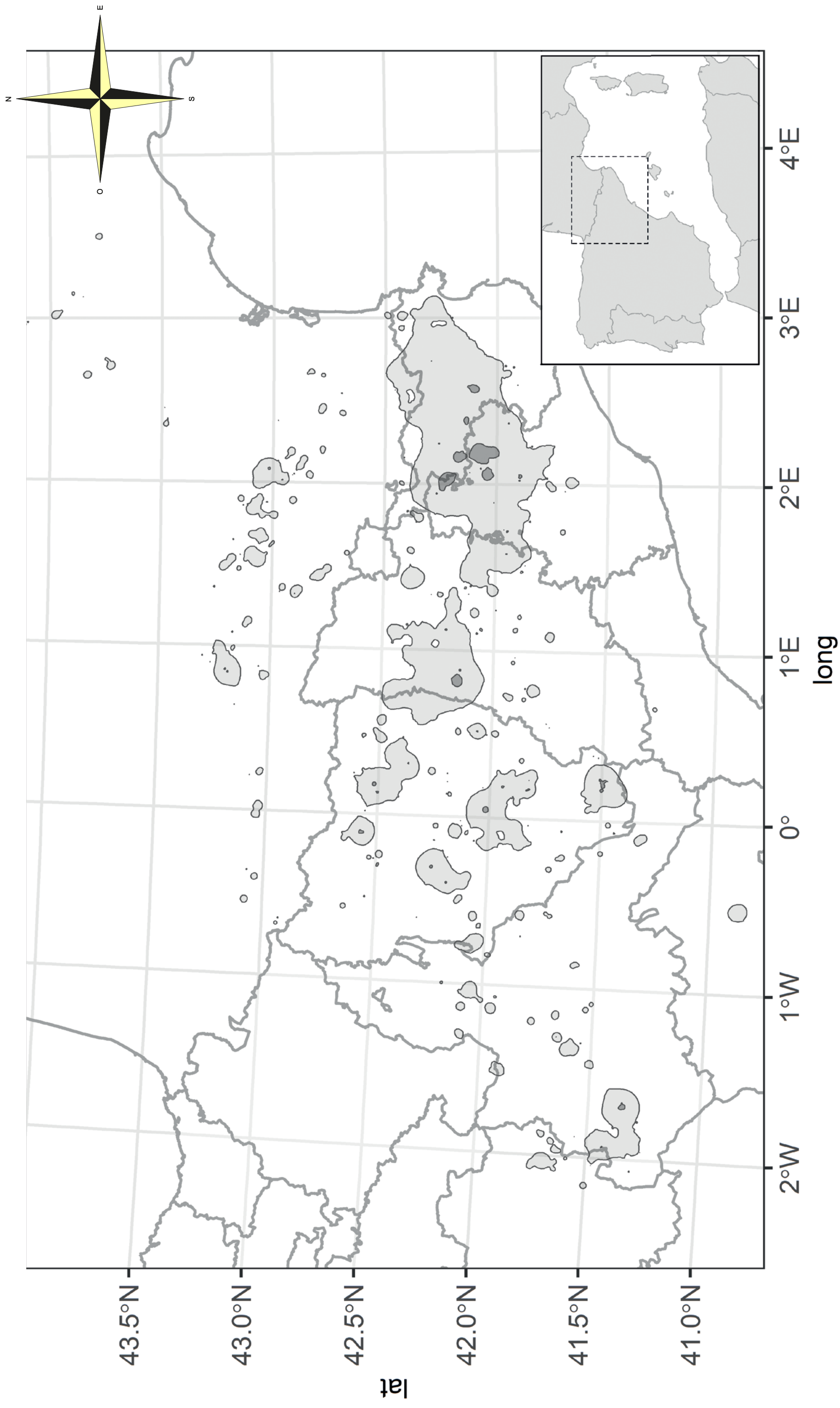

Figure S1. Dynamic Brownian Bridge Models home ranges at 50% (dark grey) and 95% (light grey) of 10 non-breeders and 6 breeders of Egyptian vulture tagged in Catalonia (Northeast Spain) at the population level.

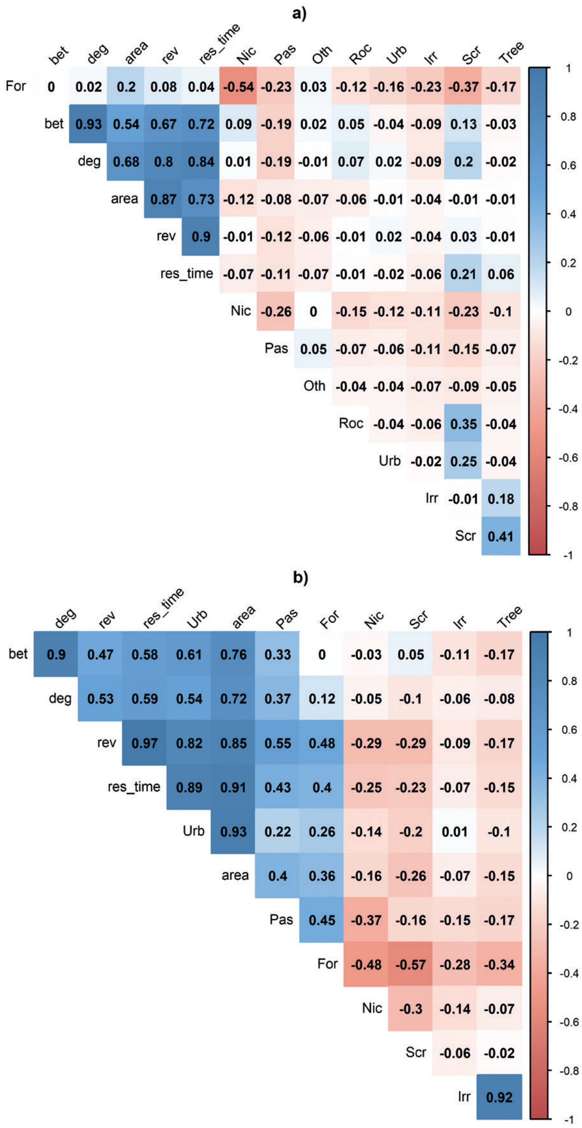

Figure S2. Correlation between nodes' features and the parameters related to node fidelity (number of revisits and accumulated residence time) and local network metrics (*degree* and *betweenness*) for the focal **a**) non-breeders and **b**) breeders. Positive correlation is showed in blue, negative correlation in red. bet: *betweennes*. deg: *degree*. area: surface of nodes. rev: number of revisits performs to one specific node. res_time: accumulated residence time on one specific node. For: cover of forest per node. Nic: cover of non-irrigated crops per node. Pas: cover of pasturelands per node. Roc: cover of bare rock per node. Urb: cover of forest per node. Irr: cover of irrigated crops per node, Scr: cover of scrublands per node. Tree: cover of permanent crops per node. Other: cover of other typologies of land uses per node.

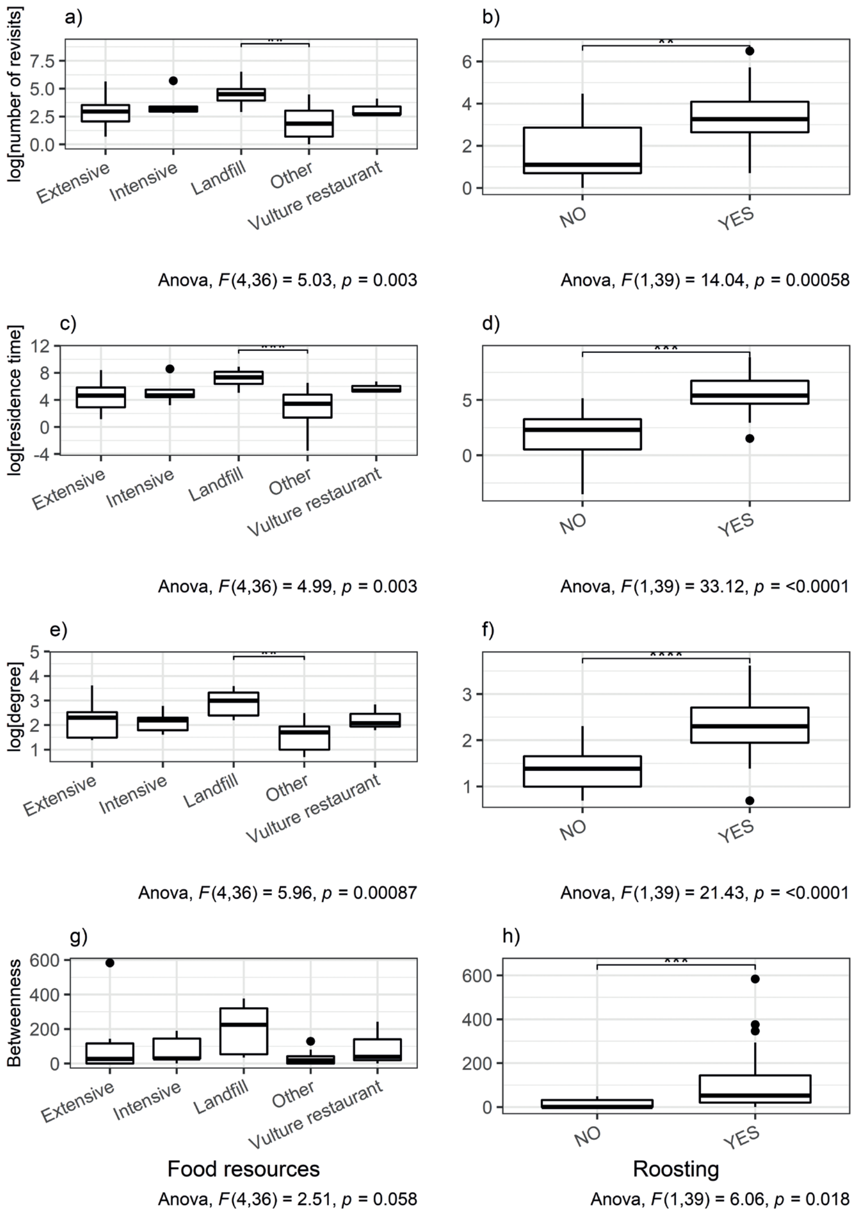

Figure S3. Boxplots of non-breeders node fidelity. Boxplots showing the number of revisits (**a-b**) and the residence time (**c-d**), and spatial-use networks topology represented by *degree* (**e-f)** and *betweenness* (**g-h**) are plotted for non-breeder population. Values are calculated for each node of the non-breeder spatial-use network. ANOVA test was carried out. Aesthetics show significant differences (**P<0.05, ** P <0.01, *** P <0.001*) with Bonferroni adjustment.

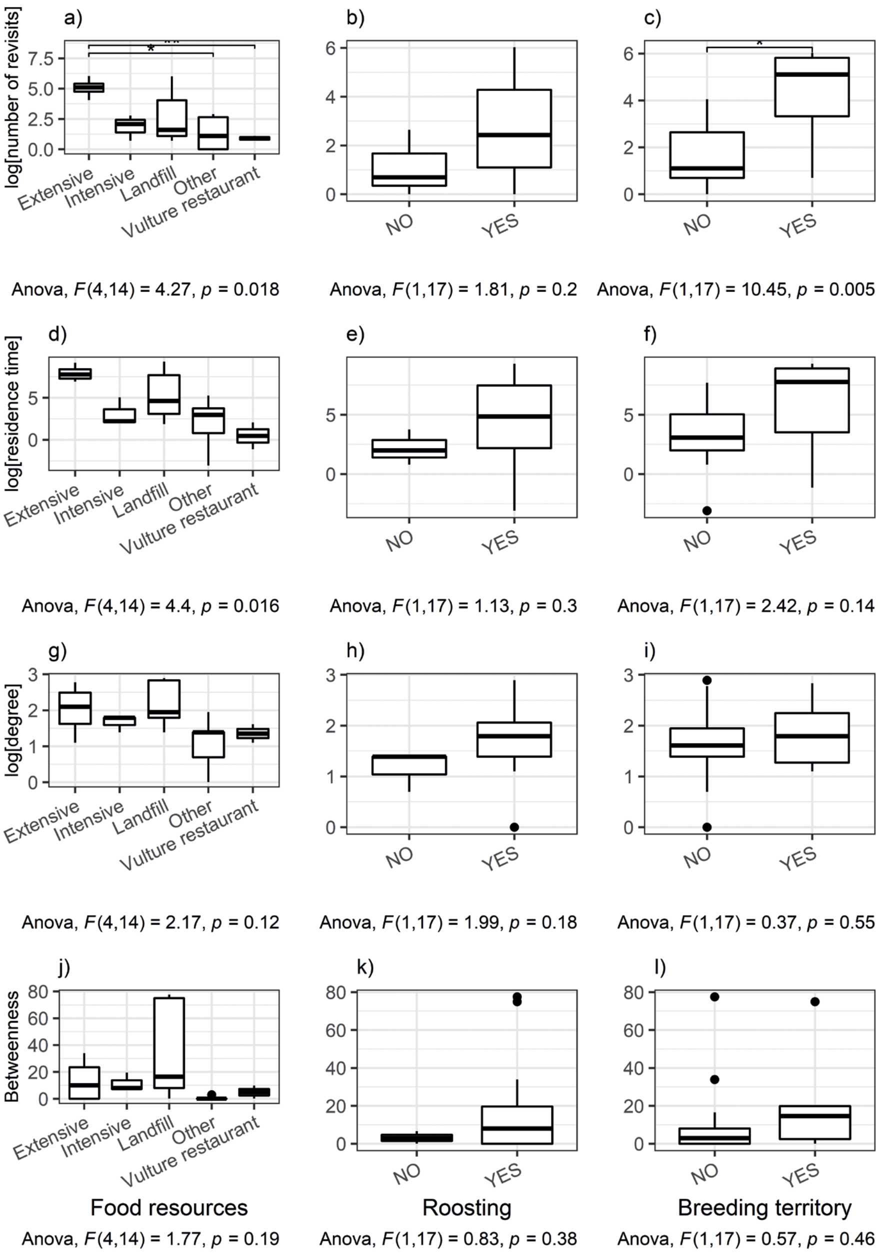

Figure S4. Boxplot of breeders nodes fidelity represented by the number of revisits (**a-b**) and residence time (**c-d**), and spatial networks topology represented by *degree* (**e-f**) and *betweenness* (**g-h**) are plotted for breeder population. Values are calculated for each node of breeder spatial network. ANOVA test was carried out. Aesthetics show significant differences (*$P<0.05$, ** $P<0.01$, *** $P<0.001$*) with Bonferroni adjustment.

Additional file 2. Topology parameters of spatial networks

Degree

The *Degree* of a node is 'the number of links connected to a node' (Newman, 2003). Sociologists use the 'six degrees' theory to demonstrate that we are all well connected. Any person in the world is connected to any another by just six other people (on average; Watts, 2004). Ecologically, node *degree* indicates the 'connectivity' and refers to how easily one can move to a specific node ('reachability', Jacoby et al., 2012). For example, an animal would tend to return to a node with a high *degree* value and use in a sporadic way the nodes with a low *degree* value.

Betweenness

Betweenness has been used by authors in several different areas of knowledge (e.g. sociologists, physics and biologists) as 'the count of how many of geodesic paths between nodes run along each link in the network' (Newman, 2003). Geodesic paths refer to 'the shortest path through the network from one node to another' (Newman, 2003). For example, in a simple network of five nodes (A-B-C-D-E), the shortest path between A and B is the one that passes through fewest nodes (e.g. A-C-B) as opposed to any other path from A to B with a greater number of nodes (e.g. A-C-E-D-B). So, *betweenness* is measured by counting the combination of all shortest paths in the spatial network that pass through a particular node. Ecologically, this measure defines which locations are most beneficial in core movements because they occupy a central place in movement networks (Jacoby *et al.,* 2014) and so are potentially important areas for conservation and management (Fortuna et al.*,* 2009).

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Additional file 3. Linear regression models

Table S4. Results of the top-ranked models (lowest AIC) for non-breeder and breeder Egyptian vultures accounting for site fidelity (number of revisits and accumulated residence time) and spatial-use network topology (*degree* and *betweenness*). Model **in bold** was selected.

	Model	AIC	R2	P
Non-breeder network	log(number of revisits) ~ PC1 + PC2 + Feeding + Roosting	128.39	0.61	< 0.001
	log(number of revisits) ~ PC1 + Feeding + Roosting	126.64	0.61	< 0.001
	log(number of revisits) ~ PC2 + Feeding + Roosting	127.98	0.6	< 0.001
	log(number of revisits) ~ Feeding + Roosting	**126.18**	**0.6**	**< 0.001**
	log(residence time) ~ PC1 + PC2 + Feeding + Roosting	171.34	0.65	< 0.001
	log(residence time) ~ PC1 + Feeding + Roosting	**169.34**	**0.65**	**< 0.001**
	log(residence time) ~ PC2 + Feeding + Roosting	173.04	0.62	< 0.001
	log(residence time) ~ Feeding + Roosting	171.04	0.62	< 0.001
	log(degree) ~ PC1 + PC2 + Feeding + Roosting	72.36	0.6	< 0.001
	log(degree) ~ PC1 + Feeding + Roosting	72.33	0.58	< 0.001
	log(degree) ~ PC2 + Feeding + Roosting	71.54	0.59	< 0.001
	log(degree) ~ Feeding + Roosting	**71.49**	**0.57**	**< 0.001**
	log(betweenness) ~ PC1 + PC2 + Feeding + Roosting	475.15	0.44	0.005
	log(betweenness) ~ PC1 + Feeding + Roosting	474.69	0.42	0.004
	log(betweenness) ~ PC2 + Feeding + Roosting	473.36	0.44	0.002
	log(betweenness) ~ PC2 + Feeding	473.12	0.42	0.002
	log(betweenness) ~ Feeding	**473.12**	**0.42**	**0.002**

Table S4 *Cont.*

	Model	AIC	R2	P
	log(number of revisits) ~ PC1 + PC2 + Feeding + Roosting + Breeding territory	77.51	0.68	0.072
	log(number of revisits) ~ PC1 + Feeding + Roosting + Breeding territory	75.55	0.68	0.035
	log(number of revisits) ~ PC2 + Feeding + Roosting + Breeding territory	75.51	0.68	0.035
	log(number of revisits) ~ Feeding + Roosting + Breeding territory	73.55	0.68	0.015
	log(number of revisits) ~ Feeding + Breeding territory	**71.69**	**0.68**	**0.006**
	log(numer of revisits) ~ Breeding territory	76.24	0.38	0.004
	log(residence time) ~ PC1 + PC2 + Feeding + Roosting + Breeding territory	102.67	0.59	0.182
	log(residence time) ~ PC1 + PC2 + Feeding + Breeding territory	100.67	0.59	0.104
	log(residence time) ~ PC1 + Feeding + Breeding territory	99.86	0.57	0.072
Breeder network	log(residence time) ~ PC2 + Feeding + Breeding territory	98.69	0.59	0.054
	log(residence time) ~ PC2 + Feeding	96.79	0.59	0.025
	log(residence time) ~ Feeding	**96.35**	**0.56**	**0.0163**
	log(degree) ~ PC1 + PC2 + Feeding + Roosting + Breeding territory	50.67	0.41	0.565
	log(degree) ~ PC1 + Feeding + Roosting + Breeding territory	49.27	0.39	0.468
	log(degree) ~ PC2 + Feeding + Roosting + Breeding territory	48.68	0.41	0.424
	log(degree) ~ PC2 + Feeding + Breeding territory	46.87	0.41	0.302
	log(degree) ~ PC2 + Feeding	45.12	0.4	0.198
	log(degree) ~ Feeding	43.6	0.38	0.125
	log(degree) ~ 1	44.78	–	< 0.001
	log(betweenness) ~ PC1 + PC2 + Feeding + Roosting + Breeding territory	182.45	0.43	0.529
	log(betweenness) ~ PC1 + PC2 + Feeding + Breeding territory	180.52	0.43	0.394
	log(betweenness) ~ PC1 + Feeding + Breeding territory	179.29	0.4	0.306
	log(betweenness) ~ PC2 + Feeding + Breeding territory	179.49	0.4	0.325
Breeder network	log(betweenness) ~ Feeding + Breeding territory	178.17	0.37	0.242
	log(betweenness) ~ Feeding	177.29	0.33	0.191
	log(betweenness) ~ 1	**14.59**	**–**	**0.015**

Additional file 4. Distribution of degree and betweenness define scale-free networks

In network theory, power law distribution of *degree* (K) and *betweenness* (B) are prospected to evaluate the robustness of a network (Albert et al., 2000). As our data are limited, the distribution spans a single order of magnitude and we cannot show whether the underlying distributions for these measures are scale-free, so that the network does show scale-free properties (Clauset et al., 2009). These analyses were conducted using the "poweRlaw" package (Gillespie, 2014) in R.

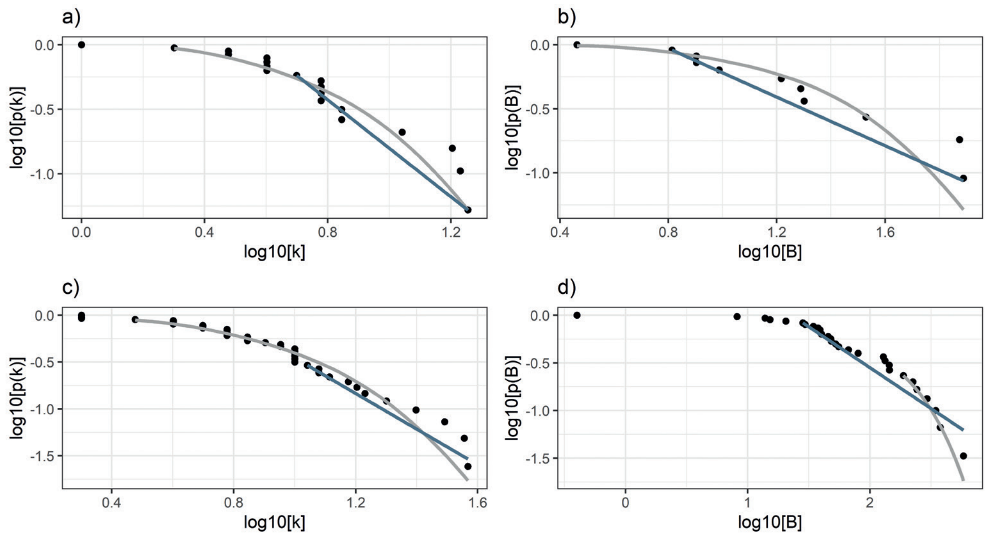

Figure S5. *Degree* (K) and *betweenness* (B) distributions of spatial-use networks for breeding and non-breeding populations of Egyptian vultures. Log-log plots of cumulative distribution functions of non-breeders for K (**a**) and betweenness (**b**). Log-log plot of cumulative distribution function of breeders for K (**c**) and betweenness (**d**). Blue line fits a power law and grey lines fit exponential distribution.

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CHAPTER 3

Assessing protected areas for avian scavengers: Insights for the conservation of an endangered long-lived and mobile species

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ABSTRACT

The establishment of Protected Areas (PAs) is a key step in wildlife conservation whose objective is to offset the rampant crisis in biodiversity worldwide. Despite the fact that approximately 17% of the Earth's land surface is protected in some way or another, a global commitment to expanding this coverage to 30% has been reached. However, the role of these PAs in protecting endangered species –especially long-lived and mobile ones– has rarely been studied. Given this lack of any full assessment of the role of PAs, we evaluate here whether or not the network of Nat2000 and ZPAEN areas provides sufficient protection for the breeding and foraging areas of a population of Egyptian vulture (*Neophron percnopterus*) in northeastern Spain. By analysing the distribution of 27 known occupied nest-site and GPS data corresponding to 16 individuals in the period 2012-2021, 1) we used a null-model approach to test whether the PAs adequately cover the distribution of nest sites and 2) analysed known foraging areas by studying the overlap between home ranges and the surface area of available PAs. We also used *Resource Selection Functions* to analyse (3) whether or not the tracked vultures actively select areas within PAs. Our results indicate that while 64% of nests are within Nat2000 boundaries, only 2% fall within ZPAEN areas. However, the distribution of the PAs does not significantly coincide with the distribution of the nests ($P > 0.5$). Additionally, we found that when foraging, only breeding birds tended to select the Nat2000 sites and that the ZPAEN network –designed to protect feeding areas– was rarely used by either breeders or non-breeders. In fact, non-breeders were only infrequently present in PAs, which leaves these birds vulnerable to human-related risks. Consequently, we recommend that the coverage of PAs be reevaluated by taking into account the foraging behaviour and ecological needs of this highly mobile species as a means of preserving whole populations, both breeders and non-breeders.

Keywords: Egyptian vultures, home ranges, Natura 2000 Network, movement ecology, protected areas, *Resource Selection Functions*, ZPAEN.

INTRODUCTION

Protected areas (PAs) are a key tool in wildlife conservation worldwide that aim to mitigate biodiversity loss. As of the 2020 Aichi Biodiversity Target 11, ~17% of the Earth's land and freshwater habitats enjoy some kind of protected status or other effective area-based conservation measures (Maxwell et al., 2020). Despite this, the global PA network to date seems to be incapable of stemming the current biodiversity crisis, especially in the case of those species that have already been declared as clearly endangered (Zeng et al., 2023). As a result, more than 50 nations have recently signed international agreements and committed themselves to protecting 30% of the planet's land and oceans by 2030 (Dinerstein et al., 2019).

The European Natura 2000 network (hereafter Nat2000) is the largest network of nature protection areas in the world (Hochkirch et al., 2013). It was designed based on the conservation objectives determined by the European Biodiversity Conservation legislation, which is backed by the Birds and Habitats Directives (Directive 79/409/EEC, 92/43/EEC, respectively). These Directives have generated a legal framework for establishing areas within Nat2000 that use multi-approach prioritisation: i) a species-level approach through the creation of Special Protected Areas for Birds (SPAs) under the Birds Directive and ii) a non-species-level approach via the creation of Sites of Community Importance (SCIs) and Special Areas of Conservation (SACs) under the Habitat Directive. In terms of the species-level approach, Nat2000 aims to ensure the long-term survival and reproduction of all European species listed in Annex I of the Birds Directive by protecting their key habitats (Directive 2009/147/EC). Additionally, to guarantee the effectiveness of habitat and species conservation, the Member States of the European Union are obliged to evaluate and assess the conservation status of all relevant sites and species. As outlined by the Bird Directive, each Member State must prepare a report for the Commission every three years outlining how relevant national provisions have been implemented and adopted (the Habitat Directive requires a report every six years). Hence, the goal of expanding the global PA network –coupled with the responsibility for evaluating this network– implies the urgent need to develop methodologies that will assist policymakers and managers identify optimal locations for establishing new conservation areas or expanding existing ones, with the overall objective of halting habitat and, ultimately, species loss (Butchart et al., 2012).

One of the main objectives of PAs is to protect all life stages of relevant species (Possingham et al., 2006; Primack, 2006); however, achieving this goal is a serious challenge in the case of many mobile species. These species often require large, interconnected areas (e.g. raptors; Bosch et al., 2010) and the mobility they exhibit makes the establishment of appropriate PAs much more complicated than for species with more restricted home ranges (e.g. endemic species; Bonn et al., 2002). This complexity arises from the fact that during the process of establishing PAs management objectives are often assumed to remain static over both temporal and spatial dimensions (Pressey et al., 2007). However, ecological systems, especially those involving mobile animals, are inherently dynamic. As a result, existing PAs may not meet the requirements of long-lived, mobile or migrant species. The conservation of these species will rely heavily on the management of far-away areas (Delgado-González et al., 2022) and requires knowledge of the behaviour of individuals in these areas of special interest in which they perform most of their life cycles (e.g. breeding, feeding or wintering areas; Burgas et al., 2014; Runge et al., 2014).

In particular, it has been found that the ecological requirements of endangered species may vary across space and time (e.g. trophic resources) and they may not necessarily be present in existing PAs (Roe et al., 2004; Manning et al., 2007; Probst et al., 2021). This is the case of vultures, globally the most endangered functional vertebrate guild (Buechley & Şekercioğlu, 2016; McClure et al., 2018). As obligate scavengers, vultures search for carrion, whose presence varies both spatially and temporally, by surveying large areas, some of which have no figures of protection (Santangeli et al., 2019; Moleón et al., 2020). Hence, during their foraging movements, vultures are exposed to multiple threats such as poisons (Safford et al., 2019), human persecution (McKean et al., 2013) and collision with and electrocution on human infrastructures (Angelov et al., 2013), all factors that have led to severe declines in many vulture populations worldwide (Santangeli et al., 2019). In fact, the disappearance of certain populations has seriously affected human well-being due to these birds' crucial ecosystem functions. For instance, vultures help ensure healthy ecosystems by preventing the spread of infectious diseases (Ogada et al., 2012) and facilitating proper nutrient cycling (DeVault et al., 2016), and also bring economic benefits to local communities through birdwatching activities (Becker et al., 2005; García-Jiménez et al., 2021). Unfortunately, in Europe, new threats have emerged since the outbreak of bovine spongiform encephalopathy in 2001, which caused a serious decline in

European vulture populations. In light of this crisis, the European Commission approved sanitary measures (EC 1774/2002) (i.e. the ban on the abandoning of livestock carcasses in the wild) that led to the disappearance of food sources. To counteract the negative effect of this legislation on the viability of populations (Margalida et al., 2010, 2012; Morales-Reyes et al., 2017), European Commission has now approved a regulation (EC 142/2011) that allows farmers to abandon extensive livestock carcasses in specific feeding areas known as Protection Zones for the Feeding of Necrophagous Species of Community Interest (hereafter ZPAEN, its acronym in Spanish).

Furthermore, given that the anthropisation of the environment is advancing at such a rapid pace (Hermoso et al., 2018), it is to be expected that existing PAs may even be inadequate or not coincident with current key areas for endangered species (Zeng et al., 2023). One particular concern involves the non-breeding fraction of populations, often overlooked in the establishment of PAs, given that breeders and non-breeders tend to occupy different habitats (Runge, 2014; Mott et al., 2021). In addition, non-breeders frequently approach highly anthropised areas (Cerecedo-Iglesias et al., 2023) and these human-altered landscapes are generally excluded from conservation frameworks, which leads to ineffective conservation strategies for non-breeding individuals (see review Penteriani et al., 2011).

Here, our main goal is to examine whether the key areas for an endangered vulture species, the Egyptian vulture (*Neophron percnopterus*), are spatially covered by the current network of PAs. Specifically, we evaluated whether or not the Nat2000 (the conservation tool in Europe) and ZPAEN (the regional tool established for feeding scavenger species) networks cover both the nesting and feeding areas of Egyptian vultures in Catalonia (NE Spain), one of the main breeding quarters of this endangered migrant species (BirdLife International, 2021). First, we tested whether or not the known locations of 27 regularly monitored breeding nests are well covered by the Nat2000 and ZPAEN areas. Next, we studied whether or not the foraging movements of tagged vultures (both breeders and non-breeders) take place within these PAs. Finally, we assessed whether the 16 GPS-tagged birds select preferentially the areas included in the PA network during their movements. To do this, we used information collected during the annual monitoring of the breeding population and the GPS locations of tracked Egyptian vultures (breeders and non-breeders). Given that international organisations have committed themselves to the ambitious task of expanding the global PA network (Dinerstein et al., 2019) and that all PAs should be periodically evaluated to check whether proposed conservation goals are being fulfilled (López-López et al., 2007), this study aims to be one of the first to identify and assess pivotal zones for conserving endangered species. This research will help identify the biases in PA coverage underlying EU legislation and guide planning on the future extension of the PA network. Furthermore, this research will also provide useful management methodologies for successfully preserving this Egyptian vulture population and those of other vulture species.

MATERIALS AND METHODS

Focal species and study area

The Egyptian vulture is a long-lived medium-sized scavenger distributed throughout the Palearctic region that is considered to be globally Endangered (BirdLife International, 2021). The primary threats to its survival are poisoning, human disturbance at breeding sites, electrocution and collisions with infrastructures (BirdLife International, 2021). Due to its declining European populations, the Egyptian vulture has been declared Vulnerable in Europe (BirdLife International, 2021). Furthermore, it has been listed as a target species for conservation under Annex I of the European Birds Directive (EC 2009/142/2011) in an attempt to ensure its survival and successful reproduction within its breeding distribution. In Spain, the Egyptian vulture is classified by the national government on the Spanish Catalogue of Threatened Species as Vulnerable due to its rarity and the risk of extinction (Legislative Decree 2/2008). In our study area, Catalonia (NE Spain), the species is classified as Vulnerable in the Catalan Catalogue of Endangered Autochthonous Wildlife (Legislative Decree 172/2022) –despite the fact that the local population has increased by 65% over the last two decades (Tauler et al., 2015; Franch et al., 2021, García et al, 2018). The study area consists of a large lowland region, chiefly covered by farmland, forest and scrubland, with Nat2000 sites distributed intermittently throughout the area and ZPAEN sites concentrated mainly in the north-west pre-Pyrenean and Pyrenean ranges (**Fig. 1**). The Nat2000 network occupies a surface area of 2,932 km^2 and the ZPAEN network 1,072 km^2; however, given the partial overlap (649 km^2) between these two networks, the total surface area of the PAs in the region covers 3,484 km^2, 32.3% of the whole study area.

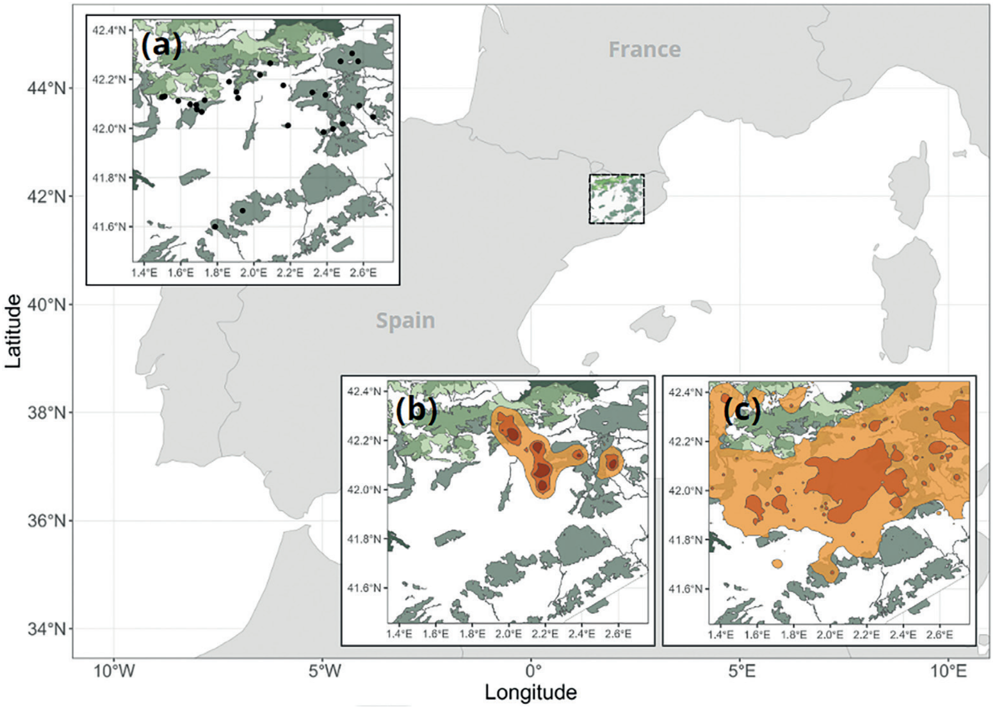

Figure 1. Study area of the monitored local population of Egyptian Vultures in northern Spain (Catalonia). The Protected Areas (PAs) represented are the Nat2000 (dark green) and ZPAEN (light green) networks. Also shown is the overlap between the two Nat2000 and ZPAEN networks. (**a**) Locations of the nests (black dots) that were occupied at least once in the period 2012-2021 (N = 27). (**b**) Combined home ranges using dynamic Brownian Bridge Movements Models (dBBMM) of the breeding fraction of the population (N = 6) and (**c**) for the non-breeding fraction (N = 10). The different 50%, 75% and 95% home ranges are indicated by a gradient of colour from yellow to red, respectively.

Data collection

From 2012 to 2021, we carried out standardised population monitoring to establish the location of nests (for more details, see Tauler et al., 2015). In March-July, an average of three visits were made to occupied territories to monitor pairs' reproductive phenology. Once breeding had been confirmed, the locations of successful nests were recorded. All observations were made with a telescope (20-60x) from a safe distance (> 500 m) to avoid interfering with birds' behaviour. In addition, during the summer in 2018-2021, we tagged 16 birds with GPS-GSM devices (6 breeders and 10 non-breeders) at a landfill in the centre of the study area (**Supplementary Material**: **Table S1**). We programmed the GPS devices to emit one location every 30 minutes. To optimise the energy efficiency of the devices, we configured a sleep interval of e-obs tags to operate on an 18-hour ON/6-hour OFF cycle (from 6:30 to 22:30 Coordinated Universal Time). Similarly, for the Ornitela tags, sleep intervals were determined relative to the position of the sun, specifically at an angle of 18° above or below the horizon. As we were focused on feeding movements, we only analysed the locations during daylight hours (see Cerecedo-Iglesias et al, 2023). Birds were also ringed with conventional rings and a distance-reading coloured ring, each on a different leg. The age of individuals was determined by their plumage (Blasco-Zumeta and Heinze, 2006). In all, we analysed a total of 386,073 locations (MEAN ± SD = 14,849 ± 9,064 location per bird).

Statistical analysis

Spatial distribution of nests and PAs

We assessed the distance between nests and the nearest PA to evaluate whether the observed distribution of nests is statistically attributable to the spatial arrangement of PAs or whether they are situated purely by chance (see Tauler-Ametller et al., 2017 for more details). Thus, we compared the distribution of observed nests with the distribution of the same number of simulated nests obtained from random locations (i.e. the same number of observed territories as other ‘potential’ locations). To ensure that simulated nests were in suitable breeding areas for Egyptian vultures, we applied three ecological constrains: 1) the simulated nests had to be inside ‘potential’ areas of observed Egyptian vulture nests (we used buffers around the observed nests in the study area with a radius of 21.91 km, equivalent to half the mean distance between occupied nests of neighbouring breeding pairs); 2) the simulated nests had to be located in a forest or in bare rocky areas (based on a 10-m resolution of the Land Cover Map *Cobertes del Sòl de Catalunya*; Generalitat de Catalunya), which are the two land cover layers in which known nests are located (Tauler-Ametller et al., 2017); and 3) as this species only nests on cliffs, we ensured the existence of a ‘potential cliff’ by selecting locations whose degree of slope is greater than the average of slopes for the observed nests. Our null model selected a set of 27 ‘potential’ nests; we then calculated the mean of all Euclidean distances between each 'potential' breeding nest and the nearest border of the PA polygons. This process was repeated 999 times to generate a histogram of distance frequencies for a 'potential' nest distribution, which we then compared with the mean of the distance between observed breeding nests and the PA border. Finally, we calculated the probability value (*P*).

Overlapping between home ranges and PAs

We conducted a comprehensive analysis of the overlap between the home ranges of breeding and non-breeding individuals and the two PA networks: Nat2000 and ZPAEN. To do so, we employed the dynamic Bowenian Bridge Movement Models (dBBMM; Horne et al., 2007; Kranstauber et al., 2012) to calculate the home ranges for each individual and year. Only GPS information for individuals with a complete summer period (i.e. February-October) was used to calculate home ranges. Utilisation Distributions (UD, Kranstauber et al., 2012), a 500-m^2 grid-cell raster, were employed to determine the probability of use in a specific area at individual and year levels. Subsequently, we averaged the UDs of different years for each bird to obtain a unique home range per individual. Then, we identified the 50, 75 and 95% probability densities of the UDs to represent the varying degrees of use, ranging from core areas (50% contour) to extensive areas (95% contour; Buechley et al., 2018). Next, we quantified the overlap defined as the proportion of home ranges of each tracked bird included in the PAs (Nat2000 and ZPAEN; **Supplementary Material: Table S2**). To assess differences at breeding level (breeders vs. non-breeders), we conducted a Welch test that takes into account unequal variances and sample sizes; a suitable approach for very small sample sizes (De Winter, 2019). Finally, to account for unbalanced samples, we applied a Bonferroni correction.

Evaluating the selection of Protected Areas by Egyptian vultures

Resource Selection Functions (RSFs; Johnson, 1980) were used to assess whether vultures use PAs differently from non-PAs when performing their vital activities. RSFs are an analytical framework that can be used to model and understand how habitat and/or resource preferences affect the movement of animals, and allow positive spatial and temporal correlations between locations during the analytical process to be controlled for (Fieberg et al., 2010). In this framework, several modelling approaches can be used to create the RSFs. In our case, we built 16 different weighted logistic regression models (binomial distribution, logit link function; Zuur et al., 2009), one per individual, to avoid any correlation between individuals. The dependent variable was composed of two sets of locations: locations where the animal was observed and 'potential' locations generated for each bird within the spatial range where the animal can be at any given time (DeCesare et al., 2012). 'Potential' locations were generated by creating 10 random points per each observed location within individuals' home ranges (see details in **Supplementary Material**: **Appendix S2** and **Fig. S1**). In addition, observed and 'potential' locations were assigned weights (1 and 1000 respectively) when fitting logistic regressions, which helps address issues related to sample bias, data imbalance and model performance in ecological modelling (see Fithian and Hastie, 2013). We controlled for between-individual correlation by estimating individual-specific coefficients (βi) modelled by a logistic distribution (assuming individuals to be independent), and controlled for within-individual correlation by subsampling the locations ($\sim$ 2-hour fix rate) based on the assumption that individuals have time to select independent sites across consecutive locations. Since we were not interested in which environmental features favour habitat selection by these vultures but, rather, aimed to test whether or not there is any preference for areas inside or outside the PAs, we used as independent variables two binomial covariates: Nat2000, which indicates whether a location was inside or outside the Nat2000 network, and ZPAEN, which indicates whether a location was inside or outside the ZPAEN network. Finally, we extracted from the logistic regression the coefficients (βi) that represent the degree of selection ($\beta i > 0$) or avoidance ($\beta i < 0$) that an individual has for specific areas inside or outside the PAs. If there was no PA available for the bird, the individual was excluded from the analysis. We also compared the coefficients between breeders and non-breeders using a Welch test with a Bonferroni correction in order to check the differences in usage of PAs.

RESULTS

Spatial distribution of breeding nests and PAs

Of 27 occupied nests in 2012-2021, 17 (63%) were located within the Nat2000 network and only 2 (7%) within the ZPAEN network. The mean distance between observed nests and the nearest Nat2000 was 495 m (max-min: 0-3,791 m) and 14,488 m (max-min: 0-56,945) for ZPAEN. Null models showed that there were no significant differences between distances for observed and for simulated territories for both the Nat2000 network (mean distance of simulations = 338 m; 95% CI 59-684; P = 0.837) and ZPAEN network (mean distance of simulations = 6,608 m; 95% CI 2,285-12,190; P = 0.099; **Fig. 2**). As the null hypothesis was accepted in both cases, our results support a random relationship between the spatial distribution of nesting sites and PAs. However, we found that the observed distance from nests to ZPAEN areas was marginally higher than was randomly expected (**Fig. 2b**), thereby indicating that these areas probably lie further from nest sites than could be expected. Although there were no significant differences, there did seem to be a pattern in the distribution of the ZPAEN nests that was not random but could not be simply explained by how nest sites were distributed.

Overlap between home ranges and PAs

The average size of the home range for breeders was 21.6 km^2 (SE = 5.82), 104 km^2 (SE = 19.1) and 341 km^2 (SE = 62.8) on the 50%, 75% and 95% contours, respectively, whereas the average for non-breeders was 53.2 km^2 (SE = 8.71), 555 km^2 (SE = 77.1) and 5 047 km^2 (SE = 694) on the same contours, respectively. Welch tests show that the home ranges of breeders were significantly smaller than those of non-breeders (50% contour: t(23.9) = -3.01, P = 0.006; 75% contour: t(17.9) = -5.68, P = < 0.001; 95% contour: t(16.3) = -6.76, P = < 0.001). The average percentage of overlap between breeders' home ranges and Nat2000 sites was 22.5%, 25.7% and 23.5%, and for ZPAEN was 0.97%, 7.79% and 9.22% on the 50%, 75% and 95% contours, respectively. By contrast, non-breeders exhibited in most cases lower average overlaps with Nat2000 (11.6%, 18.5% and 25.7%) and ZPAEN (1.72%, 3.96% and 5.96%) at respective contour levels (see **Table 1**). Additionally, there was significant individual variability within both the breeder and non-breeder groups, indicated by the large standard deviations

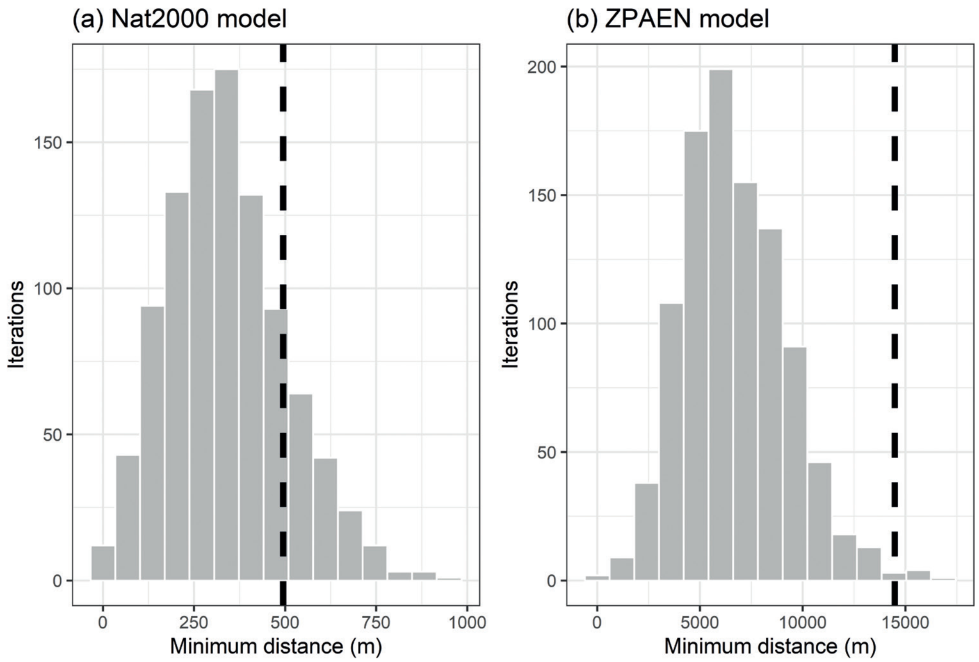

Figure 2. Histogram of minimum distance between 'potential' breeding nests and (**a**) the Nat2000 and (**b**) ZPAEN boundaries, obtained from the null models. The number of iterations were 999. The black dashed lines indicate the distance from the observed nests to the nearest Nat2000 and ZPAEN boundaries.

in the average percentage of overlap of all PAs. Consequently, the Welch test did not show any significant differences ($P > 0.05$) between overlapping percentages for PAs between breeders and non-breeders (**Fig. 3**; **Supplementary Material: Table S3**).

Evaluating the Selection of Protected Areas by Egyptian vultures

The average (± SE) of regression coefficients for all tagged vultures was negative: $\beta_{Nat2000}$ = -0.3 (± 0.33) and β_{ZPAEN} = -2 (± 0.68). This showed a relative weaker selection of areas within PAs during movements (**Fig. 4**). All vultures spent more time in Nat2000 sites (21.2% of observed locations) than in ZPAEN sites, where they rarely stayed for long (3.38% of observed locations), although there was great inter-individual variability. However, if we consider breeding status, breeders used on average more often Nat2000 (19.17% of observed

Table 1. Home range sizes (± SE) of GPS-tracked Egyptian Vultures in the PAs (Nat2000 and ZPAEN) using 50%, 75% and 95% contours. Reproductive status are breeders (B; N = 6) and non-breeders (NB; N = 10). Home ranges (dBBMM) were calculated in km^2 at three contour levels (50%, 75% and 95%). The overlap between Nat2000 and ZPAEN areas was calculated using percentages (%) at three contour levels of home ranges (50%, 75% and 95%).

Reproduct. status	Home ranges (km^2)			Overlapping (%)					
				Nat2000			ZPAEN		
	50%	75%	95%	50%	75%	95%	50%	75%	95%
B	22 ± 6	104 ± 19	341 ± 63	22.9 ± 10.3	25.7 ± 8.12	23.5 ± 6.39	0.97 ± 0.5	7.79 ± 4.17	9.22 ± 4.9
NB	53 ± 9	555 ± 77	5047 ± 694	11.6 ± 3.38	18.5 ± 2.44	25.7 ± 2.07	1.72 ± 0.97	3.96 ± 1.18	5.69 ± 1.31

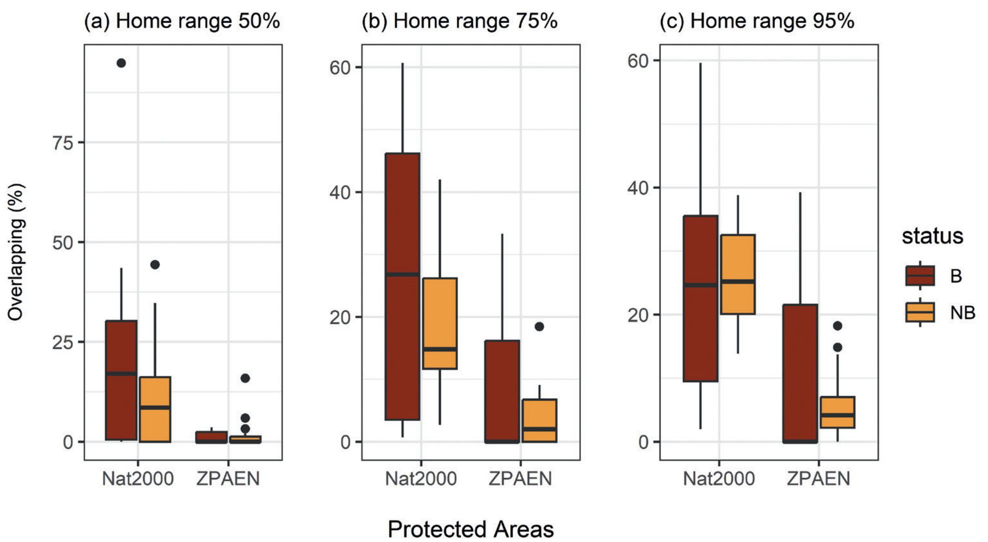

Figure 3. Percentage of overlapping home ranges in the protected areas of 16 tagged breeding Egyptian Vultures. The overlap was calculated for different home range contours: (**a**) 50%, (**b**) 75% and (**c**) 95%. The ZPAEN areas totally contained within Nat2000 areas are shown. B: Breeders; NB: Non-breeders.

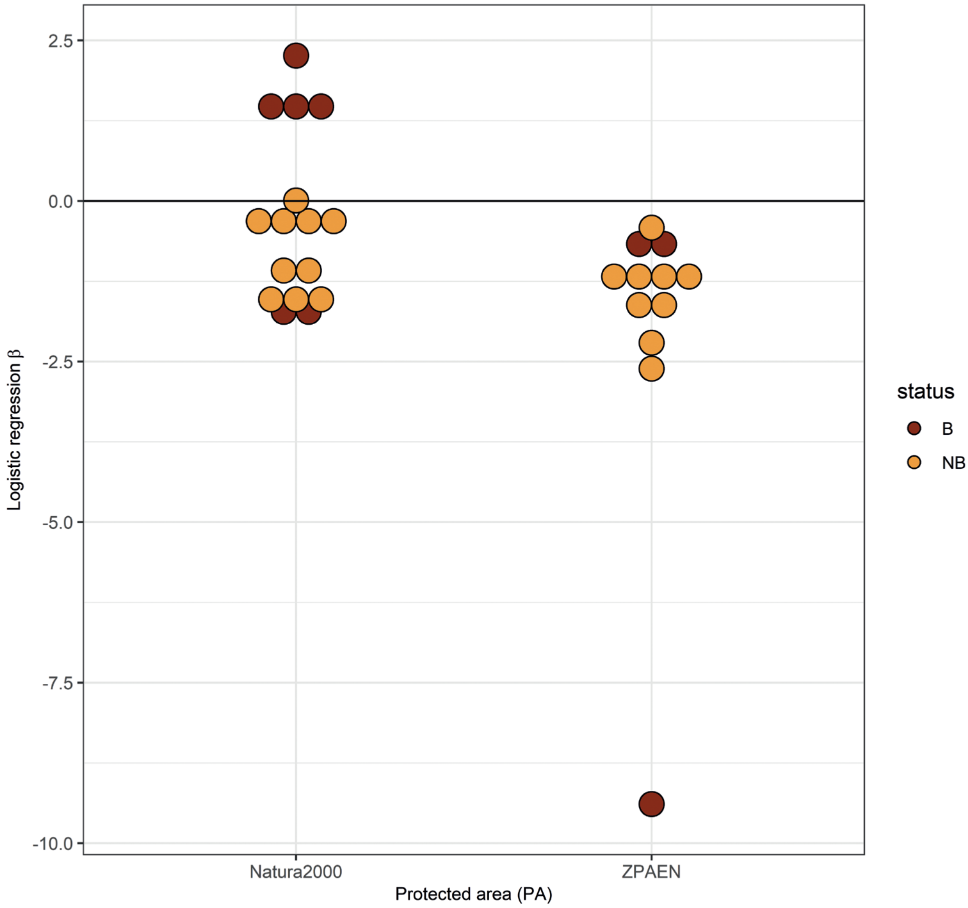

Figure 4. Logistic regression coefficients from the habitat selection model based on the *Resource Selection Functions* for each Egyptian Vulture (N = 16). Each dot is coloured by the reproductive status of the focal individual (B: breeder, NB: non-breeder). Four individuals were excluded from the selection models because the ZPAEN was not available for these individuals ($N_{breeders}$ = 3, $N_{non\text{-}breeders}$ = 9).

locations) than ZPAEN (0.06% of observed locations) areas, and positively selected areas within the Nat2000 network ($\beta_{Nat2000}$ = 0.57 ± 0.73) and avoided areas within the ZPAEN network (β_{ZPAEN} = -3.31 ± 2.62). The average regression coefficients of non-breeders was negative for both Nat2000 and ZPAEN ($\beta_{Nat2000}$ = -0.82 ± 0.21, β_{ZPAEN} = -1.56 ± 0.25), indicating that this subset of the population tends to avoid both PAs during their movements. Additionally, the comparison between the regression coefficients of breeders and non-breeders showed no significant differences in the areas used within the Nat2000 (t = 1.83, df = 5.84, P = 0.118) and within the ZPAEN (t = -0.663, df = 2.04, P = 0.574) networks, which suggests that the space used inside or outside of PAs by individuals is not distinguishable between breeders and non-breeders.

DISCUSSION

Better identification of optimal sites as a means of creating new conservation areas and/or expanding existing ones has become essential if the goal of covering 30% of the Earth's surface with PAs and improving conservation effectiveness is to be met (Butchart et al., 2012; Dinerstein et al., 2019). Given that certain taxa in terrestrial environments remain poorly represented by the global PA network (Zeng et al., 2023), a trend also observed in freshwater organisms (Hermoso et al., 2015), an examination of the degree of protection currently offered by PAs is key to determining the success of conservation actions in preserving wildlife under today's scenario of biodiversity crisis. PAs generally fail to adequately support the survival of mobile species requiring large areas in which to complete their life cycles, which exposes them to multiple threats over the vast distances they cover (López-López et al., 2007; Bosch et al., 2010; Runge et al., 2014, Delgado-González et al., 2022; Gangoso et al., 2021). This scenario is common among many vertebrates, not just vultures (Phipps et al., 2013), and includes animals such as shorebirds (Choi et al., 2019), elephants (Li et al., 2023) and marine megafauna (Conners et al., 2022). These species all suffer the same limitations since most of their ranges are much larger than existing PAs. Consequently, migratory or foraging movements often encounter specific threats beyond PA boundaries (Runge et al., 2014), as well as conflicts with humans (Nyhus, 2016).

Here, we assessed the coverage of Nat2000 and ZPAEN sites in the preservation at a local scale of key habitats for an Egyptian vulture population, work that is equally applicable to other mobile species with similar breeding and foraging behaviour whose space usage varies between breeding and non-breeding fractions of the same population. We found that the current distribution of Nat2000 sites closely matches the distribution of nests of the studied population. However, ZPAEN sites fail to adequately cover either nesting sites or the larger areas in which these vultures (both breeders and non-breeders) live and move. In other words, the Nat2000 network, created for the recovery of our focal species and other scavenger species, is rarely frequented by non-breeding vultures, while ZPAEN sites, designed to providing feeding areas for endangered avian scavenger species, are too small.

Specifically, our findings show that 63% of nests are in Nat2000 areas, which thus fulfils the objective of preserving the breeding areas of species included in the European Directives (EC 2009/142/2011). Interestingly, however, our null models showed no spatial relationship between the locations of observed nests and the Nat2000 areas. This may seem to contradict the fact that 63% of the observed nests are found within Nat2000 sites; however, we believe that this lack of statistical association can be explained by four main arguments. First, it appears that, while 37% of the nests were identified outside Nat2000 areas, their average distance from the boundaries of Nat2000 areas was only 500 m, which is a relatively short distance for this species. Consequently, even though these nests were outside the Nat2000 network, their locations were close to the borders of a PA. Second, the Nat2000 designations were strongly influenced by the preservation of physical and landscape features based on *ad hoc* criteria, while socio-economic and aesthetic criteria typically played a more significant role in determining the locations of PAs (Pressey, 1994). Third, the establishment of the Nat2000 network followed a multi-approach prioritisation whose main goals were to preserve either habitat and landscapes of ecological interest (driven by the Habitat Directive) or vulnerable birds and related species such as the bearded vulture or Bonelli’s eagle (driven by the Birds Directive). Therefore, a possible explanation could be that not all Nat2000 sites considered the presence of Egyptian vultures as a criterion for their selection: when a particular area was declared protected (or not), this vulture may not have been present then or had not been detected, or was not given priority over other endangered species such as the bearded vulture. For instance, in our study area, in nine out of 12 declared Nat2000 sites the Egyptian vulture was present when they were established, even though now we are aware of its presence in all 12 Nat2000 sites. Fourth, there are several factors affecting the distribution of nesting sites that we did not consider in our analysis. For example, it is known that nesting sites can be situated near humanised landscapes, usually close to built-up areas without any designation in terms of wildlife preservation (Tauler-Ametller et al., 2017). In these areas predictable and anthropogenic food resources such as landfills are often available. As a result, certain nests are situated close to these clusters of food sources and hence outside the boundaries of the Nat2000 network. Consequently, the presence of these anthropogenic resources can shape the distribution of nesting sites in our focal species and study area (Tauler et al., 2015) but also the nesting site of other species (Carrete et al., 2006; Robb et al., 2008). However, breeding near landfills may have negative consequences for the long-term viability of the population as these vultures are exposed to pharmaceuticals (Krüger et al., 2022) and a greater risk of collision and electrocution as they are usually found in highly anthropised landscapes (Blanco et al., 2019; Marcelino et al., 2021).

Our research also threw light on the role of areas specifically designed as feeding areas for necrophagous species, i.e. the ZPAEN network. Surprisingly, we found that only 2% of Egyptian vulture nests were within ZPAEN areas, which contrasts with studies at regional level (89.6% nests are in ZPAEN areas in Spain; Morales-Reyes et al., 2017). Furthermore, the spatial distribution of nests cannot be attributed to the spatial distribution of the ZPAEN network. From our results, we can infer that the establishment of ZPAEN in areas at altitudes over 1,400 m (Regional Order AAM/387/2012) may not suit Egyptian vultures, whose average known nest altitude is 946.41 m.a.s.l. (± 287.53). Current ZPAEN areas may be more suitable for other necrophagous species such as the bearded vulture, a vulture that tends to locate its nest at higher altitudes (an average of 1,424 m.a.s.l.; Margalida et al., 2008). Indeed, at a finer scale (at county level, a smaller administrative division in Catalonia), all breeding bearded vultures nests were situated in the ZPAEN network (Margalida et al., 2007).

If we focus more on the foraging movements of the total birds of the studied population, we find surprisingly that most of our focal vultures barely use the Nat2000 and ZPAEN areas during their movements if, for example, we compare them to other vulture species in Africa that frequently use areas inside PA networks (Moleón et al., 2020; Kane et al., 2022). For instance, Kane et al. (2022) showed that the home ranges of marked vultures in Africa overlap with PAs by more than 50%; our findings, on the other hand, indicate a maximum overlap of only 25% of home ranges with PAs in our study area. The scarcity of food resources outside PAs results in reduced and irregular feeding opportunities for vultures in Africa. Consequently, vultures tend to extend their foraging movements into the interior of PAs (Moleón et al., 2020). However, in the Iberian Peninsula, vultures rely on rubbish dumps and supplementary feeding stations (Donázar et al., 2010; Tauler-Ametller et al., 2017), the latter situated either inside or outside PAs. Therefore, it is to be expected that the movements of vultures be concentrated not within the PAs but beyond their boundaries, as our results show.

In general, we also found that vultures tend to avoid ZPAEN areas (**Fig. 4**). In fact, some individuals never enter ZPAEN areas, which can be partially explained by the fact that the Egyptian vulture population in our study area relies on certain predictable anthropogenic sources such as landfills and extensive livestock farming (Tauler-Ametller et al., 2019), which are usually located far from ZPAEN areas and not present in these vultures' foraging ranges. In addition, given that their foraging movements are strongly influenced by the availability of predictable and abundant food sources, breeding birds are likely to nest near extensive livestock (Cerecedo-Iglesias et al., 2023), while non-breeders will roost near landfills and not travel far in search of scarcer and more unpredictable food resources in ZPAEN areas. Moreover, it is important to note that the ZPAEN surface area in our study area is the second lowest in Spain (i.e. Catalonia has only 13% of its surface area covered by ZPAEN; Morales-Reyes et al., 2017). Therefore, we believe that the ZPAEN network, which was created to compensate for the shortage of more natural food sources once the abandoning of extensive livestock carcasses was allowed again (Margalida et al., 2010), should be expanded bearing in mind not only the criterion of altitude (see above) but also a more ecological perspective. For instance, ZPAEN should consider the distribution areas of endangered scavenger species, as occurs in other parts of Spain (Morales-Reyes et al., 2017).

Finally, our research highlights concern about the preservation of the non-breeding fraction of the population. We have found that the percentage of coincidence between PAs and non-breeders is still relatively low compared to breeding individuals (**Fig. 3**), a pattern also found in other raptor species such as the African white-backed vulture (*Gyps africanus*; Phipps et al., 2013) and Spanish imperial eagle (*Aquila adalberti*; Penteriani et al., 2005), as well as in other animal species (e.g. reef fish species, Félix-Hackradt et al., 2018). Thus, since non-breeders spend more time outside than inside the PAs, their exposure to potential threats (e.g. illegal poisoning and wind farms; Sanz-Aguilar et al., 2015) will surely be greater than in the case of breeders (Sanz-Aguilar et al., 2017). In this sense our research highlights how most of the conservation efforts invested in raptors, including vultures, are currently mainly focused on breeding individuals despite the fact that non-breeders (also known as 'floaters') buffer, regularise and stabilise fluctuations in populations and are much needed as a reservoir for replacing breeding individuals (Penteriani et al., 2011). Their nomadic behaviour and their attraction to anthropogenic food sources complicates their monitoring and, consequently, the establishing of adequate PAs. Thus, we need to fill this gap in our knowledge of the distribution and size of non-breeding Egyptian vulture populations. To do so, we should consider that non-breeders are solitary individuals with large home ranges that make the monitoring of the behaviour of these birds difficult (Brown and Long, 2007), although they do concentrate in roosting places (Donázar et al., 1996). Thus, estimations of the population size and/or distribution may be inaccurate and so novel monitoring methods should be implemented to survey these nomadic birds (e.g. tracking methods).

Recommendations

Our assessment of the PA network reveals that it has certain limitations regarding the adequate safeguarding of endangered mobile species like the Egyptian vulture, which play a crucial role in ecosystem health (Gangoso et al., 2013; Cortés-Avizanda et al., 2016; Donázar et al., 2016). To address these shortcomings, we conclude and propose the following recommendations:

1) We recommend conducting local-level evaluations of PAs such as Nat2000 to gain in-depth insights into the dynamics of species and ecosystems within a region. Our research presents a unique opportunity for considering the Egyptian vulture as an indicator species and offers insights into both the challenges and potential solutions for the entire guild of scavenger birds in the study area. For instance, the new sanitary and circular economy regulations advocating the closure of landfills (2008/98/EC), one of the main food sources of this vulture population (Tauler-Ametller et al., 2019) and aimed at preventing wildlife accessing human waste, are predicted to have a direct impact on these nesting areas (Cerecedo-Iglesias et al., 2023). Under this scenario, feeding alternatives for this species must be

guaranteed. Therefore, an effective local management plan not only for Egyptian vultures but other endangered scavengers (see Arévalo-Ayala et al. 2023) should focus on promoting alternative food sources in the main areas used by these species within current or future PAs by considering the behaviour, spatial use and biological requirement of both fractions of populations, breeders and non-breeders.

2) We advocate the incorporation of new technologies into the continuous, real-time and long-term monitoring of endangered mobile species. In this research, the use of GPS data has highlighted the urgent need to review and redefine PA networks. Additionally, GPS information represents a great opportunity to infer the 'potential' distribution of future PAs through actual knowledge of the areas most used by animals when they forage or migrate (Kays et al., 2015). Moreover, the use of new technologies is particularly valuable for identifying crucial areas for the under-protected fraction of the population, i.e. non-breeders, whose monitoring is even more complex due to their nomadic behaviour.

3) Adjustments to the ZPAEN network are imperative and must include the significant feeding areas identified for this endangered species since our results show that the current ZPAEN network does not cover the foraging areas most frequently used by both breeders and non-breeders. Moreover, the criteria for establishing ZPAEN in our study area should change to consider more ecological aspects of this species (e.g. its movement patterns).

4) We suggest that policymakers and conservation managers acknowledge species mobility and age-dependent movements when expanding and redefining PAs for conservation purposes. The implementation of protective measures and feeding programs should be tailored to preserve crucial nesting and foraging sites for species' survival. In this sense, a whole-landscape management approach may be the most efficient strategy for conserving mobile fauna (Runge et al., 2014). Such an approach should recognise the complexity of natural systems and focus not only on the management of areas designated for conservation but also on the landscape as a whole, both outside and inside the PAs (Hobbs et al., 2014).

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SUPPLEMENTARY MATERIAL

Assessing protected areas for avian scavengers: Insights for the conservation of an endangered long-lived and mobile species

Appendix S1. Data available and exploration analysis

Appendix S2. Selection of sufficient number of 'potential' locations

Appendix S1. Data available and exploration analysis

Table S1. Details of each tagged Egyptian Vulture. We show the reproductive status (B=Breeders and NB=Non-breeders) and the number of GPS locations distinguished by protection categories (Nat2000 and ZPAEN) and the total number of locations. Non-PA is the number of GPS-location out of PAs. ZPAEN areas partially nested in Nat2000 areas are shown.

ID device	Status	Nat2000	ZPAEN	Non-PA	Total
6616	B	1 784	0	24 957	26 741
6977	B	356	23	43 203	43 559
6978	B	7 963	2 539	13 538	21 501
201397	B	9 427	0	11 534	20 961
181648	B	9 354	4 694	5 618	14 972
200666	B	20 306	0	1 760	22 066
6223	NB	1 507	0	10 100	11 607
6224	NB	2 544	169	14 250	16 794
181649	NB	2 509	883	12 709	15 218
201395	NB	14 966	761	17 276	32 242
201452	NB	3 726	1 534	21 437	25 163
6222	NB	7 256	634	28 723	35 979
6615	NB	7 585	634	22 403	29 988
6979	NB	2 007	964	30 222	32 229
201398	NB	5 756	872	14 712	20 468
201399	NB	1 820	126	14 765	16 585

Table S2. Home ranges and percentages of overlap of 16 Egyptian Vultures (6 breeders and 10 non-breeders) during the study period (2019-2021) in Catalonia (NE of Spain). Home ranges (dBBMM) were calculated in km^2 at three contour levels (50%, 75% and 95%) for each individual and year. The overlap between the PAs (Nat2000 and ZPAEN) was calculated in percentages (%) representing the surface area of the home range of each individual covered by each PA. The overlap was also calculated on three contour levels of home ranges (50%, 75% and 95%).

ID device	Year	dBBMM (km^2)			Overlapping (%)					
					Nat2000			ZPAEN		
		50%	75%	95%	50%	75%	95%	50%	75%	95%
6616	2020	17	62	215	2.08	3.50	4.81	0.00	0.00	0.00
	2021	11	43	146	0.51	3.69	1.97	0.00	0.00	0.00
6977	2020	3	64	202	0.00	0.69	9.51	0.00	0.00	0.00
	2021	5	75	245	0.00	2.42	9.93	0.00	0.00	0.00
6978	2020	44	186	553	17.02	26.80	24.62	2.75	16.17	21.54
	2021	50	183	691	18.26	31.54	24.92	2.41	20.62	22.16
201397	2021	24	140	439	43.53	56.14	40.65	0.00	0.00	0.00
181648	2021	34	134	388	30.24	46.14	35.53	3.58	33.29	39.25
200666	2021	6	47	191	94.89	60.67	59.59	0.00	0.00	0.00
6223	2020	15	404	4726	34.72	11.75	17.20	0.00	0.00	0.00
	2021	13	454	4351	0.00	11.70	16.01	0.00	0.00	0.00
6224	2019	111	573	3561	2.37	23.74	27.61	2.02	1.54	3.68
	2020	69	557	3115	0.78	10.33	26.68	0.00	0.00	0.03
181649	2020	37	370	3659	13.90	21.46	38.80	3.24	8.03	13.71

Table S2 *Cont.*

ID device	Year	dBBMM (km^2)			Overlapping (%)					
					Nat2000			ZPAEN		
		50%	75%	95%	50%	75%	95%	50%	75%	95%
	2021	32	352	2113	11.70	28.34	37.92	15.89	18.46	14.85
201395	2021	38	450	5399	44.36	41.98	36.40	0.00	3.27	7.02
201452	2021	11	101	1727	0.00	13.58	21.24	0.00	9.07	18.24
6222	2019	37	389	4488	0.00	14.82	23.52	0.00	2.01	4.17
	2020	88	953	4472	22.32	30.67	20.63	0.00	0.88	2.32
	2021	97	1040	6698	8.53	15.54	25.19	5.93	3.01	6.92
6615	2020	43	281	6376	12.06	13.46	32.52	0.00	0.00	2.22
	2021	104	953	6237	30.01	28.47	27.43	1.27	1.87	3.56
6979	2020	16	201	3276	0.00	2.66	13.84	0.00	4.46	5.39
	2021	17	338	2732	0.00	11.34	14.22	0.00	7.93	8.63
201398	2021	84	859	9704	16.19	26.17	38.19	0.96	6.73	4.78
201399	2021	91	1165	13169	0.00	8.67	20.09	0.00	0.00	1.17

Table S3. Welch test comparing the overlap between the home ranges of breeding and non-breeding individuals of Egyptian Vultures in PAs (i.e. Nat2000 and ZPAEN sites). W: Welch statistic; df: degree of freedom; *P:* p-value.

PAs	Home range contour	W	df	*P*
Nat2000	50%	1.04	9.74	0.322
	75%	0.852	9.47	0.415
	95%	-0.332	9.72	0.747
ZPAEN	50%	-0.692	22.4	0.496
	75%	0.885	9.31	0.399
	95%	0.695	9.17	0.504

Appendix S2. Selection of sufficient number of 'potential' locations

Following Fieberg et al. (2021), it is essential to determine an adequate number of potential locations before developing the *Resource Selection Function* (RSF) in order to reach stable values for the parameter estimates. To assess the stability of these parameters, we applied logistic regression models to datasets featuring an incremental increase in 'potential' nest locations, ranging from one 'potential' nest per used location to 100 'potential' nest locations per used point. We found that the intercept decreased as we increased the number of 'potential' nest locations but that the slope parameter estimates (Nat2000 and ZPAEN) from at least 10 'potential' locations per used location did not change (**Fig. S1**).

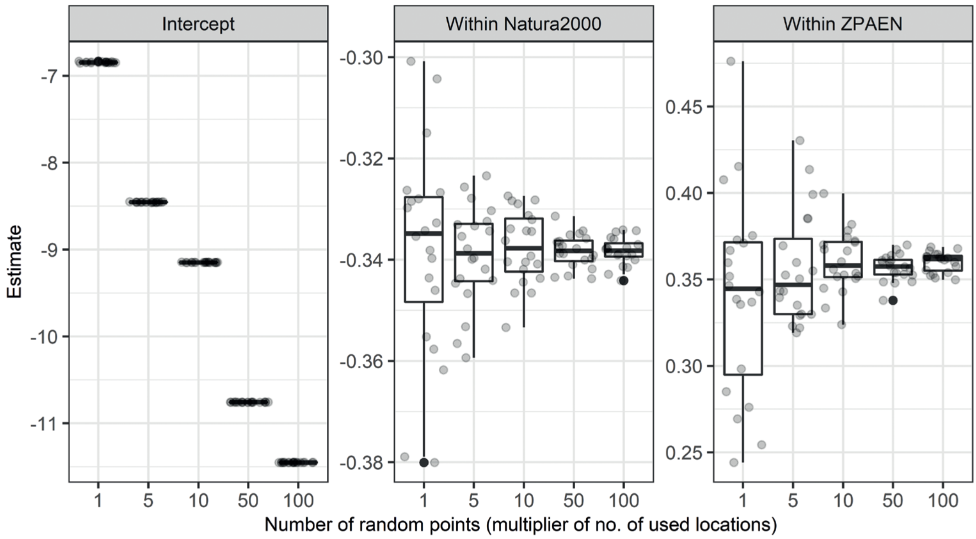

Figure S1. Estimated parameter in fitted *Resource Selection Function* using an increasing number of 'potential' locations. For each increased number of 'potential' locations, the logistic regression was fitted 20 times to obtain the distribution of the estimated parameters. Each dot represents an estimate of the regression model.

Reference

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GENERAL DISCUSSION

In recent decades, the loss of biodiversity and natural areas, largely as a result of human activity, has spiralled out of control. The rampant humanisation and destruction of the environment, coupled with numerous other factors, has led to a global biodiversity crisis (Brondizio et al. 2019; Ceballos et al., 2015; Johnson et al., 2017). The impact of this crisis extends far beyond the health of ecosystems and severely affects human societies, which depend on ecosystem services for their well-being and cultural identity (Cardinale et al., 2012; Marselle et al., 2021; Pretty et al., 2009) The European Union and the international community as a whole have implemented an ambitious plan to preserve biodiversity as part of the 2030 Agenda for Sustainable Development (UN, 2015). Some actions included in this Agenda aim to prevent the depletion of natural resources and irreversible environmental damage while maintaining socioeconomic growth (Hermoso et al., 2022). Within this context, the recognition of nature's contribution to human welfare has become one of the leitmotifs of sustainable development. However, not all species have the same relevance and importance when it comes to providing services. Avian obligate scavengers, one of the most endangered animal guilds worldwide, have attracted attention due to key role they play in regulating and cleaning ecosystems (Moleón et al., 2014; DeVault et al., 2016). As mentioned in the introduction to this thesis, several studies have shown that, despite the increasing conservation efforts to protect species and habitats, sustainable actions can have unintended harmful ecological impacts on several species, including vultures (Buchmann-Duck and Beazley, 2020; Rehbein et al., 2020; Oppel et al., 2021; Jones et al., 2022). In this thesis, we assess the novel challenges associated with species' responses to sustainable European policies and we provide guidelines for improving current conservation measures designed to protect one of the most globally threatened of all vulture species, the Egyptian vulture *Neophron percnopterus*, classified as Endangered by the International Union for Conservation of Nature (IUCN) due to its recent and extremely rapid population decline (BirdLife International, 2021). Our research focused on two populations: the continental Spanish population, one of this species' strongest, and the Catalan population, which is expanding despite overall global decline. To achieve our goals, we used innovative technologies such as tracking devices and performed novel analytical methods including networks combined with sophisticated dynamic Brownian Bridge models. This thesis expands existing knowledge of the spatial ecology of this species (mainly distribution and movement patterns) to identify practical solutions that could mitigate the impacts derived from sustainability (e.g. habitat alteration, changes in food availability and some inadequate current conservation measures). Finally, we propose a set of management guidelines that will enhance the conservation strategies devoted to preserving the Egyptian vulture and, ultimately, to other related threatened scavenger species, as well as the key ecological functions and ecosystem services they provide.

Main contributions

Spatial distribution patterns of breeding pairs according to environmental factors and at different scales

The first finding of this thesis is that the number of breeding Egyptian vultures in continental Spain has remained stable since 2000, albeit with a slight increase in the number of pairs that is not significant enough to be termed a population expansion (**Chapter 1**). However, this trend is inconsistent because human pressure and other factors threatening the species are heterogeneously distributed across the peninsula (Del Moral and Molina, 2018a). As a result, many breeding territories have disappeared and smaller populations have declined in areas such as Aragón and Basque Country (Carrete et al., 2007; Zuberogoitia, 2008). On the other hand, in regions such as Catalonia the Egyptian vulture population has expanded and reached historically high numbers of breeding pairs (Tauler et al., 2015).

This temporal stability also manifested itself in the consistency of occupancy and abundance distribution patterns of breeding territories in continental Spain. During the study period, we observed that the number of occupied cells remained almost unaltered. The few differences in the number of occupied cells over the years were either due to the expansion or contraction of the mentioned breeding areas or the product of having used different sampling efforts (see Del Moral and Molina, 2018a). Moreover, the distribution of abundances followed the same spatial patterns: the higher abundance values tended to accumulate in the same cells year after year, which could be attributable to intrinsic ecological aspects of individuals such as philopatry or strong territorial fidelity (López-López et al., 2014). These characteristics are shared with other avian scavengers such as the bearded vulture (*Gypaetus barbatus*; Krüger et al., 2015) and the cinereous vulture (*Aegypius monachus*; García-Macía et al., 2023) and help maintain population sizes and their geographical distributions. In addition, territorial fidelity forces breeding pairs to remain within areas they know well, which can help decrease the risk of mortality (García-Macía et al., 2023). Conspecific attraction, which refers to the process of gathering essential information about suitable habitats for reproduction and food resources from other individuals of the same species (Carrete et al., 2007; Mateo-Tomás and Olea, 2011), also favours the stability of species distribution. It is worth noting that certain clustered predictable sources like supplementary feeding stations and landfills also encourage the aggregation of individuals, which, consequently, could lead to an increase in the number of breeding pairs in certain areas (see below for details).

However, despite this overall regional stability, we observed that areas with a lower density of breeding pairs tend to be less stable over time. Even though natal dispersal has been defined as a density-dependent process, i.e. individuals move further where the habitat is saturated, in the particular case of the Egyptian vulture dispersal distances were inversely related to vulture density in the natal population, suggesting that birds perceive the abundance of conspecifics as a signal of high-quality habitat (Serrano et al., 2021). As a result, a lack of conspecifics in a particular breeding area could be interpreted by individuals as an indication of an unsuitable reproductive habitat. In addition, human activities that cause disturbances in breeding areas can lead to a decline in a species' population, resulting in low densities or even local extinction (Carrete et al., 2007). However, in cases where disturbances can be mitigated (e.g. recreational activities), breeding pairs may return to an empty breeding area once the disturbance disappears (Zuberogoitia et al., 2014). Another reason for this spatiotemporal instability in lower-density areas could be population stochasticity, that is, random fluctuations in population size due to probabilistic demographic processes, as has been noted in other bird species (see Sæther et al., 2004).

The second main finding of this thesis is the identification of local environmental factors that explain the heterogeneous spatial pattern of vulture populations (**Chapter 1**). In particular, the aggregation pattern in breeding territories that we noted is found in other species of birds and many other organisms, whereby a few individuals are present in most sampling sites and a few sampling sites –which can be referred to as 'hotspots'– accumulate a significant number of individuals (Brown et al., 1995). Using a spatial autocorrelation analysis, we first identified those hotspots (as well as 'cold spots') for a specific year and then determined the local environmental factors that generated this aggregation pattern in the breeding vultures. The methodological approach that we used in this chapter, which has rarely been used before in ecology for this purpose (e.g. Nelson and Boots, 2008; Martínez Batlle and van der Hoek, 2018), is very useful for distinguishing spatial patterns in the current and future distributions of a species. We found that the availability of predictable food sources (such as supplementary feeding stations) tends to aggregate breeding pairs, making it one of the most important factors in increasing the local abundance of vulture populations (Parra and Tellería, 2004; Van Beest et al., 2008; Olea and Mateo-Tomás et al., 2009; García-Heras et al., 2013). When food resources are clustered, the animals that live in the vicinities of the trophic source are more likely to survive, grow and breed, which leads to an increase in their local population (Parra and Tellería, 2004; Grande et al., 2009 but see Cortés-Avizanda et al 2009b,c). Additionally, we also observed that the griffon vulture density was also positively correlated to these hotspots for Egyptian vultures, suggesting that there could be some type of positive interaction between these two species (see below).

However, we also found that greater numbers of wind farms, one of the infrastructures used to obtain alternative 'green' energy, was highly correlated to the lower-density areas, indicating a local negative effect on Egyptian vulture distribution. Wind farms pose a significant danger to this species (BirdLife International, 2021) and to other raptors (Watson et al., 2018), and cause mortality rates to rise and population growth rates to fall (Carrete et al., 2009). To date, few studies have analysed the effect of wind farms on Egyptian vultures in our study area. Studies with other similar species have shown that, due to their distinctive physical characteristics, griffon vultures are the most vulnerable species to suffer collisions with wind farms (Martin et al., 2012; Ferrer et al., 2022). Their large size and high wing loads mean that they find it difficult to adjust their flight paths, especially when faced with obstacles such as wind turbine blades (Barrios and Rodríguez, 2004). Furthermore, vulture collisions with wind farms appear to be more frequent in areas of high breeding density, which could have severe implications for vulture populations in such regions (Carrete et al., 2012). Therefore, we consider our results to be coherent with the idea that the area of low breeding density of Egyptian vultures detected in our results may be attributable to the high risk of collision of this vulture species with this type of infrastructures. Furthermore, we observed a scale of dependence in how the analysed environmental factors affected the observed distribution of the breeding pairs of Egyptian vultures. Thus, although at local scale the appearance of wind farms and clustered trophic resources shape distributions, only two factors –the abundance of cattle and griffon vultures– significantly affected both the local and regional distribution and abundance of the Egyptian vulture (if 'regional' is taken to be the whole of continental Spain). Previous studies conducted in Spain (Tauler-Ametller et al., 2019; Cabrera-García et al., 2020) and other European countries (Arkumarev et al., 2014; Dobrev et al., 2016) have shown that extensive livestock rearing contributes to the Egyptian vultures' diet and highlight its relevance as a food source, which is supported by the results shown in **Chapter 2** of this thesis (see below). It is known that Egyptian vultures obtain most feeding success from random sources such as those provided in the wild by extensive livestock (see details in Cortés-Avizanda et al., 2012). Furthermore, although it may be anecdotal, it is known that this species consumes excrement during the pre-reproduction period, which may be another possible explanation for the importance of extensive livestock. Through the consumption of cow dung this species acquires lutein, the yellow carotenoid that is responsible for its facial colouration (Negro et al., 2018), which also plays a crucial role in its immune system as an antioxidant (Tauler-Ametller et al., 2019).

The positive relationship found between Egyptian and griffon vulture abundances is logical given that both vulture species share breeding habitats (i.e. cliffs) and feeding requirements (Margalida et al., 2007; Van Beest et al., 2008). Therefore, the abundance of the griffon vultures –the most abundant vulture species in the peninsula (data for 90% of European pairs; Del Moral and Molina, 2018b)– may signal suitable breeding habitats for Egyptian vultures, as well as an indication of areas of greater food availability. Other studies have described a similar relationship –known as heterospecific attraction– in other avian species including scavengers and raptors (Orr et al., 2019), and aquatic (Sebastián-González et al., 2010) and forest (Mönkkönen et and Forsman, 2002) species. Several theoretical and empirical studies have shown that migratory individuals use the density of related resident species as an environmental cue for profitable breeding areas (Mönkkönen et al., 1999; Thomson et al., 2023). It is reasonable to assume that this pattern is repeated in Egyptian vultures, a migratory species, and griffon vultures, resident in the Iberian Peninsula.

Effects of predictable resources on movement patterns

Human activities can modify animals' foraging and movement behaviour (Gilbert et al., 2016; Bartumeus et al., 2010; Selva et al., 2017; Shaffer et al., 2017). In this thesis, we show how predictable trophic resources shape Egyptian vultures' foraging behaviour and movement patterns (**Chapter 2**). Specifically, our findings reveal that the presence of landfills, used as habitual food sources by tagged individuals, significantly shapes the movements of foraging vultures, as has been observed in other avian species such as bald eagle (Elliott et al., 2006), white stork (Gilbert et al., 2016), California gull (Ackerman et al., 2018) and other vertebrates including jaguars (González-Gallina et al., 2018) and brown bears (Cozzi et al., 2016). By feeding in landfills, these species are potentially exposed to pollutants and toxins (De la Casa-Resino et al., 2014) and the ingestion of plastic (Plaza and Lambertucci, 2017; Ballejo et al., 2021). However, the availability of food in these anthropised environments can increase recruitment rates and breeding success in some populations (Oro et al., 2008; Tauler-Ametller et al., 2017). Despite the population's habitual use of landfills, our research revealed distinct foraging strategies in breeding and non-breeding Egyptian vultures. Non-breeders performed more heterogenous and dispersive movements, i.e. they visited more food sources more often than breeders, and concentrated their foraging efforts primarily around landfills and only secondarily on other predictable sources (e.g. intensive farms or supplementary feeding stations). Lacking the nesting obligations and constraints associated with breeding, these individuals are more nomadic in behaviour (Donázar, 1993; McGrady et al., 2018). Although breeders also regularly used landfills, particularly when their breeding territories were close by, their movement patterns reveal a more diversified foraging strategy. They do not concentrate their efforts exclusively on predictable sources, i.e. landfills, intensive farms or supplementary feeding stations, but, rather, take advantage of other more random resources such as extensive livestock (Olea and Mateo-Tomás, 2009; Aguilera-Alcalá et al., 2022). Moreover, analysing the spatial-use networks, we found that breeders exhibited homogenous and fewer dispersal movements and tended to feed constantly in the same places, usually in landfills and/or near their nests. This concurs with the findings of research on seabirds, which shows how breeding northern gannets (*Morus bassanus*) have specialised foraging behaviour, while non-breeders focus their movements around their central areas of foraging (Votier et al., 2017).

The availability of predictable food sources also plays a significant role in the formation of roosting sites where food is abundant and reliably available over both space and time (Benítez et al., 2009; García-Heras et al., 2013; López-López et al., 2014). These areas also serve as stopovers during migration and temporary settlements, and facilitate socialisation and information exchange between individuals (Donázar et al., 1996; Margalida and Boudet, 2003). As a result, it is not surprising that the primary roosting sites in our study area are located near landfills.

Avian scavengers' feeding responses and the disappearance of highly predictable trophic sources

In this thesis, we also highlight the use of spatial networks as a robust framework for understanding the dynamics of wildlife behaviour. This method, which complements traditional assessments of movement analysis and considerations of spatial connectivity, enables the behavioural responses of wild species to environmental changes and landscape transformations to be predicted (Jacoby et al., 2012; Jacoby and Freeman, 2016). In **Chapter 2**, we demonstrate the vulnerability of both non-breeding and breeding vultures to the disappearance of predictable trophic sources (particularly landfills). The disappearance of landfills in our simulations promoted changes in the movement patterns of individuals such that other food sources became the new central areas for foraging, as has been observed in certain seabird populations (e.g. Langley et al., 2021). Moreover, we found that the closure of landfills affects non-breeders more than breeders, which can be explained by non-breeders' lack of experience in exploiting and exploring more random sources and greater dependence on predictable food sources (Monsarrat et al., 2013). Furthermore, this approach also allows us to infer that individuals will increasingly come to rely on other less predictable food sources, notably extensive farms, under the hypothetical future scenario of a lack of highly predictable trophic sources. In other vulture species, such as the griffon vulture, individuals tend to maintain their food preferences by feeding on food sources similar to those they use in their original populations (Arrondo et al., 2023b). This suggests that the disappearance of predictable food sources may lead to different behavioural responses in individuals in terms of the degree to which they depend on these resources. Likewise, although we did not examine it in detail in this thesis, we believe that the disappearance of landfills could influence the sustainability of the roosting sites that have been created around these environments.

Spatial distribution of breeding birds and foraging areas in relation to protected areas (PAs)

The GPS data collected during this thesis allowed us to assess the coverage of two different types of PAs, Nat2000 and ZPAEN, to preserve endangered Egyptian vultures in Catalonia. Our results indicated that both these types of PAs fail to adequately cover essential areas of this vulture's population (**Chapter 3**), which is a common failing in other regions in the world (e.g. Ethiopia, Buechley et al., 2022) and in other vulture species (e.g. *Gyps africanus*, Phipps et al., 2013). A possible explanation for this lack of coverage is that these areas do not reflect the nature of vultures as long-lived mobile creatures. Due to their extensive movements, they are exposed to various threats outside the designated PAs (e.g. poisoning, habitat loss and collisions with human structures), like other mobile terrestrial species such as elephants (Li et al., 2023) and shorebirds (Choi et al., 2019).

We also noticed some mismatches between the coverage of PAs in terms of key habitats for both breeding and non-breeding Egyptian vultures, i.e. nesting sites and roosting sites, respectively. This pattern is not unique to Egyptian vultures and is also observed in other vultures (Phipps et al., 2013), raptors (Penteriani et al., 2005) and seabirds (Pereira et al., 2018). Despite well-protected breeding sites, breeders search for food beyond PAs. Previous research conducted in regions adjacent to our study area involving the same species have shown that the lack of food within a PA may lead birds to leave the PA and head for more humanised areas in search of food where the risk of mortality increases (Cortés-Avizanda et al., 2015b). Analogous behaviour has been documented in various other raptors such as kites in the Doñana Biological Reserve (Sergio et al., 2005), Bonelli's eagles in the Sierra de Espadán Natural Park (López-Peinado et al., 2023) and bearded vultures in certain national, natural and regional parks in northern Spain and southern France (Margalida et al., 2016). Recent experimental investigations underline how food availability within PAs limits the movements of certain eagle species, thereby reducing their exposure to human-dominated environments (López-Peinado et al., 2023). This underlines the fact that food availability and accessibility can improve the role of PAs in conserving breeding birds of prey.

By contrast, tagged non-breeding Egyptian vultures, which have a great dependence on highly predictable food sources, move from one food source to another, as occurs in other regions of the world (Phipps et al., 2013; McGrady et al., 2018). They frequented areas beyond the PAs much more often than breeding counterparts. This may be due to the location of their roosting sites in our study area: primarily near landfills, as noted above, where the greatest concentrations of individuals takes place. However, this recurrent use of anthropogenically altered environments renders these birds more vulnerable to threats such as poisoning, collisions with infrastructures and electrocution (Carrete et al., 2009; Hernández and Margalida, 2009b).

In the case of birds of prey, there are a number of reasons why conservation has focused on the breeding cohort of the population: firstly, the importance of adult raptor survival for population viability (Sergio et al., 2011; Tauler et al., 2015; Tapia and Zuberogoitia, 2018) and, secondly, the fact that information on the distribution of breeding pairs in territorial species is much easier to obtain for breeders than for non-breeders (Brown and Long, 2007). Thus, since non-breeders spend more time outside than inside PAs, they will probably be more exposed to threats than breeders (Sanz-Aguilar et al., 2015), which may adversely affect the whole population since non-breeding individuals act as a reservoir of individuals that replace breeders and help stabilise population fluctuations (Penteriani et al., 2011).

We also noted that the ZPAENs whose declarations aimed to increase the availability of food sources for necrophagous species do not in fact cover the main areas used by breeders and non-breeders. Our findings for Catalonia contrast with the results found for other regions of Spain that took into consideration the ecological factors used to establish the ZPAENs (Morales-Reyes et al., 2017, 2018). Also, our results suggest that these PAs in Catalonia were established without taking into account the main ecological needs of the study species and were designated on purely administrative criteria (e.g. altitude; Regional Order AAM/387/2012) or to protect other endangered species (e.g. bearded vultures). However, information on the movement patterns of Egyptian vultures (which did not exist in such detail when the PAs were established) will help redefine the PAs, above all in light of the scenario of population growth but with the possible closure of landfills.

Self-Review

During the work on this thesis, we identified certain limitations that should be considered in future research. It was only possible to assess some and not all of the potential environmental factors that influence the spatial ecology of the Egyptian vulture. Obtaining such information over diverse habitats and over extended periods of time is logistically challenging, above all in broad-scale studies. For instance, information on the availability of large-scale food sources (e.g. cattle at municipal scale) can only be obtained with narrow temporal resolutions (e.g. once every 10-11 years) and does not coincide with the years in which bird censuses are carried out. Furthermore, it should be noted that accessing data from third-party institutions or organisations –although common practice– does still require tackling data ownership, privacy concerns and institutional restrictions, all of which make access to this information far more difficult. As this issue is not limited to this particular thesis, but also applies to various other subjects and topics of research, we suggest that all relevant information that may prove useful for future ecological studies should be centralized by the administration and/or public organizations.

Furthermore, regarding to **Chapter 1**, we believe that other methodological frameworks such as the Cellular Automata could generate more suitable and well-fitted large-scale distribution patterns from small-scale local processes (Breckling et al. 2011). In other words, this methodology may allow for the inclusion of local ecological aspects such as territorial fidelity and conspecific attraction, which will enhance the representation of underlying processes occurring in distribution patterns (Wootton, 2001). The recognition of temporal and spatial mismatches in data is a critical aspect of ecological research and the addressing of any such disparities will require innovative approaches (see Zipkin et al., 2021).

Telemetric technology is crucial in generating high-resolution tracking information and today provides fresh opportunities for studying animal behaviour, movement patterns and ecological interactions (Kays et al., 2015). However, care must be taken when confronting the challenges associated with the use of this technology (see review Hebblewhite and Haydon, 2010). The economic costs of high-quality information gathering and maintenance can be substantial (although this technology is becoming increasingly cheaper), and requires exhaustive and dedicated monitoring and the proper exploitation of all the information generated. Additionally, capturing and tagging certain species is often complex and resource-intensive. As a result, the sample size for collecting data may be limited in some way, thereby reducing the overall scope of ecological studies. Due to these constraints, the data collected is often based on a small number of individuals. This limitation in sample size can hinder the extent to which the findings of studies can be generalised to the entire population of the species in question. Hence, researchers should carefully consider the trade-offs between the richness of data obtained from a few individuals and the ability to draw broad conclusions about the entire population.

Future research: Implications of sustainable development on vulture conservation

An important part of our findings reflects current studies exploring the adverse effects of sustainable development on wildlife (Buchmann-Duck and Beazley, 2020; Rehbein et al., 2020; Oppel et al., 2021; Jones et al., 2022). The European Union is opting for decarbonisation via a sustainable Agenda that promotes the production of renewable energy (WindEurope, 2021). Alarmingly, the European Commission recently approved a new plan called REPowerEU, which aims to accelerate the deployment of renewable energies and entails a reduction in controls on biodiversity protection (Bolonio et al., 2024). Although renewable energy is considered a sustainable and environmentally friendly strategy, it is not free from adverse environmental impacts. Therefore, we need to develop mitigation plans for reducing the mortality of species (not just those that are endangered) on existing wind farms and for evaluating the future risks associated with establishing new energy sources (e.g. Marques et al., 2014; De Lucas et al., 2012). It is also vital that these new risk assessments use a multiscale analysis approach to obtain valuable information for developing effective conservation measures at various scales, from local actions to global commitments. Thus, obtaining more telemetric data is essential for improving knowledge of wildlife movement patterns including flight paths, migratory corridors and dispersion ranges. This information is crucial if we are to effectively plan the location of the wind farms and other infrastructures contemplated in this new European sustainability plan. This will help implement a truly 'green' policy that prioritises protecting and conserving habitats and wildlife.

The transition to a Circular Economy, although necessary to promote more sustainable and more environmentally friendly economic systems, does not always translate into better biodiversity conservation (Buchmann-Duck and Beazley, 2020). In Europe, zero-waste policies such as the Landfill Waste Directive (2008/98/EC) and the Circular Economy Action Plan (European Commission, 2015) aim to close all existing landfills by 2030 as an environmental health-improving measure. In this scenario, future lines of research should attempt to determine whether other food sources for vultures such as supplementary feeding stations and the presence of wild ungulates and extensive livestock can compensate for the disappearance of landfills. Here, we have seen that individuals begin to explore unpredictable resources if there is a lack of predictable ones; more research is required into this question. Despite having been effective in preventing illegal poisoning and reversing the decline of certain vulture populations (Margalida et al., 2014), it is important to exercise caution when setting up supplementary feeding stations since they have also been found to have a negative impact on reproductive rates (Carrete et al., 2006) and individual body condition (García-Heras et al., 2013; see Cortés-Avizanda et al., 2016). A better long-term solution for the future food shortages resulting from landfills closures could be to increase the availability of more sustainable resources such as extensive livestock. This food source plays a crucial role in maintaining Egyptian vulture populations (Olea and Mateo-Tomás, 2009; Aguilera-Alcalá et al., 2022), although the abandonment of rural areas in Europe may well lead to a scarcity of this resource.

The ongoing shift towards rewilding due to rural exodus results in changes in habitats, ecosystems and biomes that could potentially affect the survival of vulture populations (Cortés-avizanda et al., 2015a). More research is required about how Egyptian vultures and other scavenger species respond to socioeconomic changes and their effects on the availability of carrion. To date, it has been found that griffon vultures tend to search for food in areas with low rewilding levels (Martin-Díaz et al., 2020), which raises several questions regarding the impact of rewilding on species distribution and movement patterns. For instance, it is unclear how rewilding-related landscape alterations may affect the movement patterns of vultures, particularly their foraging behaviour. In light of this, more research is needed to determine whether or not the individuals that have become dependent on predictable resources have lost their ability to find random ones (also taking into account the perspective of 'culture', see Arrondo et al., 2023b). We can use GPS technology and modelling (e.g. Individual Based Models) to gain a deeper understanding of the responses of the individuals dependent on predictable resources and of the rest of the individuals in the population.

Sustainable development also underlines the important role of PAs in preserving biodiversity. Under this context, more research on PAs is needed, especially studies that will answer the current need to ensure that conservation efforts are more efficient. For instance, this thesis has shown that some PAs such as ZPAEN should be expanded to better protect the main foraging habitats of Egyptian vultures in Catalonia. However, in this thesis we do not provide any guidelines as to how to proceed with any such expansion. Future research should aim to determine when and how to expand these areas in order to encompass all the areas that individuals in the population require to survive. To do so, we believe it is important to increase the sample size of the individuals tagged with GPS devices and carry out more long-term monitoring in order to gain reliable information about the distribution and movements of Egyptian vultures. This will help expand the surface area of PAs so as to encompass all the ecological aspects required for the survival of these vultures. In the present thesis we also express our concern about preserving the non-breeding fraction of the population, whose key areas are less well represented in the PAs. In light of the differences in PA coverage, which is largely based on birds' reproductive status, we suggest that further research is required and should examine whether or not there are any variations in the movement patterns of Egyptian vultures around PAs in terms of intrinsic factors such as sex and/or age. Furthermore, given that the expansion of 'green' energy infrastructures within PAs is becoming a severe concern for the conservation status of this species (Rehbein et al., 2020), we consider that additional research about the impact of the future energy projects designed for these areas is urgently required. This line of work is part of the universality of the challenges PAs face in reconciling conservation goals with the growing demand for renewable energy sources. The tension between conservation objectives and the need for energy sustainability is becoming increasingly evident and requires more attention.

Under this sustainable scenario, we believe it is crucial that society should not become detached from the conservation of this vulture species given that it is one of the main providers of ecosystem services –along with the other scavenger species– and, therefore, of our well-being. We consider that society should become more involved in the conservation of these species and to be made more aware of scientific research. This can be achieved in many ways through, for example, citizen science projects that promote the participation of local people in scientific projects (McKinley et al., 2016) or, more specifically, through advertising campaigns that advocate the consumption of food from extensive production systems (Aguilera-Alcalá et al., 2022). The success of these measures could be evaluated from socioeconomic and perception points of view.

Finally, by its very nature, sustainable development seeks to harmonise economic progress, social well-being and environmental care (Emas, 2015; Purvis et al., 2019). However, achieving this delicate balance requires an in-depth understanding of the intricate connections and feedback loops involving economic activities, societal behaviour and ecological systems (Naeem et al., 2016). To achieve this, future interdisciplinary research is imperative. Ecologists, economists, sociologists and conservationists must work together to analyse the intricate web of relationships operating between sustainable development practices and vulture conservation (or biodiversity in general). We believe that this collaboration will ensure that results are not only ecologically sound but also socio-economically influential, and will provide much-needed optimal guidelines for successful conservation efforts.

CONCLUSIONS

1. Although the number of Egyptian vulture breeding pairs in continental Spain has been stable since 2000, trends are inconsistent in certain Spanish regions. Local environmental factors explain the heterogeneous spatial pattern of the distribution of the breeding fraction and, specifically, the availability of food sources has been identified as a key factor for maintaining and establishing new breeding pairs. The abundance of griffon vultures was found to be a good indicator of suitable breeding and foraging areas for Egyptian vultures. On the other hand, wind farms were determined to correlate with areas of lower breeding pair density, suggesting that the presence of these infrastructures have a negative effect on the Egyptian vulture population. However, not all the analysed environmental factors were found to affect this species' breeding distribution at larger geographical scales, which has strong implications for the conservation of vultures.
2. Human activities significantly influence food availability and so shape the foraging behaviour and movement patterns of Egyptian vultures. Landfills in particular exert a strong influence on the movement of Egyptian vultures tagged in Catalonia. By exploiting these predictable anthropogenic food sources, individuals are exposed to numerous threats, including pollution and the ingestion of plastics. However, this behaviour also confers benefits including enhanced reproductive rates. Our findings reveal the existence of distinct foraging strategies in breeding and non-breeding vultures: non-breeding vultures primarily rely on landfills as a feeding resource, whereas breeders adopt more diversified feeding strategies including the use of unpredictable resources such as those derived from extensive livestock practices.
3. Spatial networks are an excellent tool for understanding the dynamics of wildlife behaviour. This methodology allowed us to detect vultures' vulnerability to the loss of predictable food sources such as landfills. Thus, it is clear that the closure of landfills will cause behavioural changes and force Egyptian vultures to vary their feeding strategies and search for other food sources. We show that non-breeding individuals will be most affected,

due mainly to their dependence on predictable resources. Conversely, we found that breeding Egyptian vultures, which exploit more unpredictable food sources, will be less affected by landfill closures.

4. The evaluation of the coverage of Protected Areas (PAs) reveals that the Nat2000 and ZPAEN networks do not adequately cover the key areas for protecting Egyptian vultures in Catalonia, above all in areas related to the feeding requirements of this species. However, some differences were found between breeders and non-breeders. Although breeding sites are well protected within PAs, breeders tend to forage outside of their breeding areas. This is probably due to a lack of food within their breeding areas and so within the PAs in general, which forces individuals to search for alternative resources in areas where they are exposed to greater anthropic pressure and threats. However, non-breeders, which move nomadically from one predictable source to another (i.e. they rely heavily on landfills for food), are more vulnerable to threats such as poisoning and collisions with infrastructures.

5. According to the results showed in this thesis, the conservation of Egyptian vultures may be challenged by sustainable development, which includes the expansion of renewable energy sources, the promotion of the circular economy and inadequate conservation measures. In this context, we demonstrate that spatial ecology is an optimal framework for exploring and identifying current and future limiting factors for the populations of this vulture that are linked to sustainability, which alter natural habitats, landscapes and food sources, and which shape the spatial distribution and movement patterns of this threatened species. We also show that these issues can be addressed by combining cutting-edge technology with traditional research methods, which together provide more reliable results.

6. In this thesis, we propose measures for mitigating the potential adverse effects on Egyptian vulture populations resulting from the pursuit of decarbonisation and the circular economy, and the inadequate implementation of PAs. These include:

   a. Enhance existing policies and measures that prioritise the availability of food for vultures on a large scale while limiting activities (e.g. ‘green’ energy) that may have a local impact on the preservation of vulture populations.

b. Promote extensive livestock systems with robust marketing strategies for their products and allow farmers to leave deceased livestock in the wild. This will ensure that carcasses are free from substances that are toxic to vultures such as diclofenac or antibiotics.

c. Finally, expand the PAs, i.e. the Natura 2000 and ZPAEN networks, by taking into account ecological aspects and not just administrative aspects, focusing on feeding areas that can be protected (e.g., extensive grazing areas).

CONCLUSIONES

1. Aunque el número de parejas reproductoras de alimoche común en la España continental se ha mantenido estable desde 2000, las tendencias son inconsistentes en determinadas regiones españolas. Los factores ambientales locales explicaron el patrón espacial heterogéneo de la distribución de la fracción reproductora y, específicamente, la disponibilidad de fuentes de alimento ha sido identificada como un factor clave para mantener y establecer nuevas parejas reproductoras. También se determinó que la abundancia de buitres leonados es un buen indicador de zonas adecuadas de reproducción y alimentación para el alimoche. Por otro lado, se observó que los parques eólicos se correlacionaban con áreas de menor densidad de parejas reproductoras, lo que sugiere que la presencia de estas infraestructuras tiene un efecto negativo sobre la población. Sin embargo, no todos los factores ambientales analizados afectaron a la distribución reproductiva de esta especie a escalas geográficas más grandes, lo que tiene fuertes implicaciones para la conservación de los buitres.

2. Las actividades humanas influyen significativamente en la disponibilidad de alimento y, por lo tanto, moldean el comportamiento de búsqueda de alimento y los patrones de movimiento de los alimoches. Los vertederos en particular ejercen una fuerte influencia en el movimiento de los alimoches marcados en Cataluña. Al explotar estas fuentes antropogénicas predecibles de alimentos, los individuos están expuestos a numerosas amenazas, incluida la contaminación y la ingestión de plásticos. Sin embargo, este comportamiento también confiere beneficios que incluyen mayores tasas de reproducción. Nuestros hallazgos revelan la existencia de distintas estrategias de alimentación en los buitres reproductores y no reproductores: los buitres no reproductores dependen principalmente de los vertederos como recurso alimentario, mientras que los reproductores adoptan estrategias de alimentación más diversificadas, incluido el uso de recursos impredecibles, como los derivados de la ganadería extensiva.

3. Las redes espaciales son una excelente herramienta para comprender la dinámica del comportamiento de la vida silvestre. Esta metodología nos permitió detectar la vulnerabilidad de los buitres a la pérdida de fuentes de alimentos predecibles, como los vertederos. Así, determinamos que el cierre de vertederos provocará cambios de comportamiento y obligará a los alimoches a variar sus estrategias de alimentación y buscar otras fuentes de alimento. Además, mostramos que los individuos no reproductores serán los más afectados debido a su fuerte dependencia por los recursos predecibles. Por el contrario, los alimoches reproductores, que explotan fuentes de alimento más impredecibles, se verán menos afectados por el cierre de vertederos.
4. La evaluación de la cobertura de Áreas Protegidas (APs) revela que las redes Nat2000 y ZPAEN no cubren adecuadamente las áreas clave para la protección del alimoche en Cataluña, sobre todo las áreas relacionadas con las necesidades alimentarias de esta especie. Sin embargo, se encontraron algunas diferencias entre reproductores y no reproductores. Aunque los sitios de reproducción están bien protegidos dentro de estas áreas, los reproductores tienden a buscar alimento fuera de sus áreas de reproducción. Probablemente esto se deba a la falta de alimento dentro de sus áreas de reproducción y, por ende, dentro de las AP en general, lo que obliga a los individuos a buscar recursos alternativos en áreas donde están expuestos a mayores presiones y amenazas antrópicas. Sin embargo, los no reproductores, que se desplazan de forma nómada de una fuente predecible a otra (es decir, dependen en gran medida de los vertederos para obtener alimentos), son más vulnerables a amenazas como el envenenamiento y las colisiones con infraestructuras.
5. Según los resultados de esta tesis, la conservación de los alimoches puede verse amenazada por el desarrollo sostenible, que incluye la expansión de las fuentes de energía renovables, la promoción de la economía circular y ciertas medidas de conservación inadecuadas. En este contexto, demostramos que la ecología espacial es un marco óptimo para explorar e identificar factores limitantes actuales y futuros para las poblaciones de este buitre que están vinculados a la sostenibilidad, que alteran los hábitats naturales, los paisajes y las fuentes de alimento, y que configuran sus patrones de distribución espacial y de movimiento. También mostramos que estos problemas se

pueden abordar combinando la tecnología telemétrica con métodos de investigación tradicionales, que en conjunto brindan resultados más fiables.

6. En esta tesis, proponemos medidas para mitigar los posibles efectos adversos sobre las poblaciones de alimoche resultantes de la búsqueda de la descarbonización y la economía circular, y la implementación inadecuada de las Áreas Protegidas (APs), como la Nat2000 y ZPAEN. Éstas incluyen:

    a. Mejorar las políticas y medidas existentes que priorizan la disponibilidad de alimentos para los buitres a gran escala y al mismo tiempo limitar las actividades (e.g. la energía 'verde') que puedan tener un impacto local en la preservación de las poblaciones de buitres.

    b. Promover sistemas ganaderos extensivos con sólidas estrategias de comercialización de sus productos y permitir a los agricultores abandonar los cadáveres de sus ganados libres de sustancias tóxicas para los buitres, como el diclofenaco.

    c. Por último, ampliar las APs, es decir, las redes Nat2000 y ZPAEN, teniendo en cuenta los aspectos ecológicos y no sólo los administrativos, poniendo el foco en las áreas de alimentación que se puedan proteger (e.g. zonas de ganadería extensiva).

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APPENDIX

animals

Article

Key Factors behind the Dynamic Stability of Pairs of Egyptian Vultures in Continental Spain

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Simple Summary: Understanding and modelling species distribution is crucial for conservation efforts, especially in light of the global biodiversity crisis. Here, we focus on the worldwide endangered Egyptian vulture (*Neophron percnopterus*), a large long-lived raptor, in order to explore ways of developing effective conservation strategies. We analyzed interesting differences in trends at the local level within the context of a regionally stable pattern over the past two decades in Spain, one of the most important breeding areas for this vulture. Through our analysis, we discovered that the regional stability in Egyptian vulture breeding pairs was positively associated with the abundance of griffon vultures (*Gyps fulvus*) and cattle. We also found that the presence of wind farms had a negative impact on the number of breeding pairs at the local level and that factors relating to food resources had a positive effect at both local and larger scales. To effectively conserve the Egyptian vulture, management plans should adopt a hierarchical approach and address the factors influencing breeding populations at various spatiotemporal scales.

Abstract: Conservation science aims to identify the factors influencing the distribution of threatened species, thereby permitting the implementation of effective management strategies. This is key for long-lived species that require long-term monitoring such as the worldwide endangered Egyptian vulture (*Neophron percnopterus*). We studied temporal and spatial variations in the distribution of breeding pairs and examined the intrinsic and anthropic factors that may be influencing the abundance of breeding territories in continental Spain. Based on the census data of breeding pairs from 2000, 2008, and 2018, we used Rank Occupancy–Abundance Profiles to assess the temporal stability of the population and identified the spatial heterogeneity through a Local Index of Spatial Autocorrelation analysis. The GLMs showed that the abundance distribution was mainly influenced by the abundance of griffon vultures (*Gyps fulvus*) and cattle at a regional scale. Nonparametric comparisons showed that the presence of wind farms had a significant negative effect on local breeding pairs abundance, but that supplementary feeding stations and food resource-related variables had a positive impact. In light of these findings, we recommend a hierarchical approach in future conservation programs involving actions promoting regional-scale food resource availability and highlight the need to address the negative impact of wind farms at local levels.

Keywords: abundance distribution; Egyptian vultures; LISA; ROAPs; spatial autocorrelation; trophic resources; supplementary feeding stations; vulture conservation; wind farms

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1. Introduction

The species–environment relationships determining the current distribution of endangered species within their geographic range are a key ecological process; therefore, examining and understanding these species–environment relationships may be essential for the development of effective conservation strategies devoted to recovering endangered species [1–3]. However, the study of the distribution patterns of large long-lived species presents exceptional challenges, as it requires the integration of spatial and temporal shifts in abundances [4,5]. Furthermore, species–environment relationships depend greatly on the scale at which they are studied [6–8], and the neglect of appropriate spatial and temporal considerations can lead to inaccuracies in forecasts of species distribution [9]. Species distribution is a dynamic phenomenon, characterized by spatial contractions and expansions over time, that is influenced by the interplay of biological, ecological, and biogeographic factors. In this context, the application of species distribution models (SDMs; see review [10]) has been widely used to study species occupancy and abundance patterns.

SDMs empirically examine species occupancy or abundance using grid-cells and the species–environment relationship in terms of intrinsic and extrinsic factors. Despite the advantages of using such methods (e.g., identifying important areas for species conservation; [11]), the consideration of variability in the temporal dimension is rarely addressed. The incorporation of the continuous temporal dimension (i.e., neither a static nor specific time interval; [10,12]) is a novel approach that allows us to use distinct ecological processes and time-dependent factors governing fluctuations in occupancy and abundance [13–15]. In addition, since species distribution patterns are also sensitive to factors operating in the local environment such as microclimate or food availability [16] that differ greatly from those at work at larger scales [6], SDMs require a specific spatial scale or scales under scrutiny. Additionally, landscape heterogeneity in terms of the availability of suitable breeding sites may also influence occupancy and abundance patterns [17], thereby promoting spatial aggregation and uneven distribution across a landscape [18,19].

Studying the occupancy and abundance distribution of large long-lived vertebrate species presents numerous challenges due to their wide range of different behaviors that require large interconnected habitats [20–22]. In this context, vultures are no exception, and their spatial and temporal distribution is often influenced by multiple, often environmental [23] and human-related [24,25] factors whose impact varies depending on scale. As long-lived birds, they exhibit late maturity and low reproductive rates, which leads to slow natural changes in population numbers over time [26].

Here, we use a novel approach to analyze the factors that influence temporal and spatial variation in the abundance distribution of breeding pairs of the long-lived Egyptian vulture (*Neophron percnopterus*), a species threatened worldwide at different local (i.e., specific 100 km^2 areas within a landscape) and regional (i.e., larger geographic regions such as countries) spatial scales. Despite the crucial role that Egyptian vultures play in ecosystem health, they face threats such as habitat loss, persecution, electrocution, and poisoning [27]. In Spain, human activities have resulted in local extinctions [28] but, interestingly, in some regions the number of breeding territories is now increasing [29,30]. We used long-term Egyptian vulture monitoring information in one of this vulture's main breeding areas. We aimed (1) to test whether or not Egyptian vulture occupancy and abundance has changed over time in continental Spain; (2) to determine the spatial patterns, i.e., the spatial heterogeneity, of the abundance of breeding territories in the study region; (3) to identify the factors contributing to spatial variation at the local scale; and (4) to investigate the factors responsible for changes in abundance over both time and space at the regional scale. Based on the hypothesis that both temporal and spatial factors influence species distribution, we predicted that the abundance of breeding pairs of Egyptian vultures would vary over time (i.e., a non-stationary distribution) and space (i.e., an aggregated distribution). Furthermore, we anticipated that the factors driving this species' distribution would differ depending on the spatial scale employed [6]. The findings of this study will help develop targeted conservation plans for declining vulture populations and facilitate efforts to increase the occupancy rate of their breeding populations.

2. Materials and Methods

2.1. Study Species

The Egyptian vulture is a long-lived migratory scavenger that is globally "Endangered" [27]. During the breeding period (March–August), it establishes territories in southern Europe, the Middle East, and central and southern Asia, but spends the winter in various parts of Africa. The Spanish population, which represents 12% of the world's total [27] and 27% of the European total, suffered a serious decline in 1987–2000 [31] due to multiple causes, including poisoning [32], disturbance at breeding territories [24], electrocution [33], collision with human infrastructures such as power lines and wind turbines [34], and reduced food availability [35]. Here, we used data from the last three censuses (2000, 2008, and 2018) from continental Spain (493,719 km^2, Figure 1), but excluded data from the Canary and Balearic Archipelagos where this vulture is a resident species [33]. Censuses were conducted using a standardized methodology in which territorial breeding pairs in potential breeding areas were searched for [36–38]. For each breeding territory, the location and status (occupied vs. unoccupied) was recorded. To obtain the abundance data for each census year, these locations were incorporated into a spatial Universal Transversal Mercator (UTM) grid with a resolution of 10 × 10 km and the abundance of each cell was calculated by summing the locations of confirmed breeding territories. During the analysis, we only took into account cells where the species was present in at least one year in the period 2000–2018 (n = 1033).

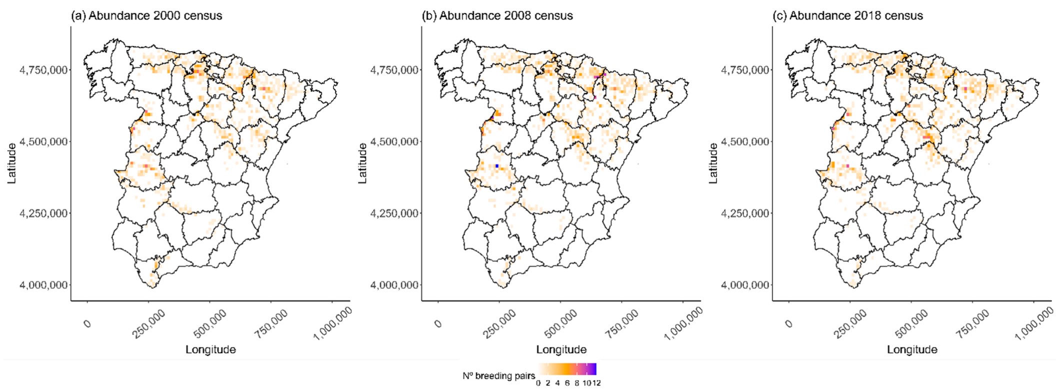

Figure 1. The distribution of Egyptian vulture breeding pairs in three different years: (**a**) 2000, (**b**) 2008, and (**c**) 2018. Each 100 km^2 grid shows the number of occupied territories during the breeding period.

2.2. Analytical Procedure

2.2.1. Analyzing the Temporal Variation in Distribution

The Rank Occupancy–Abundance Profiles (ROAPs; [39]) approach was used to test the null expectation that the regional population of Egyptian vulture can be considered stable over the years or, conversely, that significant changes have occurred (either increase or decrease) in both abundance and occupancy patterns. ROAPs are a graphical procedure based on the position of cells in a rank according to their occupancy and abundance that is similar to a classical ranking of species within communities (see [39]). They consist of scatterplots in which the X-axis (values range from 0 to 1) corresponds to the relative ranks of grid-cells based on their occupancy, and the Y-axis corresponds to the absolute abundance of pairs per grid-cell. To obtain the relative ranks, we assigned the rank position 1 to the highest abundance and divided each rank by the total number of cells (n = 1033). Three profiles were built separately from the abundance of pairs data for each 10 × 10 km cell (2000, 2008, and 2018).

Additionally, to test for differences in the occupancy and abundance distribution between the three censuses, we followed the procedure described by [39], which consists of pooling the abundance data of the three censuses and randomly assigning a year. We iterated this routine 100 times and calculated the D* statistic (the area under the curve of abundances of each year) for each run to obtain a reference random distribution. Furthermore, we compared the observed statistic D* with the random distribution and tested to see whether or not it could be considered within the scope of randomized distribution at a significance level of $\alpha = 0.05$.

2.2.2. Analyzing the Spatial Heterogeneity

To investigate the spatial variation in abundance, i.e., the spatial heterogeneity, we first identified the cells exhibiting aggregation patterns. To do so, we first checked for the existence of spatial autocorrelation by using the global Moran's I test [40], a preliminary procedure for detecting at which scales a significant spatial positive dependency occurs. We further identified the cells with spatially aggregated patterns using the procedure known as the Local Index of Spatial Autocorrelation (LISA; [41]). For this two-step analysis, we analyzed the 2018, 2008, and 2000 censuses separately. Moran's I Index reflects the degree of similarity or dissimilarity between abundance values based on the distances between the central points of the cells. The values in this index range between −1 (regular distribution, negative autocorrelation) and +1 (aggregated distribution, positive autocorrelation), zero being the reference random distribution. This index was calculated using the distance matrix between the central points of the cells that had been occupied at least once during the census (n = 1033). Then, we used a Monte Carlo simulation and 999 permutations to obtain the significance of the spatial autocorrelation at a regional level. Once we had detected the spatial autocorrelation of the abundance data, we used the LISA to detect spatial aggregation areas in which the number of breeding pairs was greater or lower than in nearby areas. The LISA measures allow us to distinguish between spatial aggregation units and non-aggregation units using the scatterplot resulting from Moran's I Index and by dividing it into four quadrants with the abundance values plotted against spatial distances [42,43]. These values are classified according to the quadrant in which they are located on the scatterplot: High–High (high surrounded by high), Low–Low (low surrounded by low), High–Low (high surrounded by low), and Low–High (low surrounded by high). Then, we combined classified the High–High and High–Low cells as High cells, and Low–Low and Low–High cells as Low cells. High cells represent the clusters where the number of breeding pairs is significantly higher than in neighboring cells (spatial aggregation), while Low cells represent clusters in which abundances are significantly lower than the abundances in neighboring cells (spatial non-aggregation).

2.2.3. Analyzing the Factors That Shape Recent Abundances at Local and Regional Scales

At local scale, once we had identified the cells with aggregated patterns, we then analyzed the factors driving this aggregation. To do so, we used a nonparametric Kruskal–Wallis test to compare each of the 16 variables relating to habitat, food availability, human pressure, and heterospecific attraction that explain the differences in abundance between the High and Low cells (Table 1). The significance level was adjusted using the Bonferroni correction.

To determine the factors that shaped the abundance distribution of Egyptian vultures in the 2018 census in continental Spain at a large scale, we performed generalized linear models (GLM; negative binomial distribution and log link function; [44]). The challenge of limited fine environmental data is a common issue in studies analyzing diverse environmental and anthropic variables across lengthy time spans. Our study encountered this limitation, with a temporal mismatch between the explanatory variable data and species abundance data collected in 2000, 2008, and 2018. Notably, data for explanatory variables were available only after 2008, such as 2009 census data for livestock and 2018 data for wind turbines and landfills. To address this, we focused our analysis on the year 2018, postulating that this later data would yield stronger models for associating Egyptian vulture distribution compared to earlier years. Additionally, we considered only explanatory variables with significant differences between High and Low cells and used the abundance of breeding pairs per cell as a dependent variable to analyze whether or not the same factors drive the abundance distribution at different scales. Moreover, in our analyses, we considered two key assumptions regarding the relationship between Egyptian vulture abundance and environmental factors. Firstly, we assumed that most of the variability in abundances observed in 2018 could be explained by the abundances registered during the previous census and therefore we considered the abundance of the previous census to be a proxy for habitat quality, based on the findings of [45]. Secondly, we incorporated a temporal term into our statistical model to account for changes in abundance distribution over time. We assumed that any independent variable (e.g., food availability) that was found to have a significant effect on abundance distribution after accounting for temporal changes was a potential driver of abundance changes between censuses. Therefore, apart from variables with differences between High and Low cells, we also considered spatial and temporal terms. The spatial term was the third-degree polynomial derived from coordinates, longitude (x), and latitude (y) of the central point of the 10 × 10 km cells in order to, on the one hand, avoid the false correlation between species and its environment and, on the other hand, to identify if there were spatial patterns in the abundance data that could not be accounted for or explained by the environmental variables [46]. The temporal terms corresponded to the abundance of breeding pairs of Egyptian vultures according to data from the 2000 (hereafter, NP00) and 2008 (hereafter, NP08) Egyptian vulture censuses. These two temporal terms were included separately in two different models.

We developed the analysis in the R environment [47] using the "adespatial" [48], "MASS" [49], and "MuMIn" packages [50]. To select the best models, we used the Corrected Akaike Selection Criterion (AICc; see the average model with a ΔAIC threshold of <2 in Appendix D; [51]).

2.2.4. Explanatory Variables

Grid cells were characterized by 16 variables relating to habitat, food availability, human pressure, and heterospecific relationships to determine the factors potentially shaping the abundance distribution. Habitat was represented by land-use coverage in several different categories (see Table 1). In addition, we included elevation as a habitat-related variable since it is associated with the reproductive habitat of breeding pairs such as cliffs [26]. We used the number of cows and sheep per 10 × 10 km cell as a proxy for potential food resources following [52]. We also considered the locations of landfills and supplementary feeding stations (specific places where carcasses are deposited to feed avian scavengers to increase the availability of food resources as a vulture conservation measure; see review [53]) as predictable anthropogenic food sources [54]. Human pressure was evaluated using various sources of information, including the location of wind farms, the number of poison-related mortality events [55], and the coverage of urban areas, all of which have been shown to be relevant factors in the breeding distribution of Egyptian vultures [56]. Finally, we used the number of breeding pairs of the dominant species in the scavenger guild, the griffon vulture (*Gyps fulvus*), as a proxy for controlling heterospecific effects [57,58]. These variables were chosen to comprehensively represent the factors potentially shaping the abundance distribution of the scavenger guild in the study area. A summary of the specific variables and their sources can be found in Table 1 (see Appendix A for details of data preparation). All units of food availability, human pressure (except urban areas) and heterospecific relationship-related explanatory variables refer to densities, i.e., the quantity or concentration of some abiotic or biotic factor within a given 100 km^2 grid-cell.

Table 1. Explanatory variables used to describe the spatial aggregation patterns and the regional distribution model of the Egyptian vulture in continental Spain. All variables were obtained at a resolution of 10 × 10 km cells (more information in Appendix A).

Acronym	Definition	Source of Information
(1) Habitat		
ALT	Altitude (meters above sea level)	Digital Elevation Model (DEM)
NIC	Cover (%) of non-irrigated crops (e.g., regular annual crops, cereals, leguminous crops)	CORINE Land Cover
IRR	Cover (%) of irrigated crops (e.g., arable, crops, rice fields, non-permanent grass)	CORINE Land Cover
TREE	Cover (%) of permanent crops (e.g., olive groves, orchids, vineyards, fruit trees)	CORINE Land Cover
DEH	Cover (%) of agroforest systems (named *dehesas* in Spain)	CORINE Land Cover
ROC	Cover (%) of bare rocks (e.g., stable rocks with limestone pavements)	CORINE Land Cover
FOR	Cover (%) of forests (e.g., broad-leaved, coniferous, and mixed forests)	CORINE Land Cover
PAS	Cover (%) of pasturelands (e.g., permanent grasslands)	CORINE Land Cover
(2) Food availability		
COW	Number of cows surveyed on national census	National Institute of Statistics (INE)
SHEEP	Number of sheep surveyed on national census	National Institute of Statistics (INE)
LAND	Number of landfills	MAPAMA
SFS	Number of supplementary feeding stations	MAPAMA
(3) Human pressure		
URB	Cover (%) of urban areas (e.g., residential and commercial/industrial buildings, parking lots, small squares)	CORINE Land Cover
WTG	Number of wind turbines	*Asociación Empresarial Eólica* (AEE)
POIS	Number of poison-related mortality events of wild fauna	WWF and SEO/Birdlife [55]
(4) Heterospecific relationship		
GF	Number of breeding pairs of griffon vultures	SEO/Birdlife [59]

3. Results

3.1. Temporal Variation on Distribution

From year 2000 onwards, censuses (every 8–10 years) showed a slight increase in the total number of breeding pairs of Egyptian vultures in continental Spain, with a total of 1270, 1364, and 1372 pairs in 2000, 2008, and 2018, respectively. Occupancy also increased over the years, with a total of 700, 725, and 731 occupied cells in 2000, 2008, and 2018, respectively. Visual inspection of ROAPs, in combination with the D* statistic, showed an almost exact profile of the three different censuses, indicating that the overall abundance and the frequency of abundances are statistically indistinguishable over the years (Figure 2; Table 2). In addition, the abundance maps for the Egyptian vulture showed a temporal variation in cells despite a similar occupancy and abundance distribution across the study area.

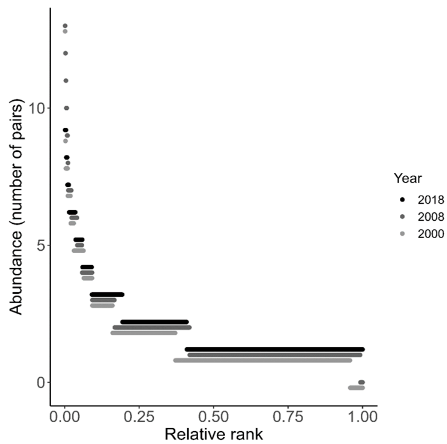

Figure 2. Rank Occupancy–Abundance Profiles (ROAPs) of Spanish national census data of Egyptian vultures in three different years. Local abundance was measured as the number of breeding territories on a 100 km^2 grid. Relative rank was calculated by dividing the rank descending order of cells by the total number of grid cells in which species has been present at least once during the study period (n = 1033). Grid cells where species were not present in any census.

Table 2. Egyptian vulture breeding pairs abundance and occupancy changes in Spain in 2000, 2008, and 2018. The D* statistics represent the area under the curve of the ROAPs. *P* is the *p*-value. The abundance change is calculated by subtracting the absolute abundances between years, while the occupancy change is calculated by subtracting the total number of occupied grid cells between years.

Years	D*	*P*	Abundance Change	Occupancy Change
2018–2008	0.992	0.648	8	6
2008–2000	0.970	0.615	94	25
2018–2000	0.918	0.640	102	31

3.2. Spatial Variation on Distribution

The autocorrelation analysis showed a strong spatial correlation in the distribution of abundances of the Egyptian vulture. Furthermore, the spatial autocorrelation structure of the abundance distribution remained consistent over the years (see Appendix B). Moran's test was statistically significant (Moran's I = 0.075; $P = 0.001$) and the correlogram showed a diminishing positive autocorrelation with increasing distances (Figure 3a). The LISA index of the abundances of breeding pairs in 2018 showed that 57 cells were classified as High-cells, with a mean abundance (±SE) of 5.37 (±0.22) breeding pairs per cell, while 31 cells were classified as Low-cells, with a mean abundance of 0.65 (±0.09) pairs per cell. Meanwhile, the remaining 945 cells were not spatially associated with their neighboring cells in terms of abundance. In addition, the High cells represented 22.3% of the abundance (306 breeding pairs) and occupied 18.12% (5700 km^2) of the distribution area. The aggregation abundance patterns rarely occurred in isolated cells but were usually a set of two or more cells (Figure 3b).

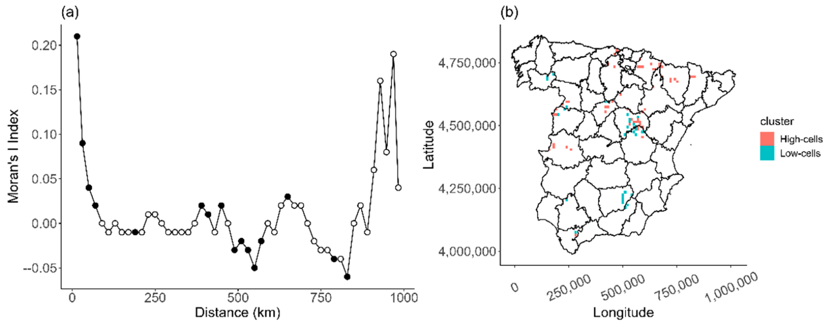

Figure 3. Spatial autocorrelation of the abundance distribution of reproductive pairs of Egyptian vultures in continental Spain in 2018. (**a**) Moran's I correlogram shows the distance lag between abundances in which spatial autocorrelation is significant (black-filled circles). (**b**) High (red) and Low (blue) cells detected by LISA analysis. High cells represent cells with significantly high abundances compared to neighboring cells, while Low cells represent cells with significantly low abundances compared to neighboring cells.

3.3. *Local Drivers of Abundance Patterns at Different Spatial Scales*

The Kruskal–Wallis comparison between High and Low cells revealed that the densities of cows (ca. heads/100 km^2), *dehesas* (wood pasture) (%), supplementary feeding stations (units/100 km^2), and griffon vultures (ca. number of breeding pairs/100 km^2) were significantly higher in High than in Low cells. Conversely, the number of wind turbines (ca. units/100 km^2) was significantly lower in the High than in the Low cells, this number being almost seven times higher in the Low cell areas (Figure 4). The remaining variables showed no significant differences (see Appendix C).

By contrast, both GLMs conducted at the regional scale revealed the range of factors affecting the vulture distribution (Table 3). The average models showed statistically positive associations between the abundance of breeding pairs of Egyptian vultures and the abundance of griffon vultures, as well as a weaker association with the number of cows (Appendix D). The model, which included the Egyptian vulture abundance in 2008 as an independent variable, exhibited a better goodness-of-fit (Model 1; pseudo-R^2 = 0.315) compared to the model that used the abundance in 2000 (Model 2; pseudo-R^2 = 0.245). Our GLM analysis indicated that the abundance of breeding pairs is primarily explained by previous census variables, while the variation not accounted for by the previous census data is influenced by the abundance of griffon vultures and cows. These latter variables are identified as the principal drivers of changes in Egyptian vulture abundance.

Table 3. Top 10 competing models for GLM from abundance distribution of Egyptian vultures in continental Spain. The abundance of 2008 (NP08) was included as an independent variable in Model 1 and the abundance of 2000 (NP00) was included as an independent variable in Model 2. Y- and X-related variables correspond to the third-polynomial spatial terms of the model.

Model	Variables	df	Loglik	AICc	Delta	Weight
1.1.	COW + GF + NP08 + Y + Y^2	7	−1365.67	2745.44	0.000	0.0046
1.2.	COW + GF + NP08 + Y + Y^3	7	−1365.69	2745.50	0.058	0.0045
1.3.	COW + GF + NP08 + Y^2 + Y^3	7	−1365.73	2745.57	0.127	0.0043
1.4.	COW + GF + SFS + NP08 + Y + Y^2	8	−1365.04	2746.22	0.785	0.0031
1.5.	COW + GF + SFS + NP08 + Y + Y^3	8	−1365.07	2746.27	0.834	0.0030
1.6.	COW + GF + SFS + NP08 + Y^2 + Y^3	8	−1365.10	2746.33	0.895	0.0029
1.7.	COW + GF + NP08 + X + X^2Y + XY + XY^2	9	−1364.14	2746.46	1.023	0.0028
1.8.	COW + DEH + GF + NP08 + Y + Y^2	8	−1365.17	2746.48	1.039	0.0027

Table 3. *Cont.*

Model	Variables	df	Loglik	AICc	Delta	Weight
1.9.	COW + GF + NP08 + WTG + Y + Y^2	8	−1365.19	2746.52	1.080	0.0027
1.10.	COW + GF + NP08 + X + X^2 + XY + XY^2	9	−1364.18	2746.54	1.099	0.0027
2.1.	COW + GF + NP00 + Y + Y^2	7	−1415.04	2844.19	0.000	0.004
2.2.	COW + GF + NP00 + Y + Y^3	7	−1415.08	2844.27	0.076	0.004
2.3.	COW + GF + NP00 + Y^2 + Y^3	7	−1415.13	2844.36	0.168	0.004
2.4.	COW + GF + NP00 + WTG + Y + Y^2	8	−1414.27	2844.67	0.479	0.003
2.5.	COW + GF + NP00 + WTG + Y + Y^3	8	−1414.29	2844.72	0.527	0.003
2.6.	COW + GF + NP00 + WTG + Y^2 + Y^3	8	−1414.32	2844.78	0.589	0.003
2.7.	COW + DEH + GF + NP00 + Y + Y^2	8	−1414.41	2844.97	0.773	0.003
2.8.	COW + DEH + GF + NP00 + Y + Y^3	8	−1414.48	2845.10	0.903	0.003
2.9.	COW + DEH + GF + NP00 + Y^2 + Y^3	8	−1414.55	2845.25	1.052	0.002
2.10.	COW + DEH + GF + NP00 + WTG + Y + Y^2	9	−1413.57	2845.33	1.132	0.002

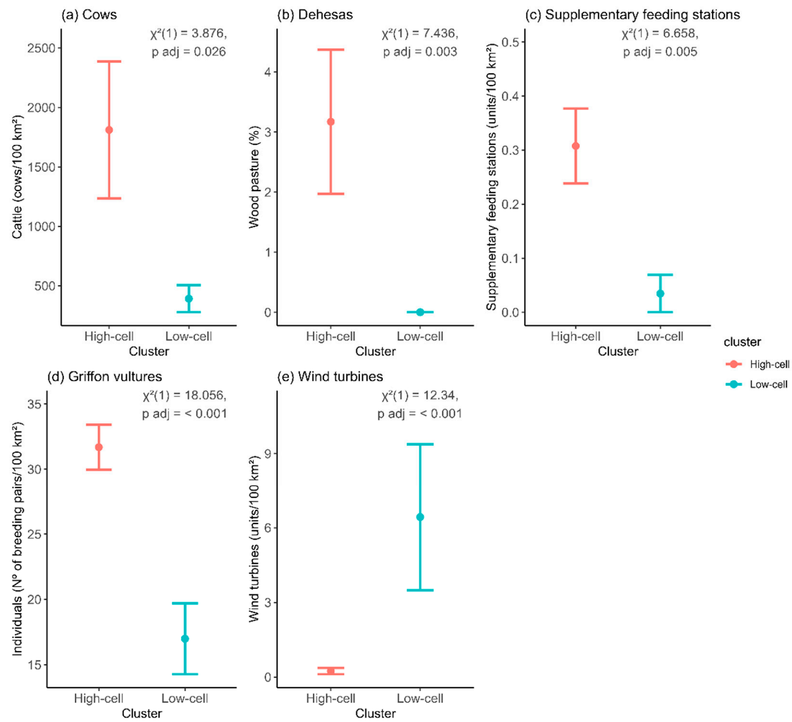

Figure 4. Plots of variables with significant differences between High (H) and Low (L) cells. High cells are areas where environmental features drive a local increase in abundance, while Low cells are areas where environmental features drive a local decrease in abundance. Each variable represents the density of that variable in each 10 × 10 km grid. Plots show mean values of each variable and 95% CIs. We only plotted the variables with significant differences between High and Low cells.

4. Discussion

This study presents an analysis of the temporal and spatial variation, as well as the distribution patterns at different scales, of breeding pairs of the endangered Egyptian vulture in one of its global strongholds. Our findings revealed stability in its breeding population in continental Spain after years of continuous decline [31,37]. However, despite this regional stability, significant spatiotemporal variation occurred. The distribution of Egyptian vultures exhibited an aggregated pattern, with the highest abundances concentrated in locations with specific environmental characteristics. This aggregation is a result of scale-dependent factors that shape the population trend. In addition, we identified a hierarchical structure of factors affecting the distribution patterns at two different local and regional scales.

Contrary to our initial expectations, we only found limited significant changes in the regional distribution of the species over time. Both the occupancy and abundance distribution patterns, assessed using ROAPs and D* statistics, exhibited a relatively stable trend during the study period. This stability can be attributed to the intrinsic and consistent fidelity of Egyptian vultures to their breeding territories [60], a characteristic observed in other raptors [61], which ensures that individuals remain in their territories for many years regardless of environmental changes. Moreover, the combination of territorial fidelity and the conspecific attraction of raptor species [62], resulting in the selection of territories near successful conspecific settlements (see *habitat-copying hypothesis* in [63]), probably confers great population stability at a regional scale. However, despite this regional stability, we did detect temporal variability expressed as a large number of cells with low abundance values (e.g., with only one breeding pair) with discontinuous occupancy over time (Figure 1). This observed variability in temporal abundance can be explained by human-related factors (e.g., illegal poisoning; [32,64]) or by demographic stochasticity (i.e., if there are few individuals, the grid cell is more likely to empty).

Additionally, the shape of the ROAP suggested a spatial aggregation of breeding territories. The steep curves indicated that breeding pairs tend to cluster in specific areas, which was confirmed by the LISA analysis that identified cells with a large number of breeding pairs. We observed more cells with low abundances (one breeding pair per cell) than cells with high abundances (five or more breeding pairs per cell), resulting in a heterogeneous distribution pattern. Moreover, this heterogeneity was also supported by our autocorrelation analyses, which revealed clear spatial autocorrelation in the census data over short distances (i.e., 20 km), consistent with patterns observed in other populations (e.g., in Turkey, [65]) and other raptors (e.g., lesser kestrel; [66]). The observed spatial aggregation was found to be a result of scale-dependent factors that shape the abundance distribution. Certain local-level factors such as the presence of wind turbines were associated with lower values of abundance, suggesting they acted as drivers of these patterns. The higher cover of *dehesas* and presence of supplementary feeding stations were associated with more breeding territories, which indicates that these factors favor the study species. However, it is worth noting that these factors only act in specific marginal areas and not throughout continental Spain. For instance, an Egyptian vulture population in southern Spain was affected by wind farm-related mortality during the breeding [34] and migration [67] periods. Additionally, the *dehesas* and agroforestry areas located only in western Spain serve as important foraging habitats for other vulture species due to the higher availability of food compared to other agricultural systems or landscapes [68,69] and support a high relative abundance of livestock grazing and other species (e.g., rabbits) that scavenging birds can exploit. The authors of [70] reported that supplementary feeding stations used as a conservation measure help both the maintenance of the closest breeding territories and breeding success. Nevertheless, these supplementary feeding sites that act as local attractors for high densities of vultures and other scavengers may have detrimental consequences. For instance, supplementary feeding stations can adversely affect the productivity of Pyrenean Bearded vultures (*Gypaetus barbatus*) due to the congregation of non-breeding individuals, leading to a decline in the quality of the reproductive habitat [71].

The main factors associated with changes in abundance at the regional scale over both time and space were griffon vulture and cattle abundances. On the one hand, our results suggest that cattle are one of the main food sources of carrion and feces at local and regional levels for the Egyptian vultures breeding in continental Spain, and play an important role in its distribution [54,72]. In addition, the coprophagous behavior of this species also explains its close association with cows. Egyptian vultures consume cow dung to obtain lutein, a yellow carotenoid responsible for its facial coloration [73] that also plays an important role in its immunological system as an antioxidant [74]. On the other hand, the positive correlation between breeding Egyptian and griffon vultures suggests a heterospecific interaction between these two species that positively impacts the number of Egyptian vulture breeding pairs. Nevertheless, in other studies, the presence of griffon vultures was not associated with the territory occupancy rate of Egyptian vultures as observed in the Balkan Peninsula [23]. In addition, both vulture species probably respond in a similar fashion to specific environmental characteristics, which means that the abundance of griffon vultures will be an indicator of the most suitable habitat for breeding pairs of Egyptian vulture [52,75]. Due to the spatial overlap between these two species, some authors define this interaction as commensalism [76] because (i) both species have similar ecological requirements (e.g., they are both cliff-nesting; [26]) and (ii) given that breeding individuals, regardless of the species, are linked to a breeding area, the abundance of breeding griffon vultures may not only indicate a suitable breeding habitat but also a habitat with food availability [52,76].

Despite the fact that our main aim was to assess the likely causes of changes in the abundance distribution of breeding Egyptian vultures at different spatial scales, other factors relating to human pressure that probably also play an important role in their distribution should not be neglected in future research (e.g., electrocution and/or collision against power lines; [33,34]). Indeed, our results underscore the importance of considering both temporal and spatial variability during the process of generating distribution models. On the one hand, we used temporal population dynamics (i.e., changes between censuses) to capture how the abundance distribution can enhance the subsequent abundance distribution in such a way that the model revealed the suitability of a breeding territory. On the other hand, we took into account spatial autocorrelation in the modelling process because ignoring spatial constraints can lead to inaccurate conclusions (see [9]). To fully understand the changes in endangered species distribution, more research is needed using other approaches, such as Bayesian INLA models, that consider the spatiotemporal variation in species abundance [77].

Conservation Implications

Our findings reveal the scale-dependent factors that influence the Egyptian vulture breeding population in mainland Spain. At the regional level, these factors require the implementation of global conservation strategies to ensure the species is protected across large areas and to serve as guidelines for developing conservation synergies between neighboring areas. At the local scale, the factors affecting populations or even individuals require specific actions related to the main threats affecting each population. Therefore, it is important to highlight the impact of hierarchical approaches on environmental policies. Thus, successful conservation programs aimed at preserving large vertebrate species over large areas should incorporate efficient local management actions [7,78]. Based on our results, we advocate the development of a national strategy promoting, at the regional level, extensive livestock farming and the abandoning of healthy carcasses (with sanitary control) as an important and unpredictable food source for not only Egyptian vultures but the whole vulture guild [79]. Although this approach is partially implemented through the ZPAEN network (Protection Zones for the Feeding of Necrophagous Species of Community Interest), local administrations use different criteria to establish these zones, which leads to a lack of coordination at the regional scale (see [80]). Additionally, some local actions should be taken to counteract the negative effect of the blades of wind turbines with which certain soaring birds including vultures are prone to collide ([81,82], personal data). Some studies have shown that the strategic placement of wind turbines and appropriate mitigation measures could help minimize the potential negative effects of wind farms on soaring birds while still allowing for the generation of renewable energy [83]. Finally, we believe it is important to underline the importance of grids with a single or few breeding pairs, since the potential for recovery and growth of endangered populations lies in these low-density areas. Conserving small populations allows them to reproduce and expand gradually, and to serve as future sources for repopulating larger areas.

5. Conclusions

The breeding Egyptian vulture pairs in continental Spain are generally stable but exhibit spatial variability in their distribution, thereby indicating a hierarchical structure of drivers affecting abundance patterns at different scales. Our data indicate that local-level factors such as the presence of supplementary feeding stations play an important role in the aggregation of breeding pairs. However, the overall stability of the population is mainly driven by the availability of natural food sources, particularly from livestock. Based on the scale-dependent factors influencing the distribution patterns of Egyptian vultures, we recommend the development of a national strategy promoting extensive livestock farming and encouraging the abandoning of healthy carcasses in the field as an important food source for these vultures. In addition, it is important to consider the potential local negative impacts of wind farms and other infrastructures on these species and the need for their strategic placement. Our findings highlight the importance of adopting a holistic approach to conservation efforts that takes into account over time both local- and regional-level factors.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Appendix A.1. Digital Elevation Model

The elevation data were obtained from the 25 m resolution Digital Elevation Model provided by the National Institute of Geography (www.ign.es, accessed on 19 December 2019). To align the resolution with our 100 km^2 abundance data, we resampled the raster by applying a grid with fewer pixels. To do so, we used the *resample*() function of the raster R package and a bilinear interpolation method that uses the distance-weighted average of the four nearest pixel values to estimate a fresh pixel value.

Appendix A.2. CORINE Land Cover Maps

We used the 2018 CORINE land cover maps from Copernicus (www.land.copernicus.eu, accessed on 16 October 2019) to obtain seven variables relating to habitat and one variable relating to human pressure. The CORINE maps include 44 land-cover classes, which we reclassified into 8 different cover classes: non-irrigated crops, irrigated crops, tree crops, agroforest systems known as *dehesas*, bare rock, forests, pasturelands, and urban areas. Table A1 shows the reassigned land-cover classes. Next, we calculated the percentage of the land cover by converting each reclassified land-cover class into polygon shapefiles, extracting the portion of the land cover in each cell, and finally rasterizing the layer with the proportion of land cover of each cell using the elevation layer as the raster base.

Table A1. Reclassification of CORINE land covers (CLC) with the new categories URB: urban areas; NIC: non-irrigated crops; IRR: irrigated crops; TREE: permanent crops; PAS: pasturelands; DEH: agroforestal systems (*dehesas*), and FOR: forests. Some categories of CORINE Land Cover were not reassigned to a new category. Modified table CORINE Land Use Covers 2018 legend (land.copernicus.eu, access on 16 October 2019).

CLC Level 1	CLC Level 2	CLC Level 3	New Code
Artificial surfaces	Urban fabric	Continuous urban fabric	URB
		Discontinuous urban fabric	URB
	Industrial, commercial, and transport units	Industrial or commercial units	URB
		Road and rail networks and associated land	URB
		Port area	URB
		Airports	URB
	Mine, dump, and construction sites	Mineral extraction sites	URB
		Dump sites	URB
		Construction sites	URB
	Artificial, non-agricultural vegetated areas	Green urban areas	URB
		Sport and leisure facilities	URB
Agricultural areas	Arable land	Non-irrigated arable land	NIC
		Permanently irrigated land	IRR
		Rice fields	IRR
	Permanent crops	Vineyards	TREE
		Fruit trees and berry plantations	TREE
		Olive groves	TREE
	Pastures	Pastures	PAS
	Heterogeneous agricultural areas	Annual crops associated with permanent crops	NIC
		Complex cultivation patterns	NIC
		Land principally occupied by agriculture, with significant areas of natural vegetation	NIC
		Agroforestal areas	DEH
Forest and semi natural areas	Forest	Broad-leaf forest	FOR
		Coniferous forest	FOR
		Mixed forest	FOR
	Scrub and/or herbaceous vegetation associations	Natural grasslands	PAS
		Moors and heathland	-
		Sclerophyllous vegetation	-
		Transitional woodland–shrub	-
	Open spaces with little or no vegetation	Beaches, dunes, sands	ROC
		Bare rocks	ROC
		Sparsely vegetated areas	ROC
		Burnt areas	-
		Glaciers and perpetual snow	-

Table A1. *Cont.*

CLC Level 1	CLC Level 2	CLC Level 3	New Code
Wetlands	Inland wetlands	Inland marshes	-
		Peat bogs	-
	Maritime wetlands	Salt marshes	-
		Salines	-
		Intertidal flats	-
Water bodies	Inland waters	Water courses	-
		Water bodies	-
	Marine waters	Coastal lagoons	-
		Estuaries	-
		Sea and ocean	-

Appendix A.3. INE

Food availability information (i.e., cows and sheep) was obtained from the agricultural census of Spain (www.ine.es, accessed on 16 December 2019), which calculates the number of different domestic animals in each municipality. We translated the density of domestic animals from each municipality into spatial information. Then, we rasterized the spatial information using a bilinear interpolation (see above) using the elevation raster as a base layer.

Appendix A.4. MAPAMA

Data on landfills and supplementary feeding stations, also used as food resources by Egyptian vultures, were obtained from the Ministry of Agriculture, Fisheries, Food and Environment (MAPAMA; www.mapa.god.es, accessed on 10 October 2019). Landfill locations were used to create a raster of landfill density. As data on landfills in Catalonia and Valencia were not available from MAPAMA, we obtained this information from the Catalan Waste Agency (www.residus.gencat.cat, accessed on 22 October 2019) and the Environment Department of the Generalitat Valenciana (www.agroambient.gva, accessed on 22 October 2019), respectively. We also obtained the geographic locations of all supplementary feeding stations and verified their operational status in 2000–2018. Information on active supplementary feeding stations was included in the data using the same procedure as for landfills.

Appendix A.5. Asociación Empresarial Eólica (AEE)

We obtained the number of wind turbines per 10 × 10 km cell from the locations of national wind farms and their corresponding number of wind turbines (available at www.aeeolica.org, accessed on 14 October 2019). We first obtained the geographic locations of all wind turbines and then created a raster by rasterizing the information on the density of wind turbines in each cell using the elevation layer as a base map.

Appendix A.6. The Poison-Related Mortality Event Database from SEO/Birdlife and WWF

The number of poison-related mortality events was calculated using the "El veneno en España "[57] database. We considered a poison-related mortality event to be the use of any chemical substance that causes the death of wildlife after ingestion. We assumed that several dead wild animals found at the same location within a 15-day period represented the same poison-related mortality event. We obtained the location of each poison-related mortality event and calculated the number of poison-related mortality events per 10 × 10 km cell.

Appendix A.7. Griffon Vulture National Census

We used the same procedure as for the Egyptian vulture to obtain the number of breeding pairs of griffon vultures (*Gyps fulvus*). For each communal breeding area or colony, we recorded the location and status (occupied vs. unoccupied). To obtain the abundance distribution, we incorporated these locations into a 10 × 10 km grid-cell and calculated the abundance in each cell by summing the locations of the confirmed communal breeding areas.

Appendix B

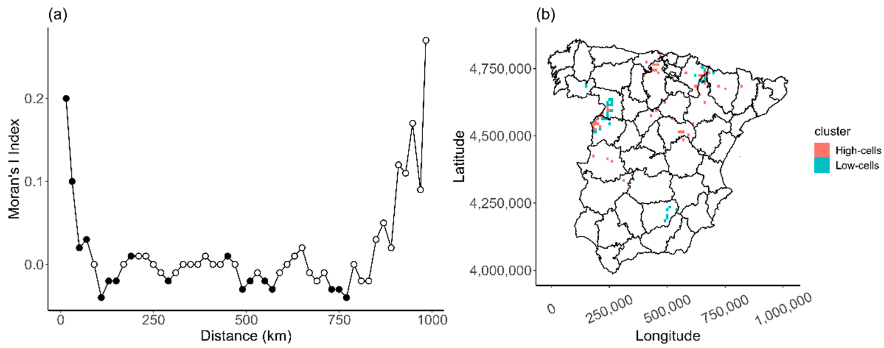

Figure A1. Spatial autocorrelation of the abundance distribution of reproductive pairs of Egyptian vultures in continental Spain in 2008. (**a**) Moran's I correlogram shows the distance lag between abundances in which spatial autocorrelation is significant (black-filled circles). (**b**) High (red) and Low (blue) cells detected by LISA analysis. High cells represent cells with significantly high abundances compared to neighboring cells, while Low cells represent cells with significantly low abundances compared to neighboring cells.

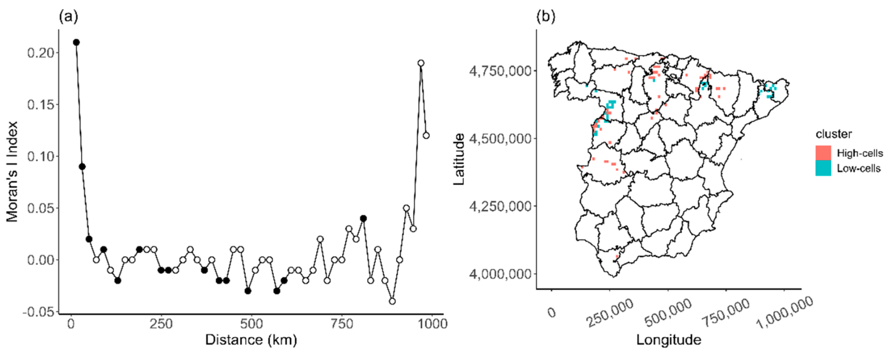

Figure A2. Spatial autocorrelation of the abundance distribution of reproductive pairs of Egyptian vultures in continental Spain in 2000. (**a**) Moran's I correlogram shows the distance lag between abundances in which spatial autocorrelation is significant (black-filled circles). (**b**) High (red) and Low (blue) cells detected by LISA analysis. High cells represent cells with significantly high abundances compared to neighboring cells, while Low cells represent cells with significantly low abundances compared to neighboring cells.

Appendix C

Table A2. Kruskal–Wallis test of no significant differences between High cells and Low cells. *P* is the *p*-value. *P adj* is the *p*-value adjusted using the Bonferroni correction.

Variables	H	df	P	P adj
(1) Habitat				
ALT	0.069	1	0.792	0.3958
NIC	16.748	1	0.650	0.325
IRR	2.654	1	0.103	0.052
TREE	0.842	1	0.359	0.179
ROC	62.978	1	0.903	0.451
FOR	93.876	1	0.761	0.381
PAS	0.400	1	0.527	0.264
(2) Food availability				
SHEEP	1.444	1	0.230	0.115
LAND	3.648	1	0.581	0.291
(3) Human pressure				
URB	2.018	1	0.155	0.078
POIS	2.449	1	0.118	0.059

Appendix D

Table A3. Estimates for average GLM (selection based on those with the lowest AICc scores, with a ΔAIC threshold of <2) describing abundance distribution of Egyptian vultures in continental Spain. Two models are specified: Model 1 incorporates the 2008 Egyptian vulture abundances (NP08) as a predictor variable and Model 2 incorporates the 2000 abundances (NP00). *P* is the *p*-value. Significant *p*-values < 0.05 are **in bold**.

	Variables	E	SE	Adj SE	Z	P
Model-1	Intercept	−36.790	74.020	74.080	0.497	0.619
	NP08	0.196	0.012	0.012	16.185	**<0.001**
	COW	1.647×10^{-5}	6.569×10^{-6}	1.647×10^{-5}	2.504	**0.012**
	GF	0.141	0.020	0.020	6.931	**<0.001**
	MUL	−0.042	0.037	0.037	1.116	0.264
	DEH	−0.003	0.003	0.003	0.981	0.327
	WTG	−0.002	0.002	0.002	1.059	0.290
	y	2.86×10^{-5}	6.46×10^{-5}	6.47×10^{-5}	0.442	0.658
	y^2	-1.91×10^{-12}	1.48×10^{-11}	1.48×10^{-11}	0.129	0.898
	y^3	-1.96×10^{-19}	1.19×10^{-18}	1.19×10^{-18}	0.164	0.869
	x	-2.19×10^{-4}	5.90×10^{-5}	5.91×10^{-5}	3.707	**<0.001**
	x^2y	-2.76×10^{-19}	1.85×10^{-19}	1.86×10^{-19}	1.488	0.137
	xy	9.56×10^{-11}	2.55×10^{-11}	2.56×10^{-11}	3.741	**<0.001**
	xy^2	-1.04×10^{-17}	2.76×10^{-18}	2.76×10^{-18}	3.762	**<0.001**
	x^2	-1.30×10^{-12}	8.80×10^{-13}	8.81×10^{-13}	1.472	0.141
	x^3	-4.23×10^{-19}	5.32×10^{-19}	5.33×10^{-19}	0.795	0.427
Model-2	Intercept	−68.530	56.810	56.850	1.205	0.228
	NP00	0.166	0.015	0.015	10.936	**<0.001**
	COW	0.000	0.000	0.000	2.492	**0.013**
	GF	0.182	0.020	0.020	9.097	**<0.001**
	MUL	−0.026	0.035	0.035	0.726	0.468
	DEH	−0.004	0.003	0.003	1.348	0.178
	WTG	−0.003	0.002	0.002	1.214	0.225
	y	3.46×10^{-5}	4.03×10^{-5}	4.03×10^{-5}	0.859	0.390
	y^2	-7.19×10^{-13}	9.99×10^{-12}	1.00×10^{-11}	0.072	0.943
	y^3	-4.71×10^{-19}	7.20×10^{-19}	7.21×10^{-19}	0.653	0.514
	x	-4.36×10^{-5}	1.06×10^{-4}	1.06×10^{-4}	0.412	0.681
	x^2y	1.89×10^{-11}	4.61×10^{-11}	4.61×10^{-11}	0.410	0.682

Table A3. *Cont.*

Variables	E	SE	Adj SE	Z	*P*
xy	-2.07×10^{-18}	5.00×10^{-18}	5.00×10^{-18}	0.414	0.679
xy^2	-1.50×10^{-13}	1.67×10^{-13}	1.67×10^{-13}	0.896	0.371
x^2	-3.10×10^{-20}	3.58×10^{-20}	3.58×10^{-20}	0.867	0.386
x^3	-1.34×10^{-19}	1.85×10^{-19}	1.85×10^{-19}	0.726	0.468

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Movement Ecology

RESEARCH

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Resource predictability modulates spatial-use networks in an endangered scavenger species

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Abstract

Background Changes in human-induced resource availability can alter the behaviour of free-living species and affect their foraging strategies. The future European *Landfill Waste Directive* and *Circular Economy Action Plan* will reduce the number of predictable anthropogenic food subsidies (PAFS), above all, by closing landfills to preclude negative effects on human health. Obligate avian scavengers, the most threatened group of birds worldwide, are the most likely group of species that will be forced to change their behaviour and use of space in response to landfill site closures. Here, we examine the possible consequences of these management decisions on the foraging patterns of Egyptian vultures (*Neophron percnopterus*) in an expanding population in the Iberian Peninsula.

Methods We tracked 16 individuals in 2018–2021, including breeders and non-breeders, and, using a combination of spatial-use and spatial-network modelling, assessed landscape connectivity between key resources based on movement patterns. We then carried out simulations of future scenarios based on the loss of PAFS to predict likely changes in the movement patterns of both non-breeders and breeders.

Results Our results show that foraging strategies in non-breeders and breeders differ significantly: non-breeders performed more dispersal movements than breeding birds across a spatial-use network. Non-breeding and breeding networks were found to be vulnerable to the removal of central foraging areas containing landfill sites, a highly predictable resource, while perturbation analysis showed dissimilar foraging responses to the gradual reduction of other predictable resources. Under a context of the non-availability of landfills for breeders and non-breeders, vultures will increase their use of extensive livestock as a trophic resource.

Conclusions Future environmental policies should thus extend the areas used by scavengers in which livestock carcasses are allowed to remain in the wild, a strategy that will also mitigate the lack of food caused by any reduction in available waste if landfills close. In general, our results emphasize the capabilities of a spatial network approaches to address questions on movement ecology. They can be used to infer the behavioural response of animal species and, also demonstrate the importance of applying such approaches to endangered species conservation within a context of changing humanized scenarios.

Keywords Egyptian vulture, Foraging movements, Landfills, Predictable anthropogenic food subsidies (PAFS), Spatial networks, Space use, Spatial connectivity

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Introduction

Many human activities result in modifications in both the spatial distribution and availability of trophic resources, thereby altering the behaviour of wildlife species [1–3]. Alterations of spatial-use strategies by individuals when exploiting resources (e.g. foraging [4, 5]) may ultimately determine the survival and reproductive performance of wildlife populations worldwide [6]. A better understanding of how species respond to human-induced changes in the availability of food resources is needed to (1) assess the expected effect of environmental policies on their food resources and (2) design conservation actions to counterbalance the negative effects of human-altered environments (see review [7]). Resource exploitation patterns in humanized environments are particularly worrying in the case of avian scavengers, for which available evidence indicates that predictable anthropogenic food subsidies (PAFS) may influence their use of space and movement patterns [8–10]. This avian guild includes vultures, one of the most world's most endangered group of birds [11] and thus their conservation management is critical [12, 13].

The term PAFS refers to resources of anthropic origin whose appearance is predictable over space and/or time [9]. The most common example of PAFS are the landfills that have become an important predictable—and unlimited—source of food for many scavenger species, and the predominant food resource for many of them [5, 14–17]. Other example of PAFS are supplementary feeding stations, also known as 'vulture restaurants', where humans intentionally offer resources to wild scavengers as part of specific conservation measures or leisure activities (e.g., [18, 19]). The relative costs and benefits of PAFS use by scavengers are controversial because, while positive effects have been described in terms of breeding success [16, 20], the increase in the number of scavenger individuals in places with great food abundance can cause a density-dependent depression of productivity parameters [21]. In this paradoxical context, although vultures as obligate avian scavengers have evolved to depend on ephemeral and unpredictable carrion resources [22–24], the intensification of livestock farming practices and the increase in the number of PAFS may have led them to adapt their foraging strategies [25, 26], especially when their main food resources originate from landfills [15]. In Europe the availability of human waste as a feeding resource is expected to decrease drastically owing to the future *Landfill Waste Directive* (2008/98/EC) and the *Circular Economy Action Plan* [27], which contemplate the closure of landfills as a health-improving measure. Therefore, the study of the movement behaviour of vulture species in relation to trophic resources in European systems is an excellent scenario for understanding how birds exploit PAFS, as well as the effects they have on feeding resources due to the implementation of waste-management measures. In addition, more detailed research on how avian scavengers respond to this reduction in food availability is urgently required to shed light on management designed to preserve populations of some of the continent's most endangered avian species.

Several approaches have been developed to study movement behaviour including state-of-the-art animal tracking by telemetry that can explore movements by wild animals [28–30]. The traditional approach to studying and analyzing animal movement with telemetry data uses kernel density estimators [31], which measure the intensity with which animals use different areas in their home ranges. A network approach has been used in ecological studies, above all to characterize food webs (e.g. [32]) and interactions between species (e.g., [33]). Yet, little attention has been paid to spatial ecology [34, 35], which focuses on the relationship between the environment and network topology. The spatial network approach using graph theory (see [36]) provides a graphic description of complex biological systems (e.g. composed of individuals) based on a set of nodes (i.e. areas with resources) interconnected by links (e.g. movement paths). Spatial networks can provide new insights into how animals interconnect in key areas (i.e. nodes) by movements (i.e. links between nodes) at landscape scale. In addition, using a novel network approach we can determine how the availability of PAFS influences vulture movement behaviour and so identify priority areas for conservation due to the strong spatial connectivity between key central areas [37]. In addition, by generating simulations based on variations in topological networks we can plausibly predict changes in spatial use caused by key alterations in spatial features (e.g. removal of well-connected nodes [35, 36]).

Here, we use spatial network analyses to investigate changes in movement behaviour in free-ranging Egyptian vultures (*Neophron percnopterus*) as responses to food availability. Firstly, we identified the key resources within home ranges and their connectivity at landscape scale (i.e. how animals forage between different food resources). Secondly, we tested the effect of different types of perturbations (i.e. resource-removal simulations) on resource prioritization and infer a population-level response.

The Egyptian vulture, an avian scavenger considered as 'Endangered' worldwide, has one of its strongest populations in the Iberian Peninsula, where its population trend is classified stable or slightly decreasing [38]. Here, we study a population in the northern Iberian Peninsula that over the past two decades has increased in size and even colonized new areas of a highly anthropogenically modified region [39, 40]. The individuals from this population exploit a wide range of food resources, ranging from small wild prey to large carcasses originating from extensive and intensive grazing regimes placed in 'vulture restaurants' [17], as well as resources obtained in large landfills [26, 39]. These sites exert an important attraction during the exploration and exploitation movements of these vultures [39, 41–43]. Thus, we used a network approach to (1) examine the foraging behaviour and spatial-use patterns of Egyptian vultures in an anthropogenically modified landscape; and (2) to predict individual foraging responses to the reduction and/or closure of PAFS. In addition, we addressed certain research and conservation measures in light of the future circular economy scenarios. Our initial hypotheses were that focal non-breeders and breeders would have different foraging strategies due to distinct spatial networks, and that the elimination of PAFS nodes would have a differential impact on non-breeders and breeders. We predicted that non-breeders, which are not tied to a particular breeding site, would have larger home ranges with a significant number of nodes of highly predictable feeding sites and would be seriously affected by the closure of PAFS, while breeders, which are tied to a nest site, would be more likely to exploit unpredictable food resources at fewer sites and be less influenced by landfill closures. Consequently, different conservation strategies are required for these two types of vulture populations.

Methods

Data collection

We tagged 16 breeding Egyptian vultures—six breeding adults (i.e. 5 year-old or older) and 10 non-breeders (1 adult and 9 immatures)—with GPS-GSM devices during the summers of 2018 and 2019. All birds were captured at a landfill site in Osona (Catalonia, Spain). We equipped eight birds with 40-g solar-powered e-Obs satellite transmitters GPS-GSM (www.e-obs.de) and eight birds with Ornitela (www.ornitela.com) digital telemetry devices using a Teflon ribbon harness. Captured birds were aged according to plumage (Additional file 1: Table S1; [44], pers. data). As we were only interested in studying movements during the summer, we discarded migration locations and winter quarters from the data. We considered the beginning of the breeding period to occur when the rectilinear migration path of individuals from Africa began to show great sinuosity on arrival in the study area, and the end of the period when we began to observe, conversely, a rectilinear southwards path. We were interested in prospecting and feeding behaviour during the day and so to optimize the energy performance of the devices the sleep interval of the e-Obs tags was set as 18 h ON/6 h OFF (6:30–22:30, Coordinated Universal Time) and for the Ornitela tags set in terms of the relative 18° sun angle above or below the horizon. We scheduled the GPS devices to record one location every 30 min and, as we were focused on foraging behaviour, we only selected locations within the daily time intervals between sunrise and sunset where birds were active. Paired individuals in adult plumage holding a breeding territory were classified as breeders whilst nomadic individuals not linked to a breeding territory were classified as non-breeders [45].

Spatial-use networks based on landscape features

We built two spatial networks based on the reproductive status of birds (non-breeders vs. breeders) composed of nodes and links to determine how animals interconnect feeding areas along movement paths. The nodes—the areas most used by all individuals—were spatially delimitated as follows. First, we measured the home range of all tagged individuals using the 50% Dynamic Brownian Bridge Movement Model (dBBMM) for each individual and year to represent the core areas in which these birds spent the most time. The dBBMM algorithm allows us to estimate the spatial-use likelihood by taking into account the temporal dependency of GPS data. The outcome of the dBBMM algorithm is a probability layer with a 500-m^2 grid cell known as the Utilization Distribution (UD [46]), a probability that refers to the likelihood of a specific area being used by an individual or individuals. Then, we calculated UDs at individual-year level by averaging all UDs to obtain a single global home range that clearly defines all the available geographical areas that any of the birds would use (Additional file 1: Fig. S1). Second, given that our home range at 50% contour at population level was composed of several polygons, each was considered to be a node. The links were the movement paths (i.e. movements of animals between nodes) that focal vultures performed when connecting a 'departure' node to an 'arrival' node. The frequency of the links between two nodes equated to the strength of the spatial connection. As we found very few movement paths between nodes with a duration of less than half an hour (less than 10% of the trips connecting two nodes), we selected only movement paths lasting one hour or more.

To analyse which environmental factors influenced the movement paths and space used in the networks, we characterized the nodes with nine land-cover categories taken from the CORINE 2018 Land Cover (www.land.copernicus.eu/) program (see Table 1) and with three ecological categories: feeding, roosting or breeding territories (the latter only for breeding birds). For feeding, we considered five types of food resources: landfill sites, intensive farms, vulture restaurants, extensive livestock, and other unpredictable resources (ordered by predictability over time and spatial heterogeneity). In addition,

Table 1 Description of the metrics of the networks (A) and the features of the nodes (B) for the non-breeders and breeders' Egyptian vultures in the study area

(A) *Network metrics*	Level	Description
Diameter	Network	The length (in number of edges) of the longest path through the network from one node to another between any two vertices
Density	Network	The average probability that two nodes that are network neighbours are themselves neighbours of another node
Degree	Nodes	The number of links joining a node to its neighbours
Betweenness	Nodes	The number of shortest paths through the network from one node to another that passes through a given node (the highest values are also called hubs)
(B) *Nodes features*	**Classes (Acronym)**	
Land-use (Acronym)	Forest (FOR)	Cover (%) of forest per node
	Pastureland (PAS)	Cover (%) of pastureland per node
	Scrubs (SCR)	Cover (%) of scrubs per node
	Irrigated crops (IRR)	Cover (%) of irrigated crops per node (e.g., rice)
	Non-irrigated crops (NIC)	Cover (%) of non-irrigated crops per node (e.g., wheat)
	Permanent crops (TREE)	Cover (%) of permanent crops per node (e.g., olives)
	Bare rock (ROC)	Cover (%) of bare rock per node
	Urban areas (URB)	Cover (%) of urban areas per node
	Others (OTH)	Cover (%) of other typologies of land uses per node
Ecological functions	Resources	Set of food sources (categorized in: landfills, extensive and intensive farms, and vultures' restaurant
	Resting	When a node is used as roosting site
	Breeding territory[a]	When a node has a known nest

[a] Only for breeders

we selected the main food resource of each node by overlapping the UD layer of all tagged individuals and the resource location layer using both the CORINE Land Cover layer and satellite images. We assigned one resource type to each node by selecting the food source with the greatest probability of use according to the UD values. Roosting sites and breeding territories are binary features indicating whether or not a roosting site or breeding territory is present within the node (Additional file 1: Table S2). Roosting sites are communal roosts where birds socialize. To verify breeding territories, i.e. the areas where breeding individuals build their nests, at least one visit to the breeding territory was made between April and July.

We characterized the network topology using two quantitative metrics at network level (*diameter* and *density*) and two quantitative metrics at node level (*degree* and *betweenness*; see Table 1 and Additional file 2). Metrics at network level describe on average the movement paths of focal birds. To measure the average length of movement paths (i.e. the movement between nodes or links), we calculated the *diameter*, which reflects the speed of movement through a network and scales up as more nodes are used by the focal birds. Therefore, a larger *diameter* implies a greater dispersing capacity in the focal birds, while *density* measures the heterogeneity of the averaged movement paths. The heterogeneity shows how movement paths and space use differ during an individual's movements inside the network. Homogeneous networks (lower *density* values) have the same number (on average) of links per node, whereas heterogeneous networks (greater *density* values) differ in the number of links per node [47]. In biological terms, *density* illustrates whether the movement paths of birds are random or non-random [35]. Metrics at node level indicate the relative importance of a node in terms of connectivity and show the core locations to which animals are attracted. Thus, by measuring the number of links of each node in terms of its interaction with neighbourhood nodes, we calculated the *degree* to identify which nodes were most heavily used by individuals. We used *betweenness* to measure the frequency of a node as an intermediate step between the path of two other nodes. Higher values of *betweenness* represent a more central position for nodes with large numbers of links to other nodes (i.e. connectivity: [47]). The nodes with the highest values of *betweenness*—known as hubs—were considered to have greater relative importance in the foraging movements of individual birds [48].

Finally, we calculated two sets of parameters: first, the node fidelity was used to understand in detail the effects of node features on the use of space and was defined by

(1) the number of revisits that individuals make to a specific node and (2) the accumulated residence time that focal birds spent at each node. Second, the spatial connectivity of non-breeders and breeders was represented by the *degree* and *betweenness*.

Statistical analyses

We used the F-statistic of analysis of variance (ANOVA) to test differences between non-breeders and breeders in the metric parameters of their foraging behaviour at network level. We compared the number of elements (nodes and links) and the network quantitative metrics at network level (*diameter* and *density*) in terms of reproductive status [49]. We performed linear regressions to identify which features of the nodes determined node fidelity (number of revisits and residence time) and node importance in terms of interconnections along movement paths (*degree* and *betweenness*). To do this, we fitted separate models for each response variable (number of revisits, residence time, *degree* and *betweenness*) and each reproductive status because the spatial-use networks of non-breeders and breeders were completely different (see Results). For each model, we estimated the importance of each explanatory variable (node features described above) by removing it from the model and then performing an F-ratio test to derive *P* values for the variable of interest [50]. In terms of ecological functions, nodes with breeding territories were only considered in the linear model for breeders. In order to avoid collinearity between each category of land cover in the linear regressions, we carried out a Principal Component Analysis (PCAs) to reduce the number of correlated explanatory variables to just a few uncorrelated variables (orthogonal). Each Principal Component (PC) was obtained from the covariance matrix of the original variables [49].

Finally, we used a perturbation analysis to assess the foraging responses of individuals under future scenarios linked to the limitation of PAFS by environmental regulations. We simulated different perturbations on the network by removing nodes of different types and computing network robustness and the presence of key nodes according to available food resources. Network robustness refers to the ability of a network to maintain its features regardless of the degradation of the network itself [48]. The structure of spatial-use networks is characterized by their elements and their distribution as any degradation of their structure may modify the movement paths of individuals and reveal the underlying robustness (or vulnerability) of the connection (or disconnection) between key areas [48]. So, we first performed a 'random removal' of nodes and the subsequent measures of *betweenness* at each iteration. We then performed 'targeted removal' by removing nodes with a specific feature (e.g. nodes where landfills are present) until there were no more nodes with a specific feature, and then recalculated the *betweenness* measures for each iteration. In both cases, each iteration refers to the gradual one-by-one removal of nodes. 'Random removal' of nodes allowed us to infer whether the foraging response to the limitation on PAFS is a stochastic process if compared to the 'targeted removal' of nodes, or whether it follows a deterministic process. Therefore, we ran each random and targeted removal iteration 1000 times to generate two different frequency histograms of the *betweenness*. Finally, we compared these histograms resulting from each random and targeted simulation using a paired T-test. In such a way, we identified which node feature drives the robustness of both the non-breeder and breeder spatial-use networks.

All analytical procedures were carried out within the R environment [51] using the *recurse* [52], *move* [53] and *igraph* packages [54].

Results

When considering all individuals, i.e. non-breeders and breeders, the spatial-use network included a total of 44 nodes scattered throughout the northeast Iberian Peninsula (Catalonia, Aragón, Navarra, and Castilla y Leon) and southern France (Additional file 1: Fig. S1). Non-breeding and breeding vultures had different patterns of space use, as illustrated by the ANOVA in the topology of the spatial-use network. For example, the number of nodes (mean ± SD; non-breeders 11.7 ± 2.31; breeders 3.5 ± 1.38) and links (mean ± SD; non-breeders 38.3 ± 10.4; breeders 7.17 ± 5.53) were significatively higher in the networks of non-breeders than in breeders (nodes: $F_{4,600} = 61.29$, $P < 0.001$; links: $F_{4,600} = 45.16$, $P < 0.001$). Moreover, comparing the *diameter* and *density* at network level between non-breeders and breeders, we found two completely different patterns of movement. Compared to breeders, non-breeders had more dispersive movement paths (Mean ± SD; non-breeders 5.4 ± 1.65; breeders 2.33 ± 1.03; $F_{4,600} = 16.61$, $P < 0.01$) and made many more random and heterogeneous movements (mean ± SD; non-breeders 0.04 ± 0.01; breeders 0.008 ± 0.006; $F_{4,600} = 45.16$, $P < 0.001$). Nevertheless, for both breeders and non-breeders landfills were central areas during their movements. Nodes in which landfills were present had the highest *betweenness* and acted as hubs connecting the other nodes with different space use and ecological features (Fig. 1).

In the non-breeder spatial-use network, multiple linear regression analysis revealed that node fidelity (number of revisits and residence time) was related to the presence of roosting sites, extensive livestock and intensive farms and landfills (revisits: $F_{5,35} = 6.61$, $P < 0.001$, $R^2 = 0.49$;

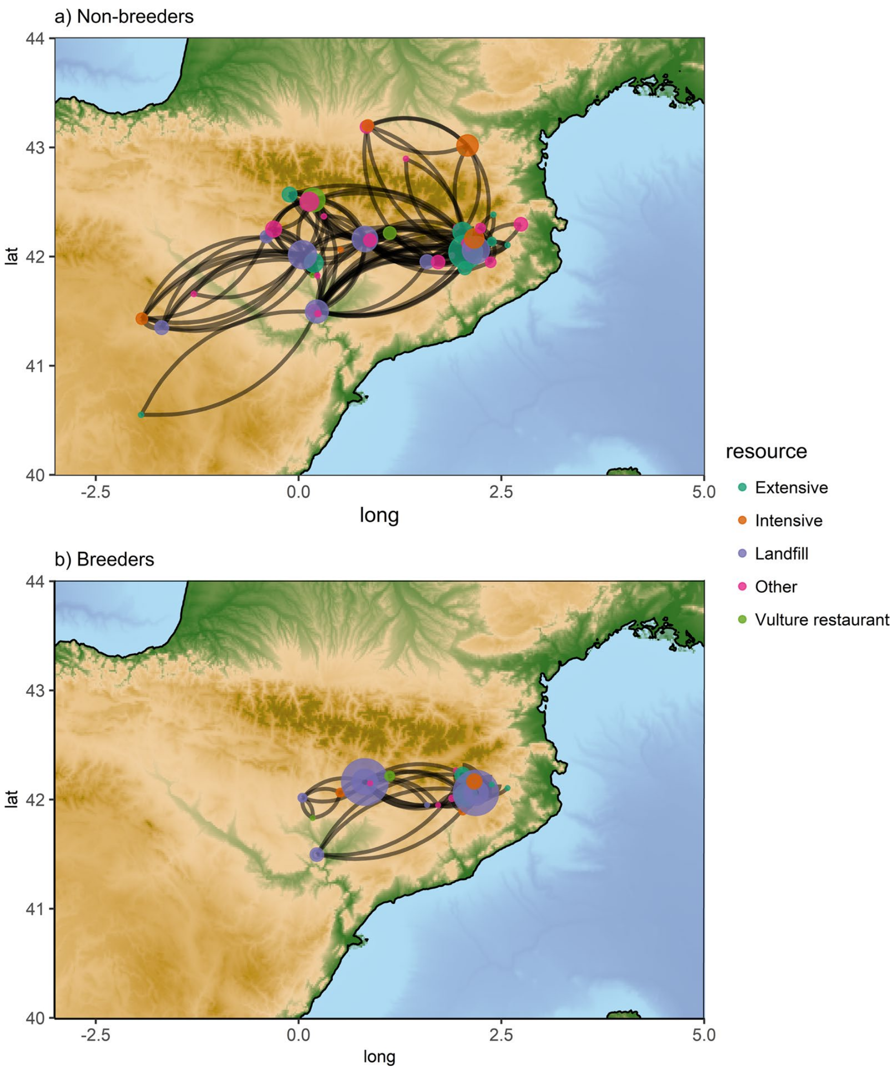

Fig. 1 Spatial-use networks of **a** non-breeding and **b** breeding Egyptian vulture populations in the study area. At the nodes the type of resources (i.e. landfill, intensive farm, extensive farm, and vulture restaurant and others that act as random or ephemeral resources) are shown. Node sizes are proportional to the *betweenness* value. Links represent the foraging trips connecting nodes. The length of the links depends on the frequency of the movement paths between the two nodes

residence time: $F_{6,34}=10.7$, $P<0.001$, $R^2=0.65$; Table 2); however, land-cover classes were not good predictors for explaining node fidelity or the relative importance of nodes within the spatial-use network (Additional file 3: Table S4). We selected two PCs in non-breeder regressions that explained a total of 75% variance. We found that PC1 relies positively on forest and negatively on non-irrigated land cover (Additional file 1: Table S3). Non-irrigated crops and forest (i.e. PC1; Additional file 1: Table S3) were selected to explain residence time but had no significant effect on non-breeders' use of networks. Moreover, the nodes most used by non-breeders were explained by roosting sites and the presence of landfills and extensive livestock (*degree*: $F_{5,35}=9.29$, $P<0.001$, $R^2=0.57$), both factors having a positive effect on the *degree.* Likewise, the nodes considered as central areas were positively driven by the presence of landfills (*betweenness*: $F_{4,35}=5.4$, $P>0.05$, $R^2=0.38$). On the other

Table 2 Multiple linear regressions analysis for site fidelity (number of revisits and residence time) and network connectivity (*degree* and *betweenness*) of non-breeder Egyptian vultures

	Non-breeders																			
	log(number of revisits)					**log(residence time)**					**log(degree)**					***Betweenness***				
Variables	***E***	***SE***	**95% CI**		***P***	***E***	***SE***	**95% CI**		***P***	***E***	***SE***	**95% CI**		***P***	***E***	***SE***	**95% CI**		***P***
			LL	**UL**				***LL***	**UL**				***LL***	**UL**				***LL***	**UL**	
(Intercept)	0.84	0.37	0–09	1.59	**0.029**	0.64	0.59	− 0.57	1.84	0.291	1.15	0.17	0.80	1.50	**< 0.001**	29.48	1.43	− 12.50	71.46	0.163
PC1	–	–	–	–	–	− 0.18	0.10	− 0.38	0.02	0.082	–	–	–	–	–	–	–	–	–	–
Resources																				
Extensive	0.91	0.44	0.02	1.79	**0.046**	1.48	0.71	0.04	2.92	**0.044**	0.52	0.21	0.09	0.96	**0.020**	14.68	0.43	− 55.28	84.64	0.673
Intensive	1.80	0.55	0.68	2.92	**0.003**	2.01	0.90	0.17	3.84	**0.033**	0.55	0.27	0.00	1.09	0.052	48.53	1.15	− 37.50	134.55	0.260
Landfill	2.09	0.51	1.05	3.14	**< 0.001**	2.51	0.87	0.75	4.27	**0.006**	1.01	0.25	0.49	1.52	**< 0.001**	167.98	4.48	91.90	244.07	**< 0.001**
Vulture rest	0.72	0.69	− 0.69	2.13	0.310	1.18	1.14	− 1.13	3.49	0.307	0.35	0.34	− 0.34	1.05	0.312	64.19	1.23	− 41.45	169.83	0.226
Roosting																				
YES	1.59	0.41	0.77	2.42	**< 0.001**	3.87	0.73	2.40	5.35	**< 0.001**	0.73	0.20	0.34	1.13	**< 0.001**	–	–	–	–	–
					$R^2 = .595$					$R^2 = .654$					$R^2 = .570$					$R^2 = .381$

Significant *P* values < 0.05 are in bold

E estimate, *SE* standard error, *CI* confidence interval, *LL* lower bound at 95% level of confidence, *UL* upper bound at 95% level of confidence, *P* values. R^2 represent the coefficient of determination for each selected model which does not include all explanatory variables

Table 3 Multiple linear regressions analysis for site fidelity (number of revisits and residence time) breeder Egyptian vultures

	Breeders																			
	log(number of revisits)					log(residence time)					log(degree)					*Betweenness*				
Variables	*E*	*SE*	95% CI		*P*	*E*	*SE*	95% CI		*P*	*E*	*SE*	95% CI		*P*	*E*	*SE*	95% CI		*P*
			LL	UL				*LL*	UL				*LL*	UL				*LL*	UL	
(Intercept)	1.33	0.60	0.04	2.62	**0.045**	1.93	1.16	− 0.56	4.42	0.119	1.68	0.17	3.21	2.11	**< 0.001**	14.59	5.42	3.21	25.98	**0.015**
Resources																				
Extensive	2.34	1.08	0.00	4.68	0.050	5.98	1.74	2.25	9.71	**0.004**	–	–	–	–	–	–	–	–	–	–
Intensive	− 0.10	1.01	− 2.28	2.09	0.924	1.16	1.90	− 2.91	5.22	0.552	–	–	–	–	–	–	–	–	–	–
Landfill	0.99	0.86	− 0.86	2.85	0.269	3.38	1.64	− 0.14	6.90	0.058	–	–	–	–	–	–	–	–	–	–
Vulture rest	− 1.36	1.19	− 3.93	1.20	0.272	− 1.48	2.17	− 6.13	3.18	0.508	–	–	–	–	–	–	–	–	–	–
Breedeing territory																				
YES	1.86	0.81	0.12	3.61	**0.038**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
					$R^2 = .680$					$R^2 = .557$										

Significant *P* values < 0.05 are in bold

E estimate, *SE* standard error, *CI* confidence interval, *LL* lower bound at 95% level of confidence, *UL* upper bound at 95% level of confidence, *P* values. R^2 represent the coefficient of determination for each selected model which does not include all explanatory variables. Models related to spatial connectivity (*degree* and *betweenness*) are not significant (null models are shown)

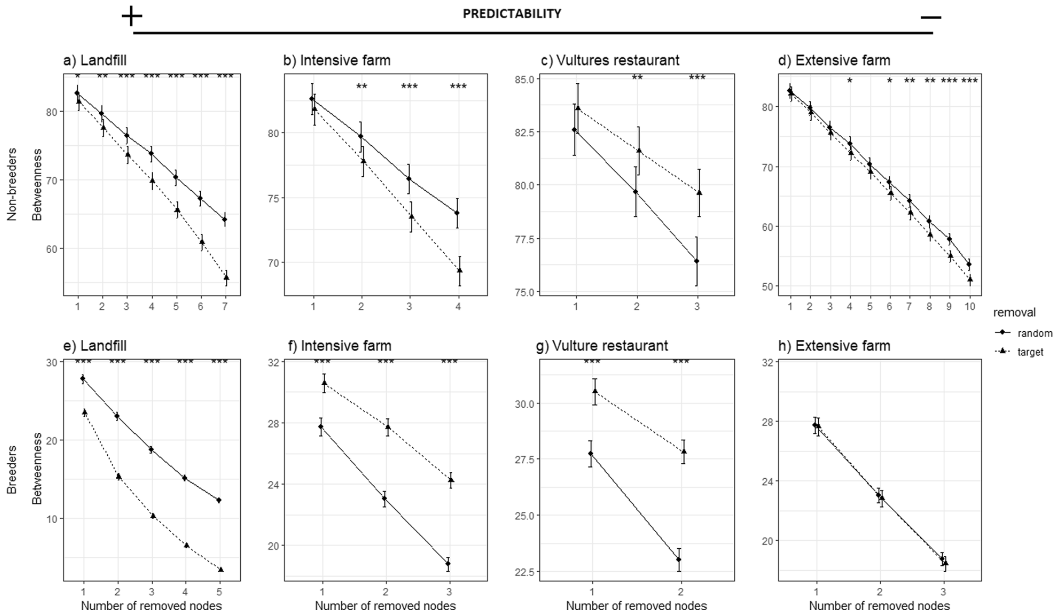

Fig. 2 Environmental perturbation analysis. Random and Targeted node removal used to examine the response of non-breeding (**a**–**d**) and breeding (**e**–**h**) Egyptian vultures to future sanitary legislation if implemented. Plots show the mean *betweenness* values and confidence intervals along, respectively, random (circle or thick line) or targeted (triangle or dashed line) node-removal simulations. Coefficient intervals (5–95%) are shown. Aesthetics show significant differences (**P* < 0.05; ***P* < 0.01; ****P* < 0.001)

hand, for breeding individuals, node fidelity was positively explained by breeding territory (number of revisits: $F_{5,13} = 5.53$, $P < 0.05$, $R^2 = 0.68$) and extensive livestock (residence time: $F_{4,14} = 4.4$, $P < 0.05$, $R^2 = 0.56$; Table 3). However, no significant effect of node features was found to explain *degree* and *betweenness* in the spatial-use networks of breeding birds (see simple ANOVA comparisons in Additional file 1: Figs. S3 and S4).

In general, the perturbation analysis showed that the gradual disappearance of PAFS will significantly alter the movement paths and the degree of relative importance of nodes (connectedness of nodes) and, in turn, modify the foraging strategy of these two subsets of this vulture population (*P* values for paired T-tests comparing random and targeted simulation were less than 0.05; Fig. 2). The removal of key nodes where landfills exist would have a deterministic effect on foraging movements at population level resulting in an increase in nodes that are poorly connected to the non-breeding and breeding networks, as shown by the significantly lower *betweenness* values of the targeted simulation compared to the random simulation (Fig. 2a, e). Moreover, the removal of nodes from the non-breeding network, where intensive or extensive farms are the main food resource, would have a similar impact on foraging strategies as landfill-site removal but at a lower intensity (Fig. 2b, d). Thus, the non-breeding network will be slightly more robust in the event of the disappearance of intensive and extensive farms. Compared to the non-breeding network, the breeding network was found to be more resilient to intensive farm removal as key nodes would become either more interconnected or there would be an increase in the number of well-connected nodes (Fig. 2f). Similar foraging responses in both non-breeding and breeding networks were found when nodes with vulture restaurants were removed (Fig. 2c, g). In addition, the perturbation analysis showed that there were no effects on foraging responses when we removed nodes with extensive farms from the breeding network (Fig. 2h).

Discussion

It is well-known that transformations of human-mediated ecosystems have the potential to alter animal movement patterns and foraging behaviour (e.g. [5, 55–57]). By studying changes in space use and connectivity in an endangered vulture species, the Egyptian vulture, we improved our understanding of how environmental and ecological conditions influence the foraging movements of different fractions of the population (i.e. non-breeders and breeders) in different ways. We show here that landfills are a key environmental factor driving spatial-use patterns and how inferred future scenarios in the event of landfill closure will generate profound changes in movement patterns in terms of connectivity in this endangered vulture's populations.

Non-breeding and breeding vultures have different foraging strategies, as illustrated by the differences in the spatial topology of their networks. Non-breeding individuals disperse more along a spatial-use network that has more nodes and links than the breeding bird networks. This could be related to the larger exploratory capacity of non-breeders as they have no nest attachments or functional constraints imposed by the demands of breeding. It is known that non-breeders have larger home ranges than breeders [42, 43] and this is probably associated with the greater number of areas they visit and more connections between them (networks with more nodes and links). The exploratory foraging behaviour undertaken by non-breeders may also explain the heterogeneity of movements found in their networks, in which individuals rarely use or connect certain spatial areas and mostly travel through well-used and well-connected areas, the so-called hub-nodes. Such heterogeneous topologies are reminiscent of the limiting case of scale-free network properties (see [58]; Additional file 4). This special type of network has been described in other species (e.g. bats, [37]) and are known to be robust against random-node removal but susceptible to (hub)-node removal [59]. In the foraging networks of non-breeding Egyptian vultures, hub-nodes are represented by landfills and intensive farms. Thus, it is not surprising that the main roosting sites in our study area are near landfills (pers. obs.), which are closely associated with predictable food sources. These roosting sites are both stopovers during migration and temporary settlement areas during the breeding season where individuals socialize and exchange information [60–62]. As well, landfills may act as highly visible and familiar landmarks or waypoints along movement paths that aid navigation between other nodes, a mechanism that has been reported in Western Gulls (*Larus occidentalis*) [57]. Conversely, the territorial behaviour of breeders is characterized by low dispersal and homogeneous movements, and individuals travel between nodes with a similar degree of usability (exploitability) and connectivity. We found a parallel in seabird literature, in which researchers also described generally more specialized foraging behaviour in breeding adult Northern Gannets (*Morus bassanus*) than in non-breeding birds, almost certainly imposed by their central foraging behaviour and habitat use [63]. The space use and connectivity emerging in breeding individuals is thus potentially vulnerable to random landscape transformation but less sensitive to targeted landscape transformations. This is probably due to the few nodes present in breeders' spatial-use networks, in which the slightest alteration spreads quickly and has a strong effect on network topology, as has been described in other kinds of networks [64]. Although the increase in our focal population over the past decades is probably linked to the appearance of landfills [26], it is known that extensive livestock can also act as one of the main food sources in breeding territories far from landfills [17]. Accordingly, our results support the idea that breeding birds are currently heavily reliant on extensive livestock [17, 65]. Overall, our findings agree with past studies regarding the interconnection between space use and reproductive status in vultures [66–68] despite our use of a novel application of a network approach to shed light on movement patterns during foraging, and use of the connectivity between distinct feeding resources in two subsets of an Egyptian vulture population. We also demonstrate here that predictable food availability affects large-scale movement behaviour in avian scavengers, as has been recognized in other species (e.g. seabirds [55]; white storks [5]; brown bears [56]; gulls [16]).

Perturbation analysis demonstrates that both non-breeder and breeder foraging strategies are vulnerable to the removal of nodes with highly predictable food sources, especially if landfills are present. Our results show that the systematic removal of landfills (hub-nodes) changes patterns of population movements such that other nodes become key in the use-of-space strategies of focal birds. Therefore, when a node with a landfill is removed, another node with a different food resource becomes the new hub. In line with our prediction, we found that this is especially important for non-breeding birds whose movements mainly target local areas with landfills (see also [43]). A possible explanation for this foraging pattern could be their lack of experience in prospecting, as well as their lack of dependency on a breeding territory, which favours the exploitation of predictable food sources (see e.g. [69]). By contrast, although we predicted that the disappearance of PAFS would not affect the foraging behaviour of breeding individuals, interestingly our results did show that an important alteration in movement patterns occurred if landfills, intensive farms and vulture restaurants were sequentially removed. The fact that breeders take advantage of less predictable resources such as extensive livestock is most likely due to their location near breeding territories [17]. Indeed, at population level, our simulations predict that, in the lack of landfill-site scenario, the core behavioural response of birds will be to switch to extensive livestock (see Fig. 3), which thus makes extensive livestock a key element in any future conservation strategy.

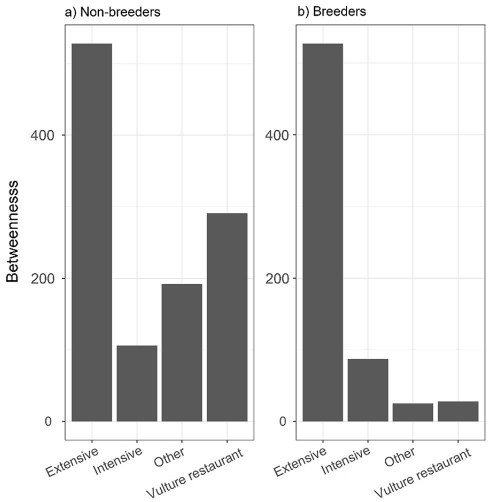

Fig. 3 Average *betweenness* of spatial-use networks for **a** non-breeding and **b** breeding Egyptian vulture populations in terms of the different sets of resources for all nodes from which landfills were removed

The studied Egyptian vulture population showed a great dependence on PAFS and our results indicate that the future closure of landfills (see 2008/98/EC [27]) will reconfigure their spatial networks and lead to a shift in home ranges in such a way that landfills will no longer be their central foraging areas. Currently, landfills concentrate large numbers of individuals of different ages and reproductive status from both local and neighbouring populations (e.g. France, Spain; pers. obs.). This makes them key places for information exchange, socialization and roosting, as well as a profitable feeding sites, particularly for non-breeders (e.g. [70]), and, in turn, for the recruitment and viability of local and regional populations ([26]; pers. obs.). An option for filling this gap in food provision if landfills close is to favour a natural supply of carrion, if necessary, by maintaining certain supplementary feeding points specifically targeting Egyptian vultures and non-breeder survival ([71, 72]) and/or guaranteeing the connection between non-breeding and breeding populations that ensures population viability. In fact, some vulture restaurants designed specifically for Egyptian vultures replace the roosting functions that landfills currently perform ([61]; pers. obs.). In any case, our findings suggest that more research is required into how PAFS affect the non-breeder subset of vultures. It is not clear to what extent landfill closure will affect the performance of breeding birds, although it is known that the occupancy of breeding areas is somehow related to these feeding sites [26]. Our results reveal that the spatial-use network of breeders is shaped above all by extensive farming and the benefits of this type of animal husbandry for vulture breeding populations have been noted elsewhere [17, 73]. Thus, future conservation farming policies should promote extensive livestock practices and allow more farmers to freely abandon livestock carcasses in the field. To do so, regional policies should focus on extending the areas in which the abandoning of extensive carcasses is permitted (e.g. in Spain, ZPAEN). Long-term monitoring is key to identifying how population numbers vary over time, and the combination of telemetric information and other tracking methods (e.g. ringing) will allow us to measure vital parameters and evaluate population viabilities under new food availability scenarios. In conclusion, we emphasize how movement ecology and network modelling are highly promising tools and can potentially play a key role in movement research. They allow us to predict the responses of wild species having to face up to environmental changes and landscape transformation (e.g. [33, 37]) and so will play a crucial role in the search for the most efficient conservation practices.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-023-00383-4.

Additional file 1: Table S1. Egyptian vultures tagged with GPS-GMS devices during the summer period between 2018 and 2019 in Catalonia (NE Spain). **Table S2**. Total of nodes used by non-breeder and breeder Egyptian vultures. **Table S3** Factor loadings after Principal Component Analysis for the nine categories assigned to land uses in the study area. **Figure S1**. Dynamic Brownian Bridge Models home ranges at 50% (dark grey) and 95% (light grey) of 10 non-breeders and 6 breeders of Egyptian vulture tagged in Catalonia (Northeast Spain) at the population level. **Figure S2**. Correlation between nodes' features and the parameters related to node fidelity (number of revisits and accumulated residence time) and local network metrics (degree and betweenness) for the focal a) non-breeders and b) breeders. **Figure S3**. Boxplots of non-breeders node fidelity. **Figure S4**. Boxplot of breeders node fidelity.

Additional file 2: Topology parameters of spatial networks.

Additional file 3: Table S4. Results of the top-ranked models (lowest AIC) for non-breeder and breeder Egyptian vultures accounting for site fidelity (number of revisits and accumulated residence time) and spatial-use network topology (*degree* and *betweenness*).

Additional file 4: Figure S5. *Degree* (K) and *betweenness* (B) distributions of spatial-use networks for breeding and non-breeding populations of Egyptian vultures.

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Author contributions
CCI, FB, ACA and JR conceived the ideas for the study. CCI and AHM conducted the fieldwork with help from JR. CCI and FB conducted the coding and data analyses. CCI and ACA wrote the first draft of the manuscript and all authors contributed substantially to revisions. All authors read and approved the final manuscript.

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Availability of data and materials
The datasets generated and analyzed during the current study are not publicly available due to sensitive information on a threatened and endangered species. Data are however available from the authors upon reasonable request and with permission of contact person of the '*Neophron percnopterus* - Central Catalonia' repository on Movebank (www.movebank.org).

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
We declare we have no competing interests.

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