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PhD Thesis

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Lleida, June 2021

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Ruth García Jiménez

Dissertation presented in fulfilment of the requirements for the Ph.D. degree in Animal Science, from the Forest and Natural Environment Management doctoral programme.

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FONDO EUROPEO DE
DESARROLLO REGIONAL
"Una manera de hacer Europa"

A mi hermana Karen,
a mis padres,
a mi abuela y a toda mi familia.

"The world as we have created it is a process of our thinking.

It cannot be changed without changing our thinking"

Albert Einstein

"You cannot get through a single day without having an impact on the world around you. What you do makes a difference, and you have to decide what kind of difference you want to make"

Jane Goodall

Photo by Juan Carlos García Gómez.
An adult Pyrenean bearded vulture just about to take off (Cogulers, Lleida).

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Así, a lo largo de toda mi infancia y adolescencia, las decisiones para mí estuvieron muy claras a la hora de elegir mis estudios, cosa que —según descubrí más adelante— en absoluto era algo evidente para la gente a esa edad. Cuando por fin llegó el momento, fui feliz estudiando la carrera de biología. La universidad fue para mí toda una revelación. Tal y como había imaginado, conocí por fin gente con la que era afín, con unos gustos compatibles, con la que era muy fácil hablar de todo y de nada, llenando el tiempo con risas y buenos recuerdos. Dejé de sentirme «un bicho raro» por ser yo misma y mostrarme como era (de ahí que *mis bichólogas*, fueran una gente tan especial). Pero, por supuesto, no fue todo jolgorio y gloria. Los trabajos y presentaciones nos desbordaban. Eso, sumado a las prácticas, las clases… nos tirábamos de sol a sol (¡literalmente!) dentro de esas mismas cuatro paredes.

Aprendimos mucho, aunque no sabíamos de nada. Y, aun siendo el estudio del funcionamiento y origen de la vida todo lo gratificante que me había imaginado, el futuro seguía reservándome sorpresas. En tercero de carrera recibí mi segundo flechazo en el terreno profesional cuando, dentro del ámbito de la biología, conocí la ecología a través de la visión de Carlos Montes (o *Charles Vowels*, según lo apelábamos con cariño algunos en *petit comité*). Él nos habló de la ecología más básica desde sus principios más filosóficos utilizando conceptos transgresores como la «torre de marfil», la metáfora del mundo «como una gran mierda» y trayendo a clase siempre debates que nos hacían cuestionar el prisma desde el que nos encontrábamos juzgando. Supongo que todo ello me llevó a lo que sería, sin saberlo, mi primer contacto cercano con los buitres durante mis prácticas externas en el Parque Nacional de Monfragüe. Y, como bien saben los cantantes de Extremoduro, «*… en Monfragüe, buitres negros*». Aunque he de decir que yo realmente solo vi allí durante el mes de agosto a los buitres leonados que se apiñaban en comunidad en torno al Salto del Gitano.

Tras ello, muchas experiencias siguieron perfilando mi vida, conduciéndome finalmente a conocer a Antoni Margalida, quien, tras hablar conmigo apenas un par de horas en una comida rápida en el clásico Punt estrella de Lleida, decidió darme una oportunidad en este mundo de la investigación en carroñeros. De modo que, gracias Antoni y Juan Ma, por la oportunidad que me brindasteis y por lo enseñado en estos años. Juan Ma, gracias por ofrecerme tu casa en algunos de mis días por Elche y especialmente gracias por presentarme a las bellísimas personas con las que conformas el equipo de ecología en la Universidad Miguel Hernández de Elche: Adrián, las Alicias, Andrés, Esther, Eva, Isa, Jomar, Lara, Nati, Paco, los Robertos, Toni Vicky y Zebensui, que me hicieron sentir bienvenida e incluida desde el primer momento y hasta el último de los días de todas mis estancias por Elche. Zebensui, ha sido un placer haber podido trabajado contigo mano a mano. No me olvido tampoco de Marcos, la gente de la escuela de teatro de Roberto (incluido su hermano Adrián) y de Margarita, que siempre aportaron muy buenos momentos también fuera del trabajo. Y hablando de mi tiempo por Elche, no puedo dejar de mencionar a Marecillo y Younes, sin duda los mejores compis de piso que haya conocido por azar. Grandes personas de gran corazón. Gracias por todos los momentos vividos, con espontaneidad y libres de prejuicios.

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Glossary

Birding: is a type of birdwatching specifically focused on compiling lists of species identified either over a specified time period (e.g. day, weeks, year, life), or in a particular region (e.g. state, country). Although birdwatching is a leisure time hobby that provides emotional and aesthetic pleasure, birding could be considered as a competitive sport in certain contexts (Cooper & Smith 2010).

Birdwatching: (also referred to as bird watching, or bird-watching) is the set of non-consumptive hobbies related with bird-based recreational activities such as feeding and photographing birds, monitoring nests, creating bird-friendly habitat around residences, travelling to see birds, and creating lists of observed birds. Sometimes birdwatching involves making lists, such as lists of identified bird species, lists of places visited for bird watching, etc. (Cooper & Smith 2010).

Carrion: a high-quality form of detritus that is composed entirely of dead animal matter (Wilson & Wolcovich 2011).

Detritus: the basal trophic level of the decomposer world composed of debris or dead organic material. Its quality ranges from the very low quality (i.e. high ratio of carbon:nitrogen or carbon:phosphorous) of dead and decaying plant materials to the high quality of carrion (Wilson & Wolcovich 2011).

Ecosystem services: direct or indirect benefits that people obtain from ecosystem functioning (Millennium Ecosystem Assessment; MEA 2005).

Ecotourism: responsible travel to natural areas that conserves the environment and improves the well-being of local people (The International Ecotourism Society; TIES 1990).

Nature's contributions to people (NCP): all the contributions of living nature to people's quality of life, including both the positive (i.e. beneficial) and negative (i.e. detrimental) inputs that people obtain from the ecosystems (Díaz *et al.* 2018). Each specific cultural setting would condition their classification through three partially overlapping groups (Díaz *et al.* 2018):

material NCP actual goods provided by nature, finite and physically consumed, such as food, energy, or medicinal products;

non-material NCP the effect of nature on the subjective or psychological aspects supporting people's quality of life sustaining individual and collective well-being, such as recreational, aesthetic, learning, and inspirational, experiential, intellectual and spiritual contributions;

regulating NCP functional and structural aspects of organisms, ecosystems and biodiversity and ecosystem processes that regulate material and non-material NCP or influence environmental conditions and those which affect humans.

Spanning these three NCP groups, there is the *maintenance of options NCP*, which includes all the processes somehow supporting the ecosystem resilience, keeping all current and future NCP available into the future.

Predator: an organism that hunts and kills its prey and then either consumes all or part of the carcasses, or hides it for a moment of starvation (Houston, 1979).

Scavenger: any organism that feeds on dead organic matter such as dead animals or plants and did not kill (Schmitz *et al.* 2008; Campbell 2015; Benbow *et al*. 2019). They can be classified in two different functional groups: *obligate scavengers*, which depend entirely on carrion for survival and reproduction, and *facultative scavengers*, that do not rely on carrion as their only food livelihood and only scavage opportunistically (DeVault *et al.* 2016; Campbell 2015; Olea *et al.* 2019).

Supplementary feeding sites (SFS): (so-called "vultures' restaurants", or feeding sites, stations, or points) scavenger feeding structures either fixed or mobile in the space that increase the availability of carrion resources in the environment with a periodical or random temporality. They are normally created for the principal purpose of scavenger conservation and so used as a conservation tool (Cortés-Avizanda *et al.* 2010; Moreno-Opo *et al.* 2015).

The International Union for Conservation of Nature (IUCN): is a membership Union composed of both government and civil society organizations (with around 1,400 Member organizations and more than 18,000 experts) and considered the global authority on the status of the natural world and the measures needed to safeguard it (IUCN 2021). On its Red List of Threatened Species, species' extinction risk is assessed as Least Concern, Near-Threatened, three progressively escalating categories of Threatened species (Vulnerable, Endangered, and Critically Endangered), and Extinct.

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Abstract

Recent research has evinced how scavenging represents a fundamental process in ecosystem functioning, playing a key role in food web, population, and community ecology, but also on evolution, biodiversity conservation, and human well-being. Despite this renewed emerging scientific mainstream focused on vertebrate scavengers, this guild is currently globally threatened. Obligate scavengers (i.e. vultures) and some species of large facultative scavengers, such as apex predators, face the most worrying situation. At present, 16 out of 23 vulture species worldwide suffer a certain degree of conservation threat, all the ecological, economic, sanitary and cultural contributions that they provide also being at risk. Yet, scavengers are currently socially valued for their nature's contributions to people (NCP) of disease control and carcass removal. Among all European countries, currently Spain boasts the most important breeding populations of the four vulture species within the Western Palearctic region (i.e. Eurasian griffon *Gyps fulvus*, cinereous vulture *Aegypius monachus*, Egyptian vulture *Neophron percnopterus* and bearded vulture *Gypaetus barbatus*), together with a wide array of facultative scavengers. Hence, at present Spain represents one of the most significant countries for the conservation of European scavengers. This thesis brings an innovative approach for the avian scavenger conservation, focusing on the movement ecology and the ecosystem services provided by the avian scavenger guild in the Pyrenees. Within this framework, the main aim of this dissertation was to study both (1) poorly known aspects of the movement ecology of the Pyrenean bearded vulture population and (2) the cultural services provided by the avian scavenger guild from a socio-ecological perspective in order to ensure the efficacy and strengthen future conservation strategies aimed at these scavenger species. The first goal was explored using the bearded vulture as a model study species to identify the drivers that determine the daily flight patterns of the Pyrenean bearded vulture population through reliable satellite telemetry data. Thanks to the studies of this thesis it was found out that both external and internal factors influenced daily flight activity of bearded vultures, as well as the proper operation of the transmitter devices with which they were tracked (*Chapters 2 and 1*, respectively). In particular, Pyrenean bearded vultures' daily flight activity was strongly influenced by daylight time, season, and territorial status, while individual sex and breeding season showed a milder effect on the birds' movement behaviour (*Chapter 2*). At the same time, the findings of

this thesis confirmed that the combined effects of technological and biological traits of a large avian species significantly influence the proper functioning of the transmitters frequently used in movement ecology studies (*Chapter 1*). Thus, these results are not only of ecological interest —being of great utility for the management and conservation of the bearded vulture, and with it, of other avian scavenger species—, but can also be helpful in the development of long-term conservation studies based on any avian species' movement ecology data. The second goal was examined by identifying and assessing the NCP provided by the European avian scavengers in the Pyrenees through scavenger-based touristic activity (i.e. birdwatching, environmental education or controlled photography activities offered when visiting the supplementary feeding sites, SFS) from a combined socio-ecological and economic approach (*Chapters 4 and 3*, respectively). The findings obtained in this thesis confirmed that people who enjoy avian scavengers by visiting SFS mostly perceived the beneficial NCP provided by these species. SFS visitors focused on non-material NCP (as it occurs with birdwatchers), particularly appreciating the supporting identity value of the avian scavenger species (*Chapter 4*). This touristic avian scavenger-based activity was estimated to represent on average an annual economic value of €4.21 ± 2.26 million (US $4.90 ± 2.67 million); including €2.18 ± 1.17 million (US $2.53 ± 1.36 million) of direct economic benefit to the local community, of which the food and accommodation costs together represented the highest contribution to the local revenue (*Chapter 3*). These results show how this specific avian-scavenger-based tourism developed in a scientifically monitored environment could comply with the aims of both the community-based conservation (CBC) strategy and ecotourism. Moreover, these recreational activities (i.e. birdwatching, educational and controlled photography) could work as potential tools to showcase non-material NCP of avian scavengers to the general public. The inclusion of the socio-cultural dimension in the conservation strategies is imperative if we want them to be successful in the long term. Environments where people can profit from non-material NCP provided by avian scavengers are important to bring the general public closer to scavenger species, increasing people's awareness and popular and ecological knowledge of the species' existence value and ecological role (including their provision of NCP), therefore promoting a favourable mindset toward this guild. We need an integrative perspective of the current socio-ecological system to encourage sustainable conservation policies that can assure key scavenger species' —such as vultures and large predators— co-existence with the human species.

Resumen

Investigaciones recientes han demostrado cómo el consumo de carroña representa un proceso fundamental en el funcionamiento de los ecosistemas, jugando éste un papel clave en la ecología de la red trófica, ecología de poblaciones y ecología de comunidades; pero también en la evolución, la conservación de la biodiversidad y el bienestar humano. A pesar de esta renovada corriente científica emergente centrada en los carroñeros vertebrados, este gremio se encuentra actualmente amenazado a nivel mundial. Los carroñeros obligados (i.e. buitres) y algunas especies de carroñeros facultativos de gran tamaño, como son los superdepredadores, enfrentan la situación más preocupante. Hoy en día, 16 de las 23 especies de buitres en todo el mundo sufren cierto grado de amenaza en su conservación, estando también en riesgo todos los aportes ecológicos, económicos, sanitarios y culturales que estas especies generan. Sin embargo, los carroñeros actualmente son valorados en la sociedad por sus contribuciones de la naturaleza a las personas (CNP) relativas al control de enfermedades y eliminación de cadáveres. De todos los países europeos, en la actualidad, España cuenta con las poblaciones reproductoras más importantes de las cuatro especies de buitres del Paleártico occidental (i.e. el buitre leonado *Gyps fulvus*, el buitre negro *Aegypius monachus*, el alimoche *Neophron percnopterus* y el quebrantahuesos *Gypaetus barbatus*), junto con una amplia variedad de carroñeros facultativos. Por tanto, en el presente, España representa uno de los países más importantes para la conservación de los carroñeros europeos. Esta tesis aporta un enfoque innovador para la conservación de las aves carroñeras, centrándose en la ecología del movimiento y los servicios ecosistémicos proporcionados por el gremio de aves carroñeras en los Pirineos. En este marco, el objetivo principal de esta disertación ha sido estudiar tanto (1) aspectos poco conocidos de la ecología del movimiento de la población pirenaica de quebrantahuesos, como (2) los servicios culturales prestados por el gremio de aves carroñeras desde una perspectiva socio-ecológica, con el fin de fortalecer y asegurar la eficacia de las futuras estrategias de conservación dirigidas a estas especies. El primer objetivo se exploró utilizando el quebrantahuesos como especie modelo de estudio, con el fin de identificar los motores que determinan los patrones de vuelo diarios de la población pirenaica de esta especie a través de datos fiables de telemetría satelital. Gracias a los estudios de esta tesis se pudo constatar que, tanto factores externos, como internos, influían en la actividad de vuelo diaria de

los quebrantahuesos, así como en el correcto funcionamiento de los transmisores con los que fueron rastreados (Capítulos 2 y 1, respectivamente). Concretamente, la actividad diaria de vuelo de los quebrantahuesos pirenaicos resultó estar fuertemente influenciada por las horas de luz, la estación y el estatus territorial, mientras que el sexo y el periodo reproductor mostraron un efecto más leve en su patrón de movimiento (Capítulo 2). Al mismo tiempo, los hallazgos de esta tesis confirmaron que los efectos combinados de los factores tecnológicos y biológicos de una especie de gran tamaño influyen significativamente en el adecuado funcionamiento de los transmisores utilizados habitualmente en estudios de ecología del movimiento (Capítulo 1). Así, estos resultados no solo son de interés ecológico —siendo de gran utilidad para el manejo y conservación del quebrantahuesos y, con él, de otras especies de aves carroñeras—, sino que también pueden ser prácticos en el desarrollo de estudios de conservación a largo plazo basados en cualquier dato de ecología de movimiento en especies similares. El segundo objetivo se examinó identificando y valorando el CNP proporcionado por las aves carroñeras europeas en los Pirineos a través de una actividad turística basada en los carroñeros (i.e. educación ambiental, observación de aves o actividades de fotografía controlada, que se ofrecen al visitar los puntos de alimentación suplementaria para aves carroñeras, PAS) desde un enfoque socio-ecológico y económico combinado (Capítulos 4 y 3, respectivamente). Los hallazgos obtenidos en esta tesis confirmaron que las personas que disfrutan de las aves carroñeras al visitar los PAS, perciben principalmente el CNP beneficioso proporcionado por estas especies. Los visitantes de los PAS se enfocaron en CNP no materiales (como también lo hacen los observadores de aves, en general), apreciando particularmente el valor de identidad de las especies de aves carroñeras (Capítulo 4). Se estimó que esta actividad turística basada en las aves carroñeras representa un valor económico anual medio de € 4,21 ± 2,26 millones (US $ 4,90 ± 2,67 millones), incluyendo € 2,18 ± 1,17 millones (US $ 2,53 ± 1,36 millones) de beneficios económicos directos para la comunidad local, de los cuales, los costos de comida y alojamiento representan, en conjunto, la mayor contribución a los ingresos locales (Capítulo 3). Estos resultados muestran cómo este turismo en concreto, basado en aves carroñeras y desarrollado en un entorno científicamente controlado, podría cumplir con los objetivos, tanto de la estrategia de conservación basada en la comunidad (CBC), como del ecoturismo. Además, estas actividades recreativas (i.e. de observación de aves, educativa y fotografía controlada) podrían funcionar como herramientas potenciales para mostrar los CNP no materiales de las aves carroñeras a la población general. La inclusión de la dimensión sociocultural en las estrategias de conservación es imperativa si queremos que éstas sean exitosas a largo plazo. Los entornos en los que las personas pueden beneficiarse de los CNP no materiales proporcionados por las aves carroñeras son importantes para acercar las especies carroñeras a la sociedad, aumentando la conciencia de la gente y el conocimiento popular y ecológico del valor de existencia de las especies y su función ecológica (incluida su provisión de CNP), promoviendo así una mentalidad favorable hacia este gremio. Necesitamos una perspectiva integradora del sistema socio-ecológico actual para fomentar políticas de conservación sostenibles que puedan asegurar la coexistencia de especies carroñeras clave, como son los buitres y los grandes depredadores, con la especie humana.

Resum

Investigacions recents han demostrat com el consum de carronya representa un procés fonamental en el funcionament dels ecosistemes, jugant aquest un paper clau en l'ecologia de la xarxa tròfica, ecologia de poblacions i ecologia de comunitats; però també en l'evolució, la conservació de la biodiversitat i el benestar humà. Tot i aquesta renovada corrent científica emergent centrada en els carronyers vertebrats, aquest gremi es troba actualment amenaçat a nivell mundial. Els carronyers obligats (i.e. voltors) i algunes espècies de carronyaires facultatius de grans dimensions, com són els superdepredadors, enfronten la situació més preocupant. Avui en dia, 16 de les 23 espècies de voltors a tot el món pateixen cert grau d'amenaça en la seva conservació, trobant-se també en risc totes les aportacions ecològiques, econòmiques, sanitàries i culturals que aquestes espècies generen. No obstant això, els carronyers actualment són valorats en la societat per les seves contribucions de la natura a les persones (CNP) relatives al control de malalties i eliminació de cadàvers. De tots els països europeus, en l'actualitat, Espanya compta amb les poblacions reproductores més importants de les quatre espècies de voltors de Paleàrtic occidental (i.e. el voltor comú *Gyps fulvus*, el voltor negre *Aegypius monachus*, l'aufrany *Neophron percnopterus* i el trencalòs *Gypaetus barbatus*), juntament amb una àmplia varietat de carronyaires facultatius. Per tant, en el present, Espanya representa un dels països més importants per a la conservació dels carronyers europeus. Aquesta tesi aporta un enfocament innovador per a la conservació dels ocells carronyaires, centrant-se en l'ecologia del moviment i els serveis ecosistèmics proporcionats per aquest gremi als Pirineus. En aquest marc, l'objectiu principal d'aquesta dissertació ha estat estudiar tant (1) aspectes poc coneguts de l'ecologia del moviment de la població pirinenca de trencalòs, com (2) els serveis culturals prestats pel gremi d'aus carronyeres des d'una perspectiva socioecològica, per tal d'enfortir i assegurar l'eficàcia de les futures estratègies de conservació dirigides a aquestes espècies. El primer objectiu es va explorar utilitzant el trencalòs com a espècie model d'estudi, per tal d'identificar els motors que determinen els patrons de vol diaris de la població pirinenca mitjançant dades fiables de telemetria satel·lital. Gràcies als estudis d'aquesta tesi es va poder constatar que, tant factors externs, com interns, influïen en l'activitat de vol diària dels trencalòs, així com en el correcte funcionament dels transmissors amb els que van ser rastrejats (Capítols 2 i 1, respectivament). Concretament, l'activitat diària de vol dels trencalosos

pirinencs va resultar estar fortament influenciada per les hores de llum, l'estació i l'estatus territorial, mentre que el sexe i el període reproductor van mostrar un efecte més lleu en el patró de moviment de les aus (Capítol 2). Al mateix temps, les troballes d'aquesta tesi van confirmar que els efectes combinats dels factors tecnològics i biològics d'espècies de gran mida influeixen significativament en l'adequat funcionament dels transmissors utilitzats habitualment en estudis d'ecologia del moviment (Capítol 1). Així, aquests resultats no només són d'interès ecològic —essent de gran utilitat per al maneig i conservació del trencalòs i, amb ell, d'altres espècies d'ocells carronyaires—, sinó que també poden ser pràctics en el desenvolupament d'estudis de conservació a llarg termini basats en qualsevol dada d'ecologia de moviment en altres espècies de similars característiques. El segon objectiu es va examinar identificant i valorant el CNP proporcionat per les aus carronyeres europees als Pirineus a través d'una activitat turística basada en els carronyers (i.e. educació ambiental, observació d'aus o activitats de fotografia controlada, que s'ofereixen al visitar els punts d'alimentació suplementària per a aus carronyeres, PAS) des d'un enfocament socioecològic i econòmic combinat (Capítols 4 i 3, respectivament). Les troballes obtingudes en aquesta tesi van confirmar que les persones que gaudeixen de les aus carronyeres al visitar els PAS, perceben principalment el CNP beneficiós proporcionat per aquestes espècies. Els visitants dels PAS es van enfocar en CNP no materials (com també ho fan els observadors d'aus, en general), i apreciar particularment el valor d'identitat de les espècies d'aus carronyaires (Capítol 4). Es va estimar que aquesta activitat turística basada en les aus carronyaires representa un valor econòmic anual mitjà de € 4,21 ± 2,26 milions (US $ 4,90 ± 2.670.000), incloent € 2,18 ± 1,17 milions (US $ 2,53 ± 1,36 milions) de beneficis econòmics directes per a la comunitat local, dels quals, els costos de menjar i allotjament representen, en conjunt, la major contribució als ingressos locals (Capítol 3). Aquests resultats mostren com aquest turisme específic, basat en aus carronyaires i desenvolupat en un entorn científicament controlat, podria complir amb els objectius, tant de l'estratègia de conservació basada en la comunitat (CBC), com de l'ecoturisme. A més, aquestes activitats recreatives (i.e. d'observació d'aus, educativa i fotografia controlada) podrien funcionar com a eines potencials per mostrar els CNP no materials de les aus carronyaires a la societat. La inclusió de la dimensió sociocultural en les estratègies de conservació és imperativa si volem que aquestes siguin reeixides a llarg termini. Els entorns en què les persones poden beneficiar-se dels CNP no materials proporcionats per les aus carronyaires són importants per apropar les espècies carronyaires a la societat, augmentant la consciència de la gent i el coneixement popular i ecològic del valor d'existència de les espècies i la seva funció ecològica (inclosa la seva provisió de CNP), promovent així una mentalitat favorable cap a aquest gremi. Necessitem una perspectiva integradora de sistema socioecològic actual per fomentar polítiques de conservació sostenibles que puguin assegurar la coexistència d'espècies carronyaires clau, com són els voltors i els grans depredadors, amb l'espècie humana.

GENERAL INTRODUCTION

Photo by Juan Carlos García Gómez.
Six adult griffon vultures in the Pyreneees.

General introduction

The role of conservation biology in the context of a global biodiversity crisis

Biodiversity losses for the mid-21st century have been predicted to be the extinction of about 30% of all species (Wilson 1992; Lawton & May 1995; Pimm *et al*. 1995). A massive degradation of habitat and extermination of many of the Earth's biota is taking place in our lifetime on an unprecedented short timescale staging what multiple scientists already name "the sixth mass extinction" (Barnosky *et al.* 2011; Pimm *et al.* 2014). Whether this trend began about 500 years ago (Pimm *et al.* 2014) or followed the losses befallen during the Pleistocene (Diamond 1989) remains to be seen. However, what the scientific community agrees on is that, unlike the previous five mass extinctions which occurred in the last 500 million years, humans have become a dominant evolutionary force in this new global biodiversity crisis (Pievani 2014). The anthropization of the planet has entailed habitat destruction and fragmentation, toxic pollutant release, overexploitation of resources (e.g. harvesting, fishing, and provisioning materials), and transport of invasive species; all in a climatic change scenario induced by greenhouse gas emissions which has unsurprisingly led to a massive decline in biodiversity (Ehrlich & Ehrlich 1981; Hughes *et al.* 1997; Vitousek *et al.* 1997). Beyond the uncertainties in Earth's species numbers and focusing on eukaryote organisms, by March 2014, the International Union for Conservation of Nature (IUCN) had assessed 71,576 mostly terrestrial and freshwater species among which threatened terrestrial species ranged from 13% (birds) to 41% (amphibians and gymnosperms) (IUCN 2014). In the same decade, Hoffmann *et al.* (2010) estimated a mean of 52 out of 22,000 species of mammals, birds, and amphibians that pass one Red List category closer to extinction each year. Accounting for these estimates, if human impacts expand at their present rate, many species not presently at risk will turn out to be threatened (Pimm *et al.* 2006).

Yet, ironically, humans are increasingly dependent on biodiversity, just as their well-being relies on the proper functioning of ecosystems (Millennium Ecosystem Assessment 2005; Guo *et al.* 2010; Hough 2014). Within this framework, conservation biology has essential work to do to ensure the future of our planet, including humanity. As a matter of fact, many biodiversity conservation accomplishments are already linked to this scientific branch. Hoffmann *et al.* (2010) calculated that were it not for conservation efforts, the rate at which mammals, birds, and amphibians have become extinct over the past four decades would have increased by 20%; and Pimm *et al.* (2006) estimated that the rate of extinctions per million species per year would be 150 E/MSY, at least three times higher than at present (< 50 E/MSY). At the same time, to confront habitat destruction (one of the major threats to species survival, IUCN 2014), conservation efforts have succeeded in increasing the < 4% of global land area protected in 1985, to 12.9% in 2009 (Jenkins & Joppa 2009). However, protected areas tend to be located where little human pressure on land degradation is exerted, covering from 4% to 25% of the 14 major biomes and < 10% of half of the 821 terrestrial ecoregions (Joppa & Pfaff 2009). Additionally, comparing these areas with some species distribution, 27% of threatened amphibians, 20% of threatened birds, 14% of threatened mammals, and 10% of threatened turtles live outside protected areas (Rodrigues *et al.* 2004). In particular for birds, only 49% of sites documented to hold the entire population of at least one highly threatened species (Ricketts *et al.* 2005) and 51% of globally important sites for birds (Butchart *et al.* 2012) are included in these protected regions (Pimm *et al.* 2014). As a result, most indicators of the state of biodiversity (e.g. covering species' population trends, extinction risk, habitat extent and condition, and community composition) show a decline with no recent significant reductions in rate, whereas indicators of pressures on biodiversity (e.g. resource consumption, invasive alien species, nitrogen pollution, overexploitation, and climate change impacts) are increasing (Butchart *et al.* 2010).

More research in basic biological and ecological science is imperative to build up the fundamentals of an effective conservation strategy in order to maintain as many of the existing living organisms and ecosystem functioning as possible. This is necessary in order to manage to understand and know the biological features of the species, and the ecological interactions that allow us to improve our knowledge about interrelations between different living beings, both among themselves and with their surrounding environment.

Birds as fundamental pieces of ecosystems

Birds are one of the best-known classes of vertebrate animals. There is a strong active social interest in these worldwide visually and acoustically notorious animals inhabiting nearly all habitats, including those highly altered by humans (Şekercioğlu 2003; Whelan *et al.* 2008; Wenny *et al.* 2011; Leong *et al.* 2020). All ≈ 10,000 species of birds already described are mobile agents that function as mobile links, connecting different types of habitats in time and space (Lundberg & Moberg 2003; Şekercioğlu 2006). This, among other biological and behavioural traits (e.g. movements, diet, etc.), makes them play certain ecological roles in nature, providing many services (either positive or negative) that were firstly appreciated by humans when they were related with both insects and plants (more specifically, bird-agriculture relationships) (Whelan *et al.* 2015). Their scientific species description started in the 1700s, exponentially increased during the 19th century, and then stabilized during the present century (figure 1, Pimm *et al.* 2006). However, birds were considered to contribute rather little to overall ecosystem productivity (Wiens 1973; Holmes & Sturges 1975) and their impact on ecosystem functioning was not studied until the last four decades. Nowadays, we have a much greater appreciation of the ways that birds function within numerous ecosystems around the world, playing roles such as predators, pollinators, scavengers, seed dispersers, seed predators, and ecosystem engineers (Şekercioğlu 2006; Whelan *et al*. 2008).

However, as a result of the global change some researchers have predicted an intermediate extinction range from 1.3% (1.1°C warming) to 30% (6.4°C warming) of 3,349 land bird species studied from the Western Hemisphere (Şekercioğlu *et al.* 2008) and variations larger than 50% of some species distribution ranges from certain avian dominated areas (Jetz *et al.* 2007; La Sorte & Jetz 2010), the ecological benefits that these species provide to humanity being at risk also with these distribution changes (Şekercioğlu 2006; Whelan *et al.* 2008). From among the major causes of extinction, introduced species (including diseases) —another significant component of human-caused global change— seem to be the main trigger of recent bird extinctions (Birdlife International, 2014). Thus, human impacts need to be considered at least as influential as natural processes on biodiversity extinction rate drivers.

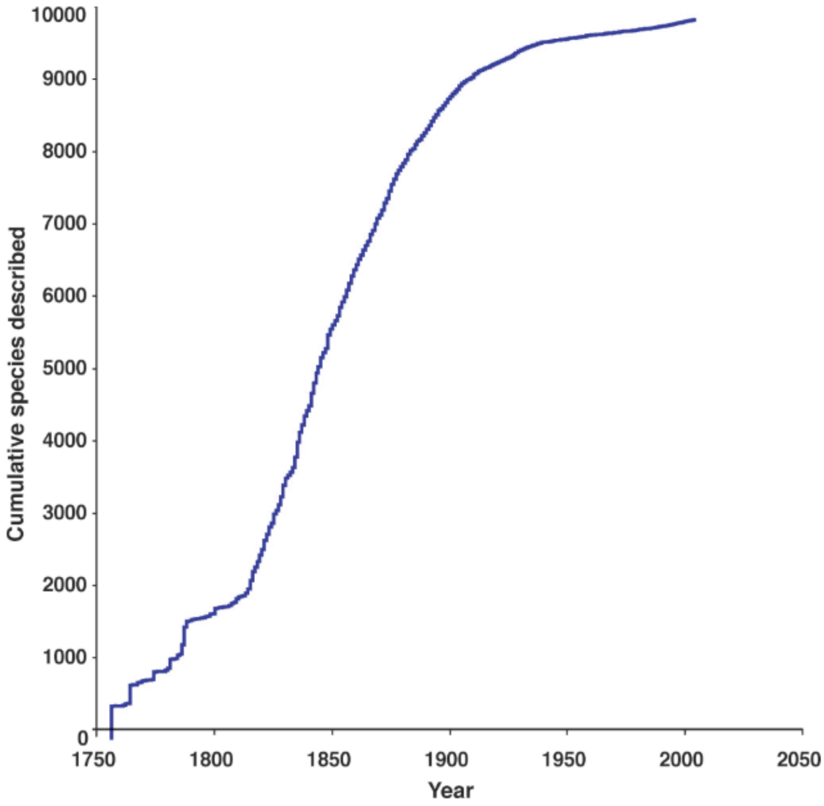


Figure 1 | Dates of description of the world's bird species. Source: Pimm *et al.* 2006.

Besides anthropic habitat degradation and the introduction of invasive species, direct human persecution has supposed (and still continues to cause) multiple species exterminations and significant population decimation not only for birds (Gittleman *et al.* 2001; Darimont *et al*. 2015; Brochet *et al.* 2019), but also, especially, for the meso and megafauna, such as large mammals and birds of prey (Taylor & Dunstone 1996; Bijleveld 1974; Bildstein 2008; Madden *et al*. 2019), thus including scavenger species (Reynolds & Tapper 1996; Ogada *et al*. 2012a). In addition, large-bodied animals generally presenting a low intrinsic rate of population increase (r) because of low fecundity, high adult survival, and long generation times, that require vast home ranges and occur at lower densities, have been proved to be more susceptible to extinction when it concerns this kind of human perturbation (Beissinger 2000). Paradoxically, several of these species remained barely studied, or even socially inconspicuous (probably due to historical human-wildlife conflicts with apex predators and to human aversion to dead flesh, in the case of scavengers), and have become critically endangered. Therefore, the current delicate status of these worldwide species calls for our ethical responsibility. They require a society wildlife conduct reorientation toward human environmental commitment. A deeper knowledge of their biology (e.g. life history traits, behavioural patterns, etc.) and ecological interactions is needed to ensure their future subsistence and population viability.

Scavengers' biological and behavioural features and conservation

Scavenging as a life strategy

A scavenger is any organism that feeds on dead organic matter such as dead animals or plants and did not kill (Schmitz *et al.* 2008; Campbell 2015; Benbow *et al.* 2019). Then, decomposers and detritivores complete this process by consuming the remains left by scavengers. However, this feeding behaviour (i.e. scavenging) is practised by organisms classified as scavengers, predators and omnivores. Therefore, how can all these feeding strategies coexist? The explanation lies in the fact that species that scavenge can be differentiated according to two major functional groups: obligate scavengers, which depend entirely on carrion for survival and reproduction, and facultative scavengers, that do not rely on carrion as their only food livelihood and only scavenge opportunistically (DeVault *et al.* 2016; Campbell 2015; Olea *et al.* 2019). Focusing on vertebrates, vultures are the only obligate scavengers known so far, while facultative scavengers are much more diverse, including mammalian carnivores, suids, raptors, gulls, and most corvids (DeVault *et al.* 2003; Mateo-Tomás *et al.* 2015, 2017; Moleón *et al.* 2014a; Pereira *et al.* 2014; Moreno-Opo *et al*. 2016).

Nowadays, 23 vulture species live all around the world: 16 from the *Accipitridae* family inhabiting the Old World and 7 from the *Cathartidae* in the New World (figure 2). Old World vultures present biological features like bills, feet and talons that position them closer to the Accipitrid raptors (hawks and eagles) than New World vultures. Still, different species appear to have different links with other raptors. Some studies based on behavioural and eco-morphological features propose competition as the main factor structuring scavengers' evolution (Attwell 1963; Kruuk 1967; König 1974, 1976; Alvarez *et al.* 1976; Grubh 1978; Mundy *et al.* 1992). Consequently, we can assume that "vulture" is more an ecological than a systematical concept (Wink 1995; Storch *et al*. 2001; Wink & Sauer-Gürth 2004). Therefore, vultures are morphologically and physiologically adapted for feeding on carcasses, showing acidic stomachs (as low as pH = 1) that probably help to decrease the pathogenic risk of high microbial loads (Houston & Cooper 1975), present feet more adapted to walking on the ground than grasping prey, and generally bare skin or down-covered heads, that

Figure 2 | Global distribution and conservation status of all 23 vulture species existing in the world. IUCN Red List categories at the global scale were used: least concern (LC, green), near threatened (NT, yellow), vulnerable (VU, orange), endangered (EN, red), and critically endangered (CR). Dashed lines were used when vultures presented breeding populations only located on one continent and solid lines for those species with breeding populations on more than one. Clockwise — New-World vultures: Andean condor (*Vultur gryphus*), greater yellow-headed vulture (*Cathartes melambrotus*), king vulture (*Sarcoramphus papa*), lesser yellow-headed vulture (*Cathartes burrovianus*), Turkey vulture (*Cathartes aura*), California condor (*Gymnogyps californianus*), and black vulture (*Coragyps atratus*). Old-World vultures: Eurasian griffon (*Gyps fulvus*), Egyptian vulture (*Neophron percnopterus*), cinereous vulture (*Aegypius monachus*), long-billed vulture (*Gyps indicus*), Himalayan griffon (*Gyps himalayensis*), red-headed vulture (*Sarcogyps calvus*), white-rumped vulture (*Gyps bengalensis*), Indian vulture (*Gyps indicus*), palm-nut vulture (*Gypohierax angolensis*), lappet-faced vulture (*Torgos tracheliotos*), Cape griffon (*Gyps coprotheres*), Rüppell's griffon (*Gyps rueppelli*), white-headed vulture (*Trigonoceps occipitalis*), hooded-vulture (*Necrosyrtes monachus*), white-backed vulture (*Gyps africanus*), and bearded vulture (*Gypaetus barbatus*). Sources: Birdlife International (2016-2020) and IUCN (2020).

reduce fouling while feeding (Houston 1979), except for the cases of the bearded vulture (*Gypaetus barbatus*) and palm-nut vulture (*Gypohierax angolensis;* Campbell 2015). They also show a keen sense of sight and/or smell (depending on the species) that helps them to find the carcasses or rotten fruits from greater distances (Houston 1979; DeVault *et al*. 2003; Potier *et al.* 2019). In addition, Ruxton and Houston (2004) evinced that, due to energy constraints, obligate vertebrate scavengers must be large soaring birds presenting efficient flight patterns that allow them to cover great home ranges that make up for the temporal and spatial unpredictability of the carrion.

Conservation and main threats

While facultative scavengers frequently present widespread distribution, obligate scavengers, which are much less numerous from the baseline, are among the most threatened functional groups worldwide (Şekercioğlu *et al*. 2004; Ogada *et al*. 2012a, 2016; Buechley & Şekercioğlu 2016). In fact, 57% of the obligate avian scavengers of the world are currently threatened with extinction (69% of the *Accipitridae* vultures and 29% of the *Cathartidae*), being classified according to the IUCN Red List categories (IUCN 2020) as seven in least concern (LC), three near threatened (NT), one vulnerable (VU), three endangered (EN), and nine critically endangered (CR) (figure 2).

The main causes of large avian scavengers' high non-natural mortality rates are originated by anthropogenic disturbances such as intoxication and poisoning (indirectly by the ingestion of fragmented lead bullets located in human hunting preys, or residues of veterinary drugs —e.g. non-steroidal anti-inflammatory drugs like diclofenac, ketoprofen, nimesulide, aceclofenac, or flunixin—; or intentional and unintentional poisoning), habitat loss and degradation resulting from human transformation (collision with wind turbines and power lines, and electrocution on the cables or dangerous pylons that hold them), food shortage (due to a decline or abandonment of traditional farming practices, or public health policy measures) and, as mentioned before, human persecution (e.g. Real *et al*. 2001; Whitfield *et al*. 2004a; Martínez *et al*. 2006; González *et al*. 2007; Kalpakis *et al*. 2009; Schaub *et al*. 2010). Among these factors, intended and unintended poisoning is at the present time probably the most worryingly and prevailing mortality cause for many populations of large raptors around the world (Whitfield *et al*. 2004b; Wobeser *et al*. 2004; González *et al*. 2007; Margalida 2012). In particular, the deliberate intoxication of carnivores with poisoned carcasses to manage game species and protect livestock (a common although illegal practice in most of the countries) is likely the most widespread cause of avian scavenger non-natural mortality worldwide (Donázar 1993; Ogada *et al*. 2012a; Margalida *et al*. 2019). Furthermore, vultures are particularly vulnerable to this threat due to their frequent behaviour of feeding communally since multiple individuals can be poisoned by the same carcass.

Like other animals from the high trophic levels, scavengers are highly exposed to the effect of accumulation of substances such as heavy metals (Pattee *et al.* 1981; Carpenter *et al*. 2003; Gangoso *et al.* 2009), pesticide residues from agriculture (Houston 2001), or drugs of veterinary origin (Oaks *et al*. 2004, Shultz *et al.* 2004, Naidoo *et al.* 2009). These toxicants generate lethal, but also sublethal effects that significantly influence the fitness of the species (Steidl *et al.* 1991; Kumar *et al.* 2003). However, the susceptibilities to these intoxicating substances are not consistent among all avian scavengers. One example is the known case of the sharp decline estimated as more than 95% of the *Gyps* vulture populations, which occurred in Asia almost three decades ago because of indirect poisoning through consumption of livestock carcasses treated with diclofenac (Green *et al.* 2004; Oaks *et al.* 2004; Shultz *et al.* 2004). Notwithstanding such a devastating precedent, in 2013 diclofenac was authorized in Spain and in 2020 the first vulture (a cinereous vulture) poisoned with this drug in Europe appeared (Herrero-Villar *et al*. 2021; Margalida *et al*. 2021). Other non-steroidal anti-inflammatory drugs (NSAID), such as ketoprofen, carprofen, flunixin, phenylbutazone and ibuprofen, have also been proved to be toxic for vultures and other facultative avian scavengers (Cuthbert *et al*. 2007; Cuthbert *et al*. 2014; Herrero-Villar *et al.* 2020).

The chain of secondary poisoning has also caused the decline of vulture populations in Africa over the last twenty years (Buechley & Şekercioğlu 2016; Ogada *et al.* 2016; Safford *et al*. 2019). Also, linked to the recent increase in rhino and elephant poaching across the continent, intentional poisoning of vultures is rising to prevent their circle-flying behaviour over the carcasses from leading authorities to the crime site (Ogada *et al.* 2015). The toxin mostly used for this poisoning is *Carbofuran, a* cheap and highly toxic easy-to-buy insecticide, although sadly several other toxicants, such as *Strychnine* and synthetic organic pesticides, have been used throughout Africa (Ogada 2014; Santangeli *et al.* 2017; Richards *et al.* 2018).

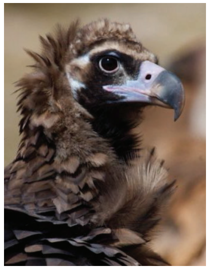
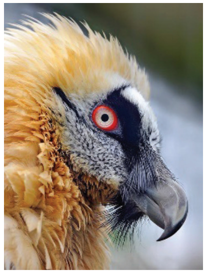
In contrast to the current critical situation of Asian and African vulture populations (Ogada *et al.* 2016; Buechley & Şekercioğlu 2016; Safford *et al.* 2019), Western Europe seems to be maintaining a recovery trend among obligate scavenger populations (BirdLife International 2017a; Deinet *et al*. 2013). The end of the legal hunting of “any meso and great predator who menaced the livestock” (which inconsistently included obligate scavengers) in the 1960s-1970s —with the consequent restriction of scientific collecting (e.g. Chapman & Buck 1893, 1910; Hiraldo *et al.* 1979)— and the later ban on poison utilization during the 1980s-1990s (Donázar 1993) allowed, in conjunction with the European Union conservation policies undertaken between the late 20th century and the beginning of the 21st (Donald *et al*. 2007) (e.g. Birds Directive 2009/147/EC and Habitats Directive 92/43/EEC), the improvement of the conservation status of all four European vulture species at the continental level (Margalida *et al.* 2010). See table 1 for the current conservation status of these scavenger species.

Scavenger conservation status in Spain

Of all European countries, Spain today boasts the most important breeding populations of these vulture species; in particular, more than 90% of the European breeding populations of cinereous (*Aegypius monachus*), 90% of the Eurasian griffon (*Gyps fulvus*), 82% of the Egyptian (*Neophron percnopterus*), and 63% of the European bearded vultures (Margalida *et al*. 2010; del Moral 2017; del Moral & Molina 2018a; del Moral & Molina 2018b; Margalida & Martínez 2020). In addition, multiple facultative avian scavenger species are present in the country, as is the case of several raptors like golden eagles (*Aquila chrysaetos*), Spanish imperial eagles (*A. adalberti*), black kites (*Milvus migrans*), red kites (*M. milvus*), common buzzards (*Buteo buteo*) and Western marsh harriers (*Circus aeruginosus*), corvids such as common ravens (*Corvus corax*), carrion crows (*Corvus corone*), Eurasian jays (*Garrulus glandarius*), and common magpies (*Pica pica*), and seabirds such as yellow-legged gulls (*Larus michahellis*) (see Moreno-Opo *et al.* 2016). Among mammalian facultative scavengers inhabiting Spain, we find carnivores such as brown bears (*Ursus arctos*), grey wolves (*Canis lupus*), Iberian lynxes (*Lynx pardinus*), red foxes (*Vulpes vulpes*), stone martens (*Martes foina*), pine martens (*M. martes*), common genets (*Genetta genetta*), Eurasian badgers (*Meles meles*) and Egyptian mongooses (*Herpestes ichneumon*), and omnivores such as wild boars (*Sus scrofa*), mostly traditional game species (Mateo-Tomás *et al.* 2015; 2017; Morales-Reyes 2018).

However, the recent history of the human-wildlife relationship in Spain has also been complicated. Coupled with the European intensive persecution of birds of prey promoted since the end of the 20th century, in 1953 Spain created 23 “*Juntas Provinciales de Extinción de Animales*

Table 1 | Conservation status for the four European vultures at a global, European and national (i.e. Spain) level. IUCN Red List categories were used: least concern (LC, green), near threatened (NT+, yellow), vulnerable (VU++, orange), and endangered (EN+++, red). For the national level, we used the *Spanish List of wild species in a special protection regime and the Spanish List of threatened species* both established in RD 139/2011 (*SLWSSPR & SLTS RD 139/2011*), that included the categories of not-threaten (NotT, green), vulnerable (as in the IUCN Red List categories, VU++, orange), and in danger of extinction (EN+++, red). Colours were assigned depending on category conservation priority, ranging from "lower" to "higher" threat degree.

Scope of assessment	 *Gyps fulvus*	 *Aegypius monachus*	 *Neophron percnopterus*	 *Gypaetus barbatus*	**Bibliography**
	LC	NT^{+}	EN^{+++}	NT^{+}	BirdLife International 2017b, 2017c, 2018, 2019
	LC	LC	EN^{+++}	VU^{++}	BirdLife International 2015a, 2015c-d
	NotT	VU^{++}	VU^{++}	EN^{+++}	SLWSSPR & SLTS RD 139/2011

Dañinos y Protección a la Caza" (Regional boards for the extinction of harmful animals and hunting protection), implementing the slaughtering of diverse carnivores and birds of prey as a systematic practice (Corbelle-Rico & Rico-Boquete 2008; Márquez Cañas 2015). Among other ordeals, between 1955 and 1961 the Spanish government paid for the carcasses of 784 vultures, 1,033 eagles, 20,228 other raptor types and more than 500,000 other birds (including corvids and non-identified raptors) in 10 provinces of Spain, representing 27 % of the country surface area (Anonym, 1962). Human pressure led to an acute decline of the main apex predators presented in Spain (both avian and mammalian, including multiple facultative scavengers) and the four aforementioned obligate scavenger species. At the same time, vulture population declines corresponded in time with a progressive regression of traditional extensive farming practices. Thus, it was popularly claimed that carrion shortage from domestic livestock was also an unequivocal cause of their population detriments, even if it was proved not to be a sustained statement (Donázar *et al.* 2009a; Donázar & Fernández 1990). Fortunately, within the framework of the European conservation policies established during the late 20th century, Spanish national legislation followed the hunting prohibition, poison ban, and species legal protection inertia, setting a departure point to reverse the declining tendency of the national mega and meso-fauna of the time (Donázar 1993).

One of the most widespread conservation actions practised for the recovery of decimated scavenger populations during the second half of the 20th century was the creation of supplementary feeding sites (SFS), so-called vulture restaurants, or feeding sites, stations, or points (Mundy *et al*. 1992; Donázar *et al.* 2009a). The rapid adaptation of avian scavenger to this habitat transformation and relatively low cost of the SFS encouraged public administrations and wildlife managers to invest in this conservation tool (Donázar *et al.* 2009a; Moreno-Opo *et al*. 2015). Nonetheless, the recent steep drop in African and Asian vulture populations evince how sensitive these large-bodied K-strategist species (see Pianka 1970 for a detailed explanation on K-strategy evolutive selection) characterized by low fecundity and high survival rates are to sudden non-natural mortality factors especially affecting adult mortality, regardless of food availability (Donázar 1993; Oaks *et al.* 2004; Green *et al.* 2006; Acharya *et al.* 2009; Ogada *et al.* 2016; McClure *et al.* 2018).

For instance, in Spain —where we find the largest European vulture population (more than 60%; Margalida *et al*. 2010) and many of the largest populations of large carnivores (usually also facultative scavengers) in Western Europe (some even threatened e.g. brown bears and grey wolves; Chapron *et al.* 2014) —, there has been a large SFS network in operation since the 1960s (Donázar 1993). Despite the plentiful carrion supply in the last 70 years in the Peninsula, three of the four European obligate scavengers remain at risk of extinction, these being the cinereous and the Egyptian vultures, vulnerable, and the bearded vulture, endangered at the national level (table 1; Spanish List of wild species in a special protection regime and the Spanish List of threatened species established in RD 139/2011). In particular, the case of the bearded vulture in the Pyrenees has been slightly more frequently studied, given that the construction of SFS (among which, some were —and still are— specifically aimed at just this species) close to their territory during some months after the hatching has been a resource frequently employed for the conservation of the species. Scientists have suggested that the aggregating effect of SFS may be contributing to the lack of geographical expansion and declining breeding output of the species. These SFS would cause the loss of habitat quality due to a conspecific attraction and consequent shrinkage of territories and increase in intra-specific competition (Carrete *et al.* 2006a, 2006b).

Despite these few recent studies, lots of the basic biological and behavioural traits of the bearded vulture remain unknown (e.g. animal physiology, population dynamics, regional mortality hotspots, etc.). Scientific research focused on this critical endangered species has been produced for 40 years now. Long-term studies that include the main species' biological traits, its behavioural patterns in this highly anthropized environment and the current ecological role of the species in nature and society, are urgently needed if we want to efficiently lead conservation investments for the species. Considering that the largest population of bearded vultures from Europe inhabits the Pyrenees (365 adult breeding birds in 2016; Margalida *et al*. 2020), and that is the only one on the continent which is naturally viable (i.e. self-sustaining, without the need for human intervention), more studies should be developed to understand the wild species' biological traits and behaviour (e.g. foraging and reproductive patterns) and to discover the specific threats that the species could be facing here. This would give us the opportunity to care for species survival and thus assure ecosystem sustainability.

Outline, structure, and objectives of the thesis

Detailed knowledge of the behavioural ecology and demographic parameters of species is imperative to apply management and conservation measures in threatened taxa, as occurs with the bearded vulture. The limited distribution range of the species since the end of the 20th century and the restrictive ecological requirements of this cliff-nesting vulture explain why the information on the wild populations of this peculiar large-bodied animal has traditionally been notoriously scarce (Hiraldo *et al*. 1979; Heredia & Heredia 1991; Bustamante 1996; Brown 1997; Margalida 2010). Notwithstanding the difficulty involved in gathering detailed data from wild populations, significant conservational efforts (mainly consisting of both economic and human contributions through reintroduction programmes and recovery plans) have already been developed in pursuit of restoring the widespread distribution and general populations' health for this species (Hiraldo *et al.* 1979; Brown 1988; Heredia & Heredia 1991; Terrasse 2001; Margalida & Heredia 2005). However, neither the social fabric where these conservation measures and management plans concerning the bearded vulture have been implemented, nor their public acceptance and impact on human population, have ever been evaluated.

This thesis uses as its model species the bearded vulture, one of the most endangered scavengers in Europe, investigating in detail its movement ecology in the Pyrenees, as well as the role that this species, along with the most common Pyrenean avian scavengers, plays in society, its acceptance and the perception that the entire avian scavenger guild inspires in certain stakeholders of society (i.e. avian scavenger tourists). The description and analysis of some basic behavioural traits (i.e. movement patterns) from the only viable population of bearded vulture in Europe, together with the evaluation of the social impact that this vulture, as well as other Pyrenean avian scavengers, has nowadays in the region, represent a meaningful and necessary knowledge that can be used to its advantage by developing powerful tools in the context of conservation biology.

The present PhD dissertation is composed of a compilation of various research articles that contribute to this previously outlined knowledge gap related with the study and analysis of basic behavioural and life history traits (*Chapters 1 and 2*) and the contributions provided and cultural role played by the bearded vulture and other avian scavengers in our current society (*Chapters 3 and 4*). The information in this thesis is structured by a general *Introduction*, a general overview of the *Materials and methods* used for the data collection and analyses, four chapters presented in the form of scientific research articles (*Chapters 1-4*) as the main body of the manuscript, an overall *General discussion*, and a closing section containing the main conclusions of the thesis (*Conclusions*). Finally, a *Bibliography* composed of all the references of the *Introduction*, *Materials and Methods* and *Discussion* is included. The *Supplementary Information* of each of the chapters can be found at the end of the dissertation, as well as two different *Appendices*: an *Appendix I* containing the three original publications corresponding to the first three chapters of this thesis and an *Appendix II* with a published research article complementary to the subject of this dissertation. All the chapters are organized following the same systematical structure officially accepted for any scientific work published in a scientific journal. On this account and to facilitate the reading comprehension of this thesis, each chapter includes its own *References* section containing all the bibliography cited in the respective texts. Thus, references may be repeated in different chapters.

The four main chapters are divided into two differentiated sections corresponding to two different research fields according to the following scheme:

Chapter distribution:

Movement ecology

- **Chapter 1**: Influence of individual biological traits on GPS fix-loss errors in wild bird tracking
- **Chapter 2**: Drivers of daily movement patterns affecting an endangered vulture flight activity

Ecosystem services

- **Chapter 3**: Economic valuation of non-material NCP to people provided by avian scavengers: Harmonizing conservation and wildlife-based tourism
- **Chapter 4**: Avian scavengers' Contributions to People: the cultural dimension of the wildlife-based tourism.

Chapters 1 and 2 are included within the movement ecology framework, a helpful tool in behavioural ecology that is spearheading much of the current scientific biological research in animal ecology. Likewise, *Chapters 3 and 4* form part of the ecosystem services domain, a relatively recent area in ecology, that tries to showcase the value that all ecosystem processes —and by extension, the ecosystems themselves— represent for human society. Both areas of expertise currently constitute priceless useful tools in conservation biology that play key roles in ensuring a sustainable and efficient conservation policy and management strategy for any threatened constituent piece of ecosystems. Hence, in these four research chapters some examples of the ecology of movement and ecosystem services disciplines' scope and applicability using avian scavengers, and particularly the endangered bearded vulture as the model species are shown. Below is a more detailed explanation of the chapters' scope.

The importance of the movement ecology

All the resources required by any living organism are heterogeneously distributed in time and space. Consequently, the position that an individual occupies in the landscape affects its chances of survival and reproduction and, with it, the dynamics of the populations (Hawkes 2009; Morales *et al*. 2010), the spread of diseases (Fèvre *et al*. 2006) and biological invasions (Cote *et al.* 2010). The movement ecology seeks to study how the species move within their habitat and in relation to other individuals. A movement is defined as any position change of either an individual, or a total or partial population (Hansson & Åkesson 2014). The completion of these movements implies a considerable individual investment of time and energy, occasionally even requiring the existence of specific morphological adaptations (e.g. legs, hoofs, fins, and wings, the latter involving the additional cost of feather shedding; Lindström *et al.* 1993; Barta *et al.* 2008; Hansson & Åkesson 2014; Coper & Blumstein 2015). Sometimes such is the energy cost that it has even been related with a reduction of fecundity in some long-distance migrant animals (Bruderer & Salewski 2009). Therefore, movement conditions the life strategy of living organisms, allowing them to reach food or habitat resources, avoiding predation and finding the optimal breeding territories. In this respect, our ability to understand ecosystem processes and undertake effective management and wildlife conservation depends, to a large extent, on our ability to interpret animal movement at the individual level.

Nevertheless, organisms' movements are complex phenomena that result from the interaction between both intrinsic and extrinsic factors (Nathan *et al.* 2008). For instance, the physiological state initially determines the individual priorities and motivations for moving to attend to some of their basic biological requirements (e.g. feeding, breeding, or seeking refuge), and then this movement is constrained by the individual morphology, especially their locomotive system characteristics (Dickinson *et al.* 2000). Movement decisions are therefore made based on intrinsic factors, but also conditioned by the physical and biotic attributes of the environment, such as relief, climate, air drafts, or the presence of predators, among others (Fortin *et al.* 2005; Boyle *et al.* 2010; Bohrer *et al.* 2012).

The movement study has been experiencing a strong boost since the end of the 20th century due to an improvement of the data sources resulting from technological upgrading (Davis 2008; Holyoak *et al.* 2008; Nathan *et al.* 2008; Gimenez *et al*. 2014). In particular, satellite telemetry has revolutionized the movement ecology (Cooke *et al.* 2004; Cagnacci *et al.* 2010). This technique enables the gathering of huge amounts of accurate data on animal movement with an unprecedented spatio-temporal resolution, informing about the animal positions in a wide diversity of environments (Rutz & Hays 2009; Urbano *et al.* 2010; Bouten *et al.* 2013). This information can then be combined with diverse environmental data measured at different scales of space and time through remote sensing (Horning *et al*. 2010). As a result, these new technologies have increased the quantity and quality of movement ecology databases providing essential information on animal ecology and behaviour, including a species' detailed patterns of spatial use (Nathan *et al.* 2008; Schick *et al.* 2008; Morales *et al.* 2010).

In this context, *Chaper 1* of this thesis evaluates the possible effects of the biological traits of a large raptor on the correct operation of the satellite technology used to track its movement. We also describe the influence that technical and geographical parameters are currently exercising on the position data record. This type of studies assessing the efficacy and potential bias of the animal telemetry tracking devices is fundamental to reach any ecological conclusions or hypotheses regarding spatial utilization, since the results can vary substantially depending on extrinsic factors (i.e. GPS transmitter model, retrieval data system, PTT usage time, season, etc.), or biological factors (such as those analysed in this study). All of these changing elements can influence the data collected and lead to errors in interpreting patterns of movement. At the same time, in *Chapter 2* we wanted to analyse the patterns of spatial use of the bearded vulture, especially important information to optimize the design of conservation and management strategies for endangered species, as is the case for our studied species. In particular, we evaluated the main drivers of the daily patterns in the daytime flight routine of the threatened bearded vulture, considering the possible influence of both internal and external factors. Understanding these basic behavioural traits is essential to predict the future dispersal, foraging and reproductive patterns of the Pyrenean population of bearded vulture, all indispensable data to develop future conservation strategies.

Ecosystem services in scavenging world

Humans depend on the ecosystems for life. This is a popularly known statement, but, paradoxically, our species does not always care about nature's health state (Newbold *et al.* 2015; Venter *et al.* 2016). From this perspective, ecosystem services play a fundamental role (Folke *et al.* 2011; Luck *et al.* 2012). This was a term formalized in 2005 by the Millennium Ecosystem Assessment (MEA 2005), based on the concept first called "nature's services" by Westman (1997). The primary term was created to conceptualize the dependence of human well-being on the maintenance of ecosystem functioning. Thus, ecosystem services were defined as the benefits that humans obtain from ecosystems (MEA 2005; Costanza *et al.* 2017). Even if this concept has been questioned for its anthropic reductionism of ecosystems, nature commodification, and the exploitative perspective with which it could be used (e.g. McCauley 2006; Brockington *et al.* 2008; Redford & Adams 2009), its value as a conservation tool is self-evident (see review in Costanza *et al*. 2017). Unavoidably, social and ecological systems have been intertwined ever since humans inhabited the planet and therefore the separation of these two spheres is unsubstantiated and artificial (Berkes & Folke 1998). In this light, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) recently gave another turn of the screw in the ecosystem services concept and introduced the term "nature's contributions to people (NCP)", which comprises both beneficial and detrimental effects of living nature on people's quality of life and considers the social systems as the matrix where all NCP occur (Díaz *et al.* 2018). Regarding their classification, three overlapped groups are proposed, called "provisioning services" (e.g. food and water), "regulating services" (e.g. flood and disease control), and "cultural services" (e.g. recreation, ethical and spiritual, educational, and sense of place) (Díaz *et al.* 2018).

Bearing this socio-ecological perspective in mind, we can confirm that scavengers provide human society with indispensable ecological services, recycling carrion biomass through the removal of waste and preventing the accumulation of dead animal biomass, thus reducing the spread of diseases and contributing to nutrient cycling (DeVault *et al*. 2003; Swan *et al*. 2006; Markandya *et al.* 2008; Ogada *et al*. 2012b; DeVault *et al.* 2016; O'Bryan *et al.* 2018). Evincing this, Markandya *et al.* (2008) estimated the human health cost of the vulture decline in India. They calculated the monetary costs (i.e. medicines, doctor remuneration, and work compensation) associated with human rabies transmitted by feral dog bites, which increased dramatically following the vulture population declines in the Indian subcontinent (around 95% of its population), at an estimated annual average of US$2.43 billion. Indeed, the NCP provided by this guild have benefited our species from the very first biped hominids (Moleón *et al*. 2014b; Morelli *et al.* 2015). Especially since the Late Pliocene (when our ancestors started to eat meat), humans and vertebrate scavengers have been directly interdependent (Moleón *et al.* 2014b). Besides the regulating NCP already mentioned, humans have, for example, traditionally obtained different ornamental resources, such as feathers, from scavengers (a material NCP) (Finlayson *et al.* 2012). Archaeological finds in Çatal Hüyük and Göbekli Tepe, in the Konya Plain (Turkey) suggest that Old World vultures have been revered in cultures ever since the Neolithic (6,000–3,000 years B.C.) (Mellaart 1963; Peters & Schmidt 2004). The wall drawings and grave positions suggest that in the early Neolithic culture of Anatolia, the recently deceased were deliberately exposed in order to be consumed by vultures and other avian scavengers. This practice would be similar to the one called "sky burials" of Buddhists in Tibet and some parts of Nepal (e.g. Mustang, Dolpa and Menang) and by Zoroastrians (Parsees) in Iran and India, already fallen into disuse (Markandya *et al.* 2008). In Hindu mythology, *Jatayu* –the vulture god– sacrificed his life to save the goddess *Sita* from the evil ten-headed demon *Ravana* (Markandya *et al.* 2008). In Maasai culture there are still some specific songs warriors sing to vultures as they prepare to attack and raid their enemies (Reson 2012) and vultures are also considered goodwill messengers. showing where missing cattle are located (Cortés-Avizanda *et al.* 2016). In ancient Egypt, *Nekhbet*, the vulture, along with the cobra, symbolized the unity of Upper and Lower Egyptian civilizations.

Scavengers have also recently been recognized as contributing to the long-term maintenance of soil structure (Wilson & Wolkovich 2011; Beasley *et al*. 2015) and reducing environmental pollution (Markandya *et al*. 2008; Morales-Reyes *et al*. 2015) thanks to their ability to dispose of waste and organic matter. For instance, it has been estimated that Spanish vultures alone remove 134-201 tons of bones and 5,500 - > 8,000 tons of meat from livestock carcasses per year, preventing release of greenhouse gases and providing estimated economic savings of up to €1.5 million ($1.86 million) (Margalida & Colomer 2012). In fact, Morales-Reyes *et al.* (2015) estimated that supplanting the natural removal of extensive livestock carrion by scavengers with carcass collection and transport to authorized plants in Spain led to annual emissions of 77,344 metric tons of CO_2 eq. to the atmosphere and payments of about $50 million to insurance companies.

Scavengers have traditionally provided important ecosystem services, helping control disease and pests, recycling nutrients, and providing cultural inspiration and recreational value. However, contrary to their regulating and material NCP, not much has been studied or measured about their cultural contributions (i.e. non-material NCP) to society, or their social role (see the few examples found in recent literature from Becker *et al.* 2005; Willemen *et al.* 2015; Aguilera-Alcalá *et al.* 2020; Echeverri *et al.* 2020). *Chapters 3 and 4* of this PhD dissertation try to solve this knowledge divide by focusing on evaluating and quantifying from different approaches how the cultural role of avian scavenger influences our society. To do so, in *Chapter 3* an economic evaluation of non-material contributions to people provided by avian scavengers through birdwatching tourism in the Pyrenean SFS is performed. In this work we propose a way to harmonize both nature conservation and economic development based on avian scavenger recreational and educational activities. *Chapter 4* deals with the socio-cultural dimensions of biodiversity conservation through the evaluation of SFS visitors' perceptions of avian scavengers as NCP providers. We identify and value the NCP provided by the European avian scavengers through a recreational activity (i.e. wildlife-based tourism) at the SFS in the Pyrenees. In addition, we describe the working strategies —beyond the originating conservative purposes— of the currently existent Pyrenean SFS, characterize the type of public visiting these SFS, and describe and analyse the perceptions, interest and knowledge of European avian scavengers held by SFS visitors. The findings of these two works should be used to highlight the important role of avian scavengers in providing non-material NCP through recreational/ educational activities to human population and hence as a tool to integrate the social sphere in biodiversity conservation.

Objectives

The **main aim** of this PhD dissertation was both to study poorly known aspects of the movement ecology of the Pyrenean bearded vulture population and the cultural services provided by the avian scavenger guild from a socio-ecological perspective in order to ensure the efficacy and strengthen future conservation strategies aimed at these scavenger species. To this effect, we used the approaches of the movement ecology and ecosystem services to address the following **specific objectives**:

1. Determine the drivers of the daily flight patterns of the Pyrenean bearded vulture population through reliable satellite telemetry data (*Chapters 1 and 2*). To this end, we aimed to investigate:
    - **I.** the potential influence of both internal (i.e. biological) and external (i.e. environmental) factors on the flight activity of the bearded vulture;
    - **II.** the potential influence of both internal (i.e. biological and behavioural) and external (i.e. technical and environmental) factors on the correct operation of the bird transmitters;
    - **III.** the potential influence of both internal (i.e. biological) and external (i.e. environmental) factors on the daily movement patterns of the Pyrenean population of bearded vultures
2. Assess and showcase avian scavenger non-material NCP (i.e. recreational and educational experiences) through an economic valuation of the monetary benefits provided by European avian scavenger tourism at Pyrenean supplementary feeding sites (SFS) (*Chapter 3*).
3. Identify and assess the NCP provided by the European avian scavengers through a recreational activity (i.e. wildlife-based tourism) at the SFS in the Pyrenees (*Chapter 4*). For this purpose, we aimed to determine:
    - **I.** a characterization of SFS visitor profile;
    - **II.** a description and analysis of the perceptions, interest and knowledge of European avian scavengers held by SFS visitors.

MATERIALS AND METHODS

Photo by Daniel Navarro Samaniego.
A close-up of two juvenile Eurasian griffon (left) and cinereous (right) vultures near El Escorial (Madrid).

Materials and methods

Study area

All the scientific research presented in this thesis was carried out in the Pyrenees, a mountain range in southwest Europe (NE Spain, SW France and Andorra) with the coordinates 42° 40′ 0″ N, 1° 0′ 0″ E (WGS84) (figure 3). This is a > 400 km-long continuous mountain range covering around 50,000 km^2 and acting as the natural boundary between France and Spain. On the northern slope, the Pyrenees stretches across the French regions of New Aquitaine and Occitania. On the southern slope it passes through the Spanish autonomous communities of the Basque Country, Navarre, Aragon and Catalonia. The small country of Andorra is nestled in the mountain range. The Pyrenees is one of the most important mountain ranges of Spain (given that it is the most extensive and the second tallest in the country), reaching more than 3,000 masl at its highest summits and containing the second highest peak of the Iberian Peninsula, the Aneto (3,404 masl). This mountain range is a tectonic chain, primarily formed during the Paleozoic Era and reshaped during the Cenozoic Era by the alpine orogeny, as a result of the pressure between the African and Eurasian plates (Comín & Rica 2007). Thus, two different zones are identified as the axial Pyrenees (the core of the range presenting the highest altitudes) and the pre-Pyrenees (surrounding the axial Pyrenees). The axial Pyrenees, which is the central area of the Pyrenees and gradually decreases in altitude from west to east, consists of granitoids and Paleozoic rocks. The main geologic elements of the pre-Pyrenees are calcareous sedimentary rocks from the Mesozoic and Paleogene period (Sanuy *et al*. 2009).

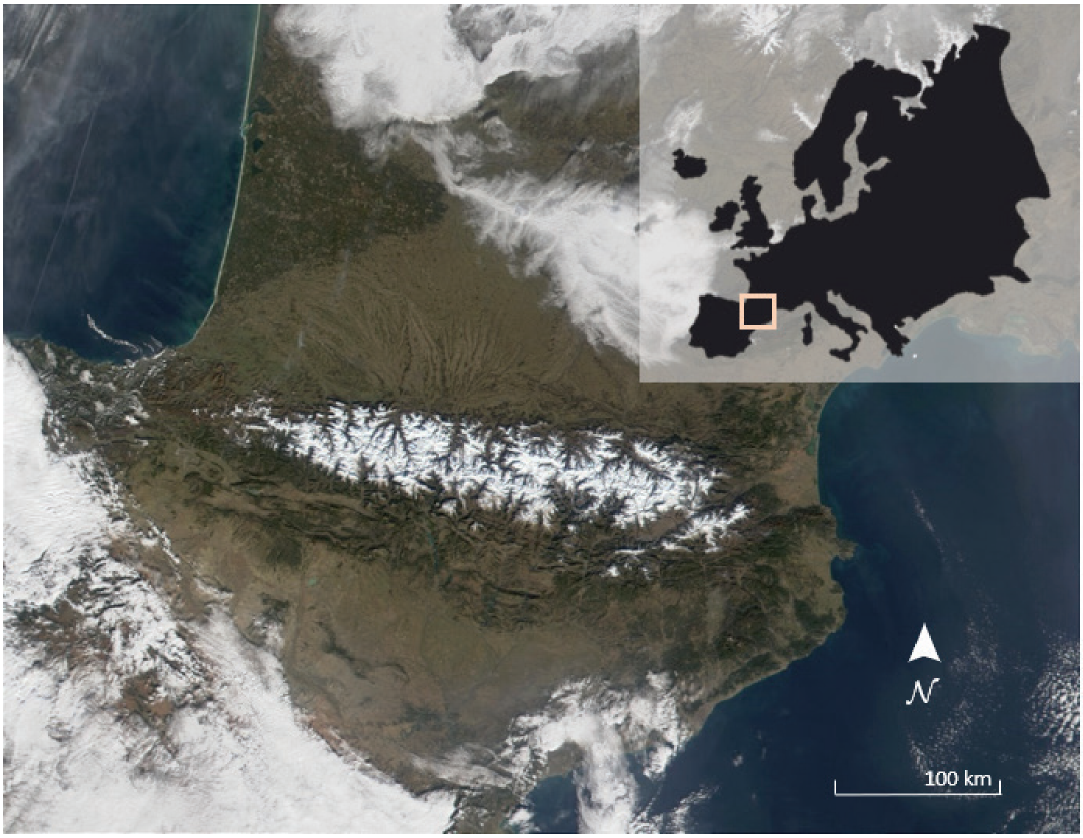


Figure 3 | The Pyrenees in a Moderate-Resolution Imaging Spectroradiometer (MODIS) image from January 18, 2002. Source: Jacques Descloitres, MODIS Land Rapid Response Team, NASA/GSFC - http://visibleearth.nasa.gov/view_rec.php?id= 2690, modified.

Since the Pyrenees forms a natural and climatic border between the Atlantic Ocean and the Mediterranean Sea, its climate is strongly regulated by both water bodies. Consequently, the northwest region shows climatic characteristics similar to the Atlantic climate (i.e. higher precipitations and lower temperatures), while those of the southeast area are more similar to the Mediterranean climate (i.e. drier and with higher temperatures). At the same time, climate varies, as usual, in terms of altitude, orientation and latitude. Thus, the Pyrenees includes three different bioclimatic areas (Montane, Sub-Alpine, and Alpine), showing four-seasonal weather conditions with average annual temperatures varying between 0°C and 16°C and precipitation ranges from 600 mm to 2,600 mm (Cuadrat *et al.* 2010). Snow is frequent in the axial zone between November and March (Rivas-Martínez 1990; Vicente-Serrano *et al*. 2007). The soil structure, the high elevation gradient and the climate condition the type of vegetation. In the west, beech (*Fagus sylvatica*) becomes dominant at montane elevations (> 1,000 masl). In the Central and Eastern Pyrenees, the climate becomes continental, and the foothills are mostly dominated by evergreen or marcescent oaks, while pines become predominant at higher elevations, and Atlantic species such as beech or fir (*Abies alba*) are restricted to the most humid valleys. Pines distribute in a clear elevation gradient according to their autoecology: Scots pine (*Pinus sylvestris*) is the most common species in the montane range (1,300 to 1,700 masl). From here the main species is the Mountain pine (*Pinus uncinata*), which reaches up to 2,200-2,300 masl, and constitutes the upper limit of the forest (treeline) throughout the massif (Améztegui *et al.* 2021).

Like other mountain ranges of the same latitude, the Pyrenees has been highly anthropized since ancient times. Rock paintings from 6,000-10,000 years ago persist on the southern slopes of the pre-Pyrenees and megalithic remains from the Bronze Age dated about 5,000 years ago have been found at many points of this range (including the subalpine belt) (Comín & Rica 2007). Urbanization development, agriculture and extensive farming were traditional practices in the area that have shaped the landscape of this mountain range, especially in the 600-1,600 masl altitudinal range. Until the mid-20th century, transport limitation obliged people to obtain resources locally, triggering an intense deforestation and consequent soil loss in the area (Comín & Rica 2007). However, over the last 60 years, the Pyrenees has undergone major changes in land organization suffering from rural depopulation that has led to farmland abandonment linked to an intense transhumance and livestock decline. Nowadays, human pressures remain intensively in the most productive areas, such as the lower valleys (Améztegui *et al.* 2010). Recreational and touristic value of the area has increased, partly in attempt to offset the low economic competitiveness of agriculture and therefore further favouring hillslope abandonment (van Leeuwen *et al.* 2019).

These kinds of socio-economic changes also have important impacts on the regional natural resources and protected areas. At present, three national parks exist in the Pyrenees (two on the southern and one on the northern slop), the first of these three —*Parque de Ordesa y Monte Perdido*— having been created in Spain in 1918. Complementarily, the Pyrenees presents a great proportion of protected areas, containing for instance at least 1.92% (i.e. 12,636.51 km^2) of the Spanish surface included in the Natura 2000 network (Otegui *et al*. 2012; Galicia *et al.* 2015). Thus, this mountain range, like many other mountains, plays a role of biodiversity reservoir and refuge for threatened species. Evidence shows that this mountain range (as well as the Spanish Cantabrian mountain chain) served as a refuge for the last populations of quaternary megafauna in Europe during the Holocene, some of these species still persisting (Comín & Rica 2007).

Nowadays, the Pyrenees is inhabited by all four European vulture species (i.e. Eurasian griffon, cinereous, Egyptian and bearded vulture) and multiple facultative avian scavenger species, including most of the species of the aforementioned scavenger guild living in Spain (in the *Scavenger conservation status in Spain* section). In the Pyrenees, we can find several raptors like golden eagles, black kites, red kites, common buzzards and Western marsh harriers, corvids such as common ravens, carrion crows, Eurasian jays, and common magpies, and seabirds such as yellow-legged gulls (especially close to dumps). Regarding mammalian facultative scavengers, there are carnivores such as brown bears, grey wolves, red foxes, stone martens, pine martens, common genets, and Eurasian badgers, and omnivores such as wild boars.

In relation to the obligate scavengers inhabiting the Pyrenees, the populations of all four vulture species have increased in this region during the last decades. In 2009, 1,115 pairs of Eurasian griffons and 67 Egyptian vulture territories were estimated in the Pyrenees (García & Margalida 2009), compared to the more than 260 pairs of Egyptian vulture and 4,774 pairs of Eurasian griffons estimated in 2018 at least in the Spanish Pyrenees (del Moral & Molina 2018a; del Moral & Molina 2018b). Cinereous vulture species was extinct in the Pyrenees, but reintroduced in 2007 in the Special Protection Area (SPA) of Serra de Boumort-Collegats (Catalonia, Spain), existing in 2017 a fixed colony of 14 pairs (del Moral 2017). At the same time, in the Pyrenees the territories of bearded vulture have increased from 45 in 1987 to 177 in 2018, 365 adult breeding bearded vultures having been estimated in 2016, representing 49% of the adult population and 36% of the total Pyrenean population (Donázar *et al*. 1993; Margalida & Martínez 2020; Margalida *et al*. 2020).

In particular, the bearded vulture (used as study model species in *Chapters 1 and 2*) occupies habitats of abrupt orography, its most important breeding areas being located on the southern slopes of the Pyrenees, where 122 territories were found in 2018 (Aragon, *n* = 74; Catalonia, *n* = 40; and Navarre, *n* = 8; figure 4). The highest nesting densities occur in steeply sloping areas over 1,000 masl (ranging between 650 masl and 2,250 masl), where human access is limited and orographic updraughts are more frequent (Margalida 2010; Margalida & Martínez 2020). Pyrenean bearded vultures feed on bones of medium-size wild mammals (e.g. wild boar, Pyrenean chamois *Rupicapra pyrenaica*, and red deer *Cervus elaphus*) and also on the abundant remains of dead extensive livestock (sheep *Ovis aries*, goats *Capra hircus* — these two being those preferred by the study species—, and also cows *Bos taurus* and horses *Equus*), especially in summer thanks to the traditional transhumance practices remaining in the Pyrenees (Margalida *et al*. 2009; Margalida 2010).

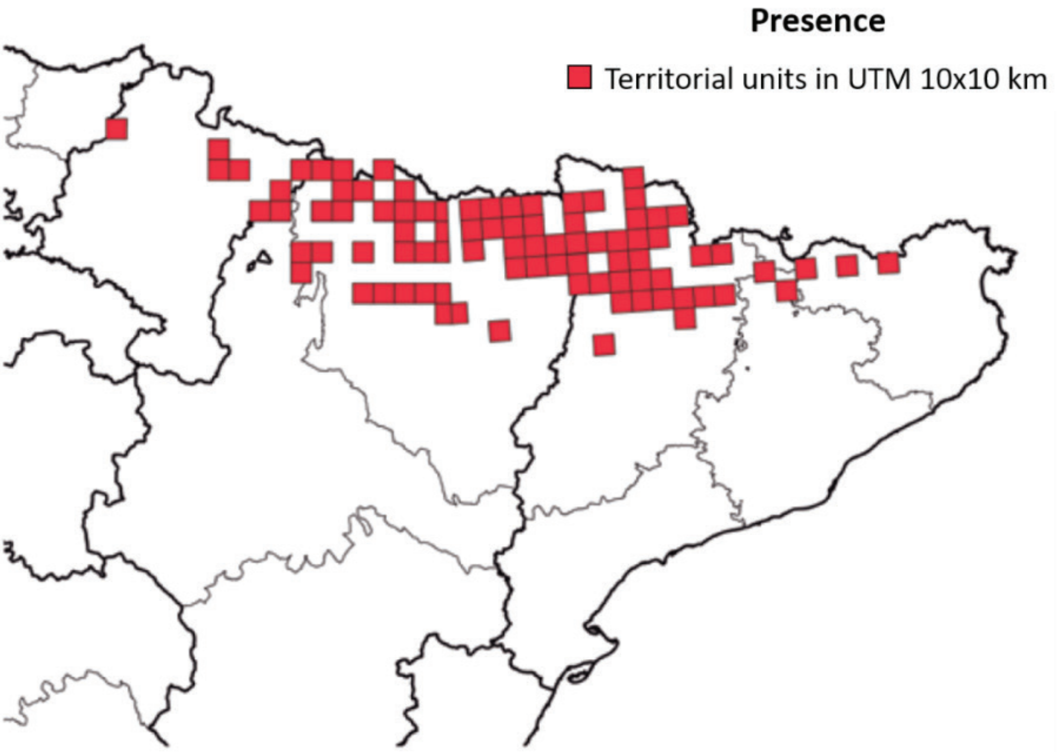


Figure 4 | Bearded vulture distribution range (n = 132 estimated breeding territories in Spain and 1 in Andorra) on southern Pyrenean slopes in 2018. These territories represent 74.6% of the Pyrenean population. There are also 44 breeding territories on the northern slope of the Pyrenees, but no map was found with such detailed information for this area. Source: Margalida & Martínez 2020.

It has been estimated that, in the Pyrenees, the proportion of carcasses of wild and domestic ungulates available to avian scavengers fluctuates between 25% and 80%, depending on the habitat occupied by the prey species (forest or open landscape; Margalida *et al*. 2011; Margalida & Colomer 2012). More specifically, Margalida *et al.* (2011) showed that, in the pre-Pyrenees region of northeastern Spain, wild ungulates do not currently provide enough food to sustain avian scavengers, and domestic animal carcasses are necessary to prevent population decline.

To achieve the current Pyrenean populations of obligate scavengers, several conservation and population rescue plans have had to be developed in order to face the sharp decline suffered by vulture populations at the end of the 20th century in Europe (Bijleveld 1974; Botha *et al.* 2017). As one of the remedial initiatives, the establishment of SFS (some specifically aimed at the bearded vulture and others at a multitude of avian scavengers) was a measure recurrently applied by administrations (Donázar 1993; see review in Donázar *et al.* 2009a). As a result, since the late 1960s, a large network of SFS started to be created in the Pyrenees, at least 67 of them currently operating in the Pyrenean and Pre-Pyrenean area (seven in France and 60 in Spain), each with very different spatial and temporal feeding routines. Besides the original conservation purpose for which these SFS were built, some have also been managed with complementary strategies in order to benefit from the non-material NCP that avian scavengers provide to society, developing scientific and recreational strategies. SFS following a scientific strategy (at least $n = 19$) were those developing scientific activities such as bird monitoring, field technicians training in visual species identification, demographic studies, etc. In contrast, SFS following a recreational strategy (around 30%, $n = 20$, located in the eastern Spanish Pyrenees, i.e. Aragon and Catalonia autonomous communities) were those receiving visitors at certain times of the year at the hides linked to these feeding structures offering recreational activities such as birdwatching, educational and photography experiences. These two strategies are not exclusive, given that both kinds of activities can be performed in the same SFS, but in different period of the year.

Study model species: bearded vulture (*Gypaetus barbatus*)

In Europe, we can only find four obligate scavenger species (i.e. griffon, cinereous, Egyptian and bearded vulture), all accipitrid raptors characterized by being long-lived K-strategist species. Among them, the bearded vulture *Gypaetus barbatus* (Linnaeus 1758, figure 5) is a non-colonial, sexually monomorphic cliff-nester that inhabits mainly mountainous regions of Eurasia and Africa (Cramp & Simmons 1980). This 4.5-7.1 kg weighted avian scavenger is distinguished from the others especially because of its territorial behaviour and its diet based mainly on bone remnants (preferably feeding on bones of medium-size domestic and wild ungulates, which constitute 70-90% of its diet), occupying a unique trophic niche within the avian scavenger guild (Hiraldo *et al.* 1979; Brown 1988; Margalida *et al*. 2009, see other species' peculiarities in figure 6). It is a mainly monogamous species, but some exceptional polyandrous cases have also been reported in different populations on diverse continents (e.g. Fasce *et al.* 1989; Heredia & Donázar 1990, Margalida *et al*. 1997; Carrete *et al.* 2006b; Krüger 2007; Margalida 2010). Diverse studies have indicated that birds first pair and become territorial at an average age of 6.5 years (Antor *et al.* 2007), although on average first breeding attempt takes place

Figure 5 | An adult Pyrenean bearded vulture. Photo by Antoni Margalida.

Figure 6 | *Pájaro de barro*. An adult Pyrenean bearded vulture flying after a mud bath. Traces of mud on the feathers of its neck, chest and legs can be appreciated. Photo, description*, and picture name provided by Pilar Oliva.

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* Bearded vultures visit ferruginous springs where they bathe and their plumage acquires a reddish or orange coloration due to the presence of iron oxides. The reason for this peculiar behaviour is unknown. However, some theories relate it to signs of dominance or territoriality status of the individuals as well as other processes such as pair formation and their long-term maintenance.

at 10.3 years (Margalida *et al*. 2020). It presents a prolonged breeding cycle during which two eggs are laid, but normally only one chick survives due to sibling aggression (Thaler & Pechlaner 1980; Margalida *et al*. 2004). The bearded vulture also shows a delayed plumage maturation, since full adult plumage is not reached until the age of 6-7 years (Sesé 2019). Based on plumage characteristics, age can be determined as juvenile for those < 1 year old, immature for those 2-3 years old, subadult for birds 4–5 years old, and adult for those ≥ 6 years old (Margalida *et al.* 2016).

Two subspecies are currently recognized (though up to five have been described in the past), based on plumage characteristics (Hiraldo *et al*. 1984; Mundy *et al*. 1992; Margalida & Martínez 2020): *G. b. barbatus* for all Eurasian and North African bearded vulture populations occurring north of the Tropic of Cancer, and *G. b. meridionalis* for the bearded vultures of Eastern and Southern Africa occurring south of the Tropic of Cancer (see figure 7). Although, a study of Godoy *et al.* (2004) based on the analysis of mitochondrial DNA does not support this subspecies distinction accepted for the bearded vulture species. In this study, they found two divergent mitochondrial lineages within the entire population of Eurasian and African bearded vultures, but not enough intraspecific genetic variation to declare two differentiated subspecies. In the past, the bearded vulture used to be widely distributed through African and Eurasian mountainous chains. However, like many other raptors (Bijleveld 1974), this vulture was persecuted and extirpated from many European mountain ranges remaining by the mid-20th century just a few isolated populations in some parts of the Pyrenees (France and Spain), Corsica, Greece and the Balkans (see Hiraldo *et al*. 1979; Heredia & Heredia 1991; Donázar 1993; Terrasse 2001; Margalida & Heredia 2005). More specifically, it was eradicated from the Alps in 1913, when the last individual was shot in the valley of Aosta, and the last bird disappeared from Andalusia in 1986. In 2009, around 162 bearded vulture breeding territories were known in Europe and this species was considered to be one of the most threatened raptors of the continent (Annex I, EU Wild Birds Directive 79/409/EEC and 2009/147/EEC, Appendix II of the Bern Convention, Bonn Convention and CITES). In order to deal with this serious risk of extinction, recovery plans consisting of *in situ* conservation actions such as nest surveillance, hunting regulation, maintenance of SFS, signalling, and modification of potentially dangerous power lines were implemented in Europe (Margalida & Martínez 2020). Parallel actions to fight against illegal poisoning bait use and all scientific research carried out so far about the species' ecology which led to management implications have also been meaningfully helping to start recover the endangered European populations of bearded vulture. In the Pyrenees

(Andorra, northeastern Spain, and southern France), conservation measures were fundamentally implemented as of the end of the 1980s, their mainstays being population monitoring as a means of understanding the breeding parameters and the installation of SFS with public funds (see reviews in Heredia & Heredia 1991 and Donázar 1993). At the same time, in terms of ex-situ conservation projects, ambitious reintroduction plans (e.g. in 1986 in the Alps —in Switzerland, Italy, France, and Austria— Hirzel *et al*. 2004; Schaub *et al.* 2009, in 2006 in Andalusia —southern Spain— Simón *et al.* 2007, in 2008 in Sardinia —Italy— Genero 2009, and currently in 2021 in French Massif Central and Pre-Alps —southeastern France— LIFE GypConnect program) are being developed. These are slow and laborious projects that undoubtedly required a high capital investment (e.g. Schaub *et al.* 2009 showed that a bird at the moment of release has accumulated costs of €70,000).

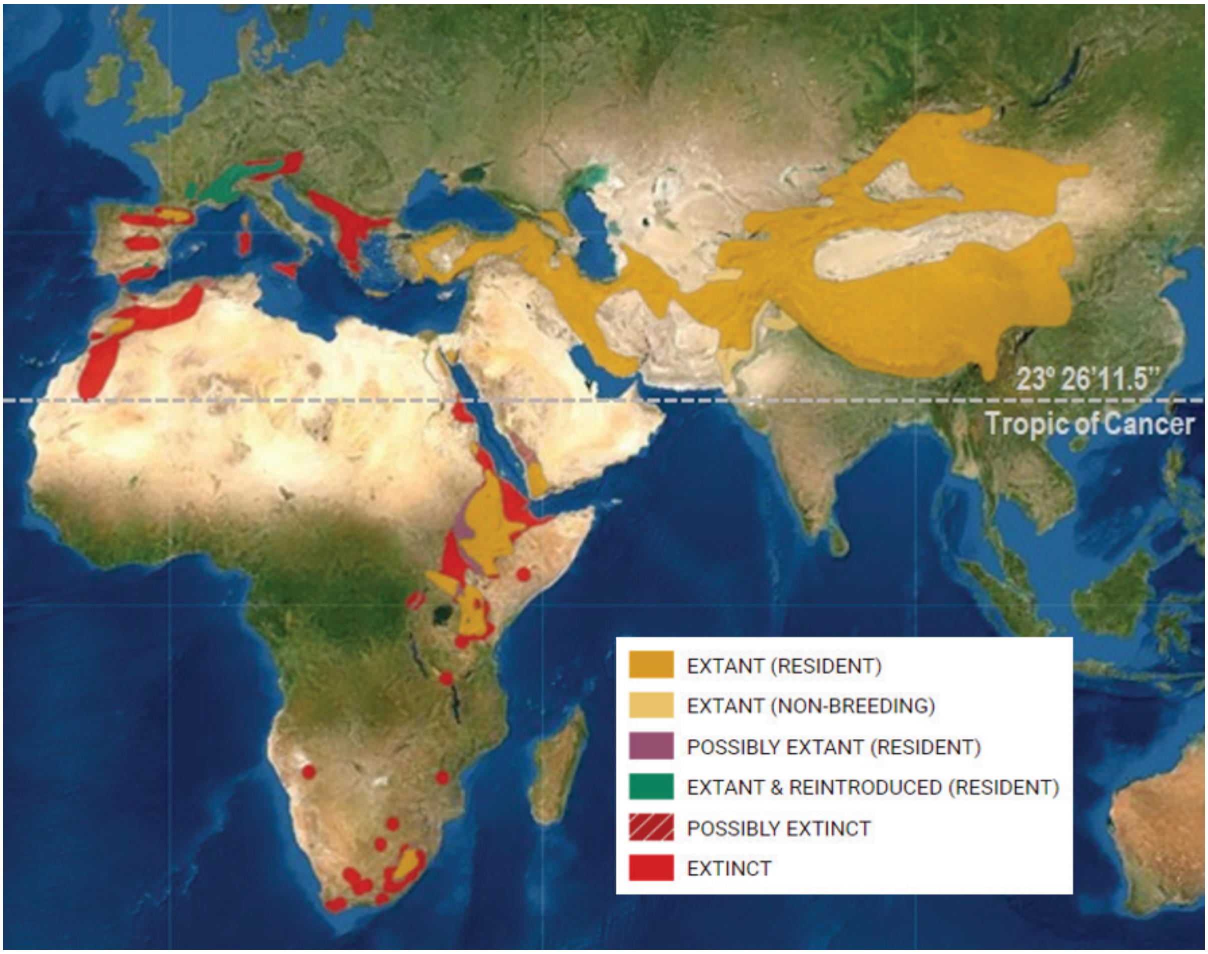

Figure 7 | World distribution of the bearded vulture. Modified from BirdLife International 2017 and Handbook of the Birds of the World (2017). *Gypaetus barbatus*. The IUCN Red List of Threatened Species. Version 2021-1.

Nowadays, the European range of the bearded vulture comprises the Pyrenees, Andalusia (southern Spain), Asturias (northern Spain), the Alps, Corsica (France), and Crete (figure 7). The Pyrenean population represents 63% of the European population, working as the dispersal nucleus of the species on this continent (Margalida *et al.* 2010; Margalida & Martínez 2020). However, despite the fact that the species is recovering in Western Europe, globally it was up-listed in 2014 from Least Concern to Near Threatened (BirdLife International 2014; table 1), because it is declining worldwide as a result of poisoning, habitat degradation, disturbance of breeding sites and collisions with power lines (BirdLife International, 2015b). Currently, the global population is estimated at 1,300-6,700 mature individuals, of which 1,200-1,600 are estimated to inhabit Europe (BirdLife International 2015b). It is suspected that the population has declined by 25-29% over the past 53.4 years (three generations), whilst within Europe the population would have decreased by at least 10% during the same time period (BirdLife International 2015b). In fact, in the Pyrenees, the breeding population experienced a geometric mean population increase of 3.3% annually, falling to 2.3% during the last 10 years (Margalida *et al.* 2020).

Significant progress was made in Europe between the end of the 20th century and the beginning of the 21st, such as the social awakening of conservationists' and people's awareness of raptor populations' state of health, the economic and management efforts made to carry forward ex-situ conservation measures for bearded vulture populations, and the information obtained from captive breeding programs (Frey *et al*. 1995; Llopis & Frey 2005). Nevertheless, in spite of the social and economic progress, research and knowledge of the ecology and behaviour of wild populations of this species is still deficient (Hiraldo *et al*. 1979; Brown 1988; Heredia & Heredia 1991; Terrasse 2001; Margalida & Heredia 2005). Yet, this information, as well as the current human perception of the species, is required to maximize the efficiency of any conservation strategy and to optimize the human and economic efforts (Caro 1998; Bennett 2016). Also, accounting for the considerable economic and human resources already invested in the conservation of the bearded vulture, this species represents an interesting and informative example when it is necessary to evaluate the effectiveness of the application of conservation measures in a seriously threatened raptor population.

Data collection

Chapters 1 and 2

For the research articles analysing any matter relating to the movement ecology of the Pyrenean bearded vulture population (*Chapters 1 and 2*), a database of 20 bearded vultures tracked from 2006 to the present day was used. These birds were captured in the Pyrenees, in the period 2006–2016, using radio-controlled bow-nets at supplementary feeding stations (n = 17), at nests (n = 1), or as injured individuals recovered at official wildlife recovery centres (n = 2), where birds are released following rehabilitation. All birds were tagged with 17 different 70 g solar-powered Argos satellite transmitters (PTT/GPS Microwave Telemetry, Inc. Columbia, MD, USA, of 2005–2008 logger generation) three of them being reused on new individuals. Transmitters were in all cases attached to the bird's back with a breakaway thoracic junction stitched with cotton thread harness made of 0.64 cm Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA). The transmitters were programmed to record a fix (manufacturer's estimated error ± 18 m) each hour from 4:00 to 22:00 UTC, with the exception of two individuals, whose transmitters recorded a GPS location every 2 h. The usage time of the transmitters was 5.34 ± 3.03 years (n = 14) on average. Regarding the biological (i.e. internal/intrinsic) factors, four parameters were analysed (see table 2):

(i) *Age*. According to plumage characteristics of individuals, four different age classes were assigned: juvenile (1 year old); immature (2–3 years old); subadult (4–5 years old); and adult (> 6 years old).

(ii) *Sex*. Determined by molecular analysis of blood samples (PCR amplification of the CHD-W gene as described in Ellergren 1996).

(iii) *Breading season*. Defined either as *breeding period* (1st January to 31st July) or *non-breeding period* (1st August–31st December).

(iv) *Territoriality*. Described as territorial or non-territorial individuals, depending on their movement patterns and breeding behaviour. Adult birds were defined as territorial when they exhibited spatially aggressive defence, nestbuilding behaviour and sexual activity in a fixed area (Burt *et al.* 1943; Börger *et al.* 2008; Margalida *et al.* 2016).

(v) *Flight activity*. Defined according to Silva *et al.* 2017 by the complementary rates of perched fixes (*RPF*, calculated from monthly fixes with instant speeds slower than 1.39 m/s) and fix in flight (*RFF*, calculated from monthly fixes with instant speeds equal to or faster than 1.39 m/s). This behavioural factor was only considered in *Chapter 1*.

Table 2 | Basic individual biological and behavioural traits for 20 birds tagged with 17 solar-powered Argos satellite transmitters (PTT/GPS Microwave Telemetry, Inc. Columbia, MD, USA) of 70 g all bought in 2005-2008. For the complementary rate of fix in flight (RFF) and rate of perched fixes (RPF), monthly mean ± SD are shown. In bold indicates transmitters (platform transmitter terminal, PTT) that were used on two different birds. For the territorial status (*T* territorial, *NT* non-territorial), the years of the beginning and ending (if any before 2019) are shown.

Individuals	PTT	Sex	Age (years)	Territorial status	Time period	Usage time (years)	RPF	RFF
Adrian	PTT1	M	4	T (2012-2016)	05/2009 - 01/2019	9.8	0.72 ± 0.26	0.28 ± 0.26
Andreia	**PTT2**	H	>7	T (2009)	03/2009 - 09/2009	0.6	0.47 ± 0.32	0.52 ± 0.32
Pocholo	**PTT2**	M	>7	NT	07/2011 - 01/2019	7.6	0.75 ± 0.23	0.25 ± 0.23
Batín	PTT3	M	>7	T (2008)	05/2008 - 04/2015	7.0	0.50 ± 0.33	0.50 ± 0.33
Cabó	**PTT4**	H	>7	T (2007)	11/2007 - 08/2008	0.7	0.53 ± 0.37	0.47 ± 0.37
Sofia	**PTT4**	H	>7	NT	11/2008 - 05/2012	3.6	0.71 ± 0.29	0.29 ± 0.29
Dulantz	PTT5	M	6	NT	04/2013 - 10/2014	1.5	0.64 ± 0.30	0.37 ± 0.30
Elisabeth	PTT6	H	18	NT	03/2015 - 01/2018	2.9	0.77 ± 0.23	0.23 ± 0.23
Garrotxa	PTT7	H	5	T (2012)	05/2008 - 06/2013	5.2	0.61 ± 0.31	0.38 ± 0.31
Gervàs	**PTT8**	H	>7	T (2007)	05/2007 - 04/2009	1.9	0.69 ± 0.28	0.31 ± 0.28
Min	**PTT8**	M	5	NT	05/2009 - 08/2017	8.4	0.73 ± 0.27	0.27 ± 0.28
Isaac	PTT9	M	5	NT	11/2010 - 01/2014	3.2	0.70 ± 0.26	0.29 ± 0.26
Jairo	PTT10	H	4	T (2014)	11/2010 - 06/2016	5.6	0.76 ± 0.27	0.24 ± 0.27
Morreres	PTT11	M	1	NT	11/2007 - 09/2012	4.9	0.62 ± 0.31	0.37 ± 0.31
Nicky	PTT12	M	5	T (2011)	06/2009 - 05/2017	8.0	0.53 ± 0.34	0.47 ± 0.34
Noah	PTT13	H	>7	NT	04/2008 - 09/2008	0.5	0.84 ± 0.23	0.16 ± 0.23
Revilla	PTT14	H	5	NT	04/2013 - 11/2013	0.6	0.87 ± 0.17	0.13 ± 0.17
Sasi	PTT15	M	1	NT	08/2007 - 06/2008	0.9	0.78 ± 0.24	0.22 ± 0.24
Subfli	PTT16	H	4	T (2012)	05/2008 - 04/2012	4.0	0.72 ± 0.28	0.28 ± 0.28
Tossal	PTT17	H	>7	T	11/2006 - 12/2006	0.1	0.82 ± 0.22	0.18 ± 0.22

The external (i.e. extrinsic) factors analysed were different in *Chapters 1 and 2:*

- In *Chapter 1* we accounted for two different types of extrinsic factors, depending on whether they were technical or environmental variables:

  Technical variables: (i) we accounted for the device usage time and (ii) duty cycle (as mentioned, of 1 or 2 h depending on the individual).

  Environmental variables: (iii) topographic altitudes were obtained using a Digital Elevation Model (ASTER Global DEM, 1 arc-second spatial resolution); and (iv) surface solar radiation and (v) total precipitation were obtained from an interim full-daily at surface forecast (European Centre for Medium-Range Weather Forecasts, 0.75° each 3 h). Monthly means of all three parameters were calculated using the Movebank Env-DATA track data annotation. More details in *Chapter 1*.

- In *Chapter 2* the external variables considered were (i) the season, defined in the Mediterranean climate as four periods (spring, from 21st March to 20th June; summer, from 21st June to 22nd September; fall, from 23rd September to 20th December; and winter, from 21st December to 20th March) and (ii) the daylight time, considering the astronomical twilight as the start and the end of a daylight length setting sunrise (i.e. the astronomical twilight is the time when the geometric centre of the Sun is 18 degrees below the horizon). More details in *Chapter 2*.

Chapters 3 and 4

For the research articles analysing a socio-ecological perspective from the ecosystem services approach of the Pyrenean avian scavengers (*Chapters 3 and 4*), data from two different sources were obtained between February 2018 and January 2020:

SFS information

We telephonically interviewed some Pyrenean SFS managers in order to obtain basic information of the management and structural characteristics of each SFS, including whether they allowed access to the general public. Specifically, for those Pyrenean SFS receiving visitors, the information obtained included the mean amount of people visiting the SFS per year, the cost, if any, of the

SFS entrance, and the activities developed beyond supplementary feeding of avian scavengers (i.e. scientific and/or recreational strategy, the latter including birdwatching, educational, or photography experiences). Given all the activities developed in the SFS, they usually count on at least one associated hide, and/or an observation point, especially for those SFS receiving visitors, given that only the entrance of the field technicians directly to the SFS is allowed. Hides built, managed, and exclusively intended for photography were not included in this study. All SFS considered here had been created for the principal purpose of scavenger conservation.

Visitor information

In the SFS receiving visitors, we conducted individual surveys to analyse the kind of visitors that enjoy the recreational activities offered in the SFS and collected information about their perceptions of the avian scavenger guild. Within the SFS accessible to the public, some were built inside a protected area (national or natural parks), and therefore we could not assume that the main reason for all the people visiting the parks was mainly to enjoy watching avian scavengers, and so we did not consider them suitable to perform the survey. However, those SFS located in a protected area, but specifically controlled by non-governmental organizations, could be included in our study, since the number of visitors that expressly went to the SFS can be assured. Thus, questionnaires (in either English or Spanish) were randomly distributed among visitors.

The questionnaire was divided into three sections: (1) the wider section, with questions about visitors' personal interest, perceptions and knowledge of the NCP provided by scavengers; (2) trip characterization; and (3) individual socio-economic characterization. Associated with this questionnaire, we showed visitors a laminated paper with printed colour images of 14 species of obligate and facultative scavengers mostly present in the Pyrenees (the four European vultures, and 10 facultative avian scavengers, including six birds of prey and four corvids; see table S2 in *Supplementary Information of Chapter 4* for list of species) to visually identify the species. The only species absent from the Pyrenees is the Spanish imperial eagle, an important icon of the Iberian Peninsula avifauna —thus, culturally representative—, easy to visually identify and hence included in the questionnaire in order to have at least two individuals from the *Aquila* genus, giving us the possibility to evaluate the visual identification and cultural recognition skills of the visitors.

We reached a mean of 10 ± 4 questionnaires completed per SFS surveyed (range 3-17). Given the diverse dynamics of the SFS (only two of the SFS surveyed present scheduled visits), the questionnaires were self-answered by the visitors, so we obtained variable usable responses depending on the question. We complied with the ethical standards ruling social surveys given that respondents were informed in writing at the beginning of the questionnaire about the nature of their voluntary participation and their ensured data anonymity. See more details in *Chapter 4.*

Data analyses

In *Chapter 1*, the possible effects of the biological traits of a large raptor on the frequency of lost fixes —the fix-loss rate (FLR)— were evaluated. To this end, we assessed the influence of biological, technical, and environmental factors on the FLR of birds' transmitters. The FLR used in this study was calculated as a monthly value for each individual, consisting of the proportion of days per month on which no fixes were recorded. First, to perform a deviance partitioning analysis, we grouped all the predictor variables: (1) age, sex, breeding and territorial status, and rate of perched fixes (RPF) (the latter describing flight activity) as biological factors; (2) PTT usage time per month and duty cycle as the technical factors; and (3) monthly means of topographic altitude, surface solar radiation, and total precipitation as environmental factors. With this analysis we evaluated the effect on FLR of the single and joint contributions of each of the three groups of variables comparing by basic algebra the percentage of the explained conditional R^2 of each of the best generalized linear mixed models (GLMMs; Nakagawa & Schielzeth 2013) built, including the aforementioned biological, technical and environmental factors as fixed factors (where applicable) and the individual as a random factor. Second, to determinate the significant variables influencing the FLR, we constructed the full model with all of the biological, technical and environmental variables as fixed factors and the individual as a random factor, considering a binomial error distribution and logit-link function, made a model selection using Akaike's Information Criterion (AIC; Burnham & Anderson, 2002), and chose the best models with a delta AIC < 2. Third, to better understand the individual flying behaviour and how it could affect FLR, we analysed the influence of all of the same biological and environmental factors on the flight activity of the birds. For this analysis, a weighted RPF (wRPF) was created combining the monthly number of perched fixes and monthly number of fixes in flight. Thus, we modelled wRPF using a GLMM (binomial error distribution and logit-link function) with all the biological and environmental variables as fixed factors and the individual as a random factor, and then selected models giving delta AIC < 2. Technical factors were not included as predictors in this model because of their obvious absence of influence over the flight activity of the birds. All the statistical analyses were computed using R statistical software. See more details in *Chapter 1*.

In *Chapter 2*, the main drivers of daily patterns in the flight activity of the Pyrenean population of bearded vultures were analysed. With this purpose, we assessed the relative influence of external factors (season and daylight time) and internal factors (sex, breeding season and territorial status) on their daily activity behaviour by computing mean hourly distance travelled, maximum displacement and cumulative distance travelled per hour. Maximum displacement was defined as the average Euclidean distance between the initial daily location and any position reached on the consecutive hours. Hourly distance was approximated as the average straight-line distances covered in an hour. Cumulative distance travelled was estimated as the sum of straight-line distances covered during each hour on a given day. To standardize the seasonal variation in daylight, we generated an index of daylight duration for each day. We computed this daylight index as the division of daylight elapsed fix time by daylight length, where the numerator is the period of daylight spent until the fix transmission, and denominator is length of daylight hours within a given 24h day. To examine the relationship between movement parameters and biological (sex, breeding season, and territorial status) and external (daylight time and season) factors we used linear mixed models (LMM) with individual as a random factor (McCullagh & Searle 2000) and then selected the best model giving delta AIC < 4 (Burnham & Anderson 2002). All analyses were conducted using R statistical software. See more details in *Chapter 2*.

In *Chapter 3*, an economic valuation of the recreational and educational experiences brought by avian scavenger-based tourism in Spain, in particular, at vulture supplementary feeding sites (SFS) in the Pyrenees and their important contribution to the incomes of the local human population is estimated. To this end, we first used the descriptive nonparametric analyses to explore whether there were significant differences in the mean trip expenses and specific trip parameters, such as distance travelled (distance by road in km) between the trip departure point and the SFS visited and trip duration between visitors who started their trip from anywhere in Spain (national visitors) and those with departure points outside the country (international visitors). Second, we calculated the specific costs of each trip parameter considering separately travel costs (T), SFS entrance cost (SFSe), accommodation costs (A), food costs (F), and opportunity costs (O). After that, we summed all these specific costs of each trip parameter for the entire trip to calculate the visitors' trip expenses and then computed a mean trip expenses/visitor value following the equations:

$$(1)\ \text{Visitors' trip expenses} = T+(SFSe+A+F+O) \times \text{trip duration}$$

$$\text{and then } (2)\ \text{Mean visitors' trip expenses} = \Sigma\text{Visitors' trip expenses}/n.$$

Based on the mean trip expenses per visitor and the mean annual number of visitors per SFS, we were able to estimate the annual expenses associated with the non-material NCP (recreational and educational experiences) provided by vultures at the Pyrenean SFS for which visits were allowed. We summed the total economic benefits estimated for the nine SFS surveyed and the estimated economic benefits for the other six, differentiating between the expenses resulting from visits made by national and international visitors to arrive at an average expense per person. See more details in *Chapter 3*.

In *Chapter 4*, an identification and valuation of the NCP provided by European avian scavengers through a recreational activity (i.e. birdwatching, educational and controlled photography) at the Pyrenean SFS were performed as well as an evaluation of SFS visitors' perceptions of avian scavengers as NCP providers. With this aim, it was first developed a descriptive study characterizing the working strategies —beyond the originating conservative purposes— of the currently existent Pyrenean SFS, especially focusing on the ones receiving visitors. Second, SFS visitors' profile was typified through a two-step cluster analysis including categorical (i.e. the reason for the visit, the previous experience with birds, the relationship between their work and the avifauna, their level of education, and their average monthly income) and numerical variables (the material brought to the SFS, the visitor's self-rated interest in the avifauna, the frequency they birdwatch in a year, and the four indices built to determine the knowledge level and perceptions that the visitors present in relation to the avian scavenger guild, i.e. species identification, species recognition, positive perceptions and less positive perceptions indices). Third, descriptive analyses were used to define and assess perceptions, interest and knowledge of European avian scavengers maintained by SFS visitors. See more details in *Chapter 4*.

MOVEMENT ECOLOGY

CHAPTER 1

Photo credits:

Movement ecology
Photo by Miguel Ángel Díaz Guillén.
The *Cañón de Añisclo* valley, in the *Parque Nacional de Ordesa y Monte Perdido* of the Pyrenees (Huesca).

Chapter 1
Photo by Juan Carlos García Gómez.
An adult bearded vulture flying over The Pyrenees (Huesca).

CHAPTER 1

Influence of individual biological traits on GPS fix-loss errors in wild bird tracking

by

Ruth García Jiménez, Antoni Margalida & Juan Manuel Pérez García

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ABSTRACT

In recent decades, global positioning system (GPS) location data and satellite telemetry systems for data transmission have become fundamental in the study of basic ecological traits in wildlife biology. Evaluating GPS location errors is essential in assessing detailed information about the behaviour of an animal species such as migration, habitat selection, species distribution or foraging strategy. While many studies of the influence of environmental and technical factors on the fix errors of solar-powered GPS transmitters have been published, few studies have focused on the performance of GPS systems in relation to a species' biological traits. Here, we evaluate the possible effects of the biological traits of a large raptor on the frequency of lost fixes—the fix-loss rate (FLR). We analysed 95,686 records obtained from 20 bearded vultures *Gypaetus barbatus* tracked with 17 solar-powered satellite transmitters in the Pyrenees (Spain, France and Andorra), between 2006 and 2019 to evaluate the influence of biological, technical, and environmental factors on the fix-loss rate of transmitters. We show that combined effects of technical factors and the biological traits of birds explained 23% of the deviance observed. As expected, the transmitter usage time significantly increased errors in the fix-loss rate, although the flight activity of birds revealed an unexpected trade-off: the greater the proportion of fixes recorded from perched birds, the lower the FLR. This finding seems related with the fact that territorial and breeding birds spend significantly more time flying than nonterritorial individuals. The fix success rate is apparently due to the interactions between a complex of factors. Non-territorial adults and subadults, males, and breeding individuals showed a significantly lower FLR than juveniles-immatures females, territorial birds or non-breeding individuals. Animal telemetry tracking studies should include error analyses before reaching any ecological conclusions or hypotheses about spatial distribution.

Keywords

ARGOS GPS telemetry, endangered vulture, environmental factors,
large-size raptor, solar-powered GPS

INTRODUCTION

Obtaining a global positioning system (GPS) fix and the reliability of location data are primarily subject to satellite acquisition, a process mainly shaped by technical, environmental, and behavioural factors (Moen *et al*. 1996). External factors such as GPS satellite geometry (satellite constellation), topography and land surface roughness, vegetation, fix interval (time lapse between successive fixes), or even GPS-tag position and orientation, all limit a transmitters' ability to make contact with at least three satellites during a period of GPS activation (Moen *et al*. 2001; Cain *et al.* 2005; Graves & Waller 2006) causing GPS misconnections. Some authors have even observed: (1) an association between resource use, habitat selection, and fix-loss rate; and (2) interactions between animal behaviour and local habitat conditions which have to be considered particularly when assessing a species' habitat use (Rempel *et al.* 1995; Dussault *et al*. 1999; Moen *et al*. 2001; D'Eon 2003; Nielson *et al.* 2009). However, one of the biggest gaps in our understanding of GPS performance is related to species-specific behavioural effects. For example, the position of an individual animal changes the orientation of a receiver, and its performance. Some studies of large mammals have demonstrated that inactive animals have higher fix-loss rates and lower fix accuracy than active ones (Moen *et al*. 1996; Bowman *et al*. 2000; Moen *et al*. 2001). But very little is known about how, or to what extent, individual biological traits such as sex, age, size, territorial or breeding status, and their associated behaviour and ecology may affect satellite connection, fix-loss and location accuracy (Kaczensky *et al*. 2010; Mattisson *et al*. 2010; Recio *et al*. 2011; Jung & Kuba 2015). This kind of information is essential to properly interpret geolocation data and to draw useful conclusions regarding animal movement patterns or species behaviour.

During the last 40 years, Argos Platforms Transmitter Terminals (PTTs) have provided the world's most commonly used tracking coverage technology for the remote study of free-ranging animal movements, mainly because of their integration of GPS fixes (i.e. satellite locations) with data transmission technologies (i.e. the Argos data transfer system), particularly from the mid-1990s when GPS receivers became able to record high spatial-resolution tracking data (Harris *et al*. 1990; Schwartz & Arthur 1999; Rodgers 2001; Tomkiewicz *et al.* 2010). However, the raw data registered through GPS-Argos telemetry still suffer from errors and biases (e.g. fix rate bias, fix-loss errors and spatial location errors) that must be considered to avoid drawing incorrect conclusions and making the wrong management recommendations (Schwartz & Arthur 1999; Kaczensky *et al*. 2010; Thomas *et al*. 2011). These tracking problems are especially relevant for threatened species where reliable information is particularly important for reintroduction projects and conservation plans.

The endangered bearded vulture *Gypaetus barbatus* represents a good case study for assessing GPS fix-loss errors—measured in this study though the monthly fix-loss rate, FLR (for more details see "Methods" section). In the first instance, this species inhabits rugged mountain landscapes (in the Pyrenees, average home range kernel 90% varying between 63 km^2 for territorial individuals to 11,600 km^2 for non-territorial ones; Margalida *et al*. 2016) that allows the evaluation of the influence of abrupt topography on GPS fix-loss. Second, the long daylight hours and sunny climatic conditions favour at the same time flying behaviour and the charging of transmitter solar batteries. Third, the territorial behaviour of breeding individuals is very different to the behavioural pattern of non-territorial individuals, which fly over greater distances due to the lack of a nest site acting as a central foraging point Margalida *et al*. 2016; García-Jiménez *et al*. 2018). Four, the changing seasonal and weather conditions in the Pyrenees allow the comparison of transmitter performance during different solar radiation conditions. Finally, bearded vultures are an endangered species (more specifically, classed by the BirdLife International 2017 as vulnerable in Europe, and globally near threatened) for which accurate GPS data is important to improve management and conservation actions. The species is being reintroduced in several European countries, and GPS transmitter monitoring is one of the main tools used by managers and conservationists to assess its habitat use and reintroduction success (Houston 2006).

Technological improvements enabling the use of Argos GPS-lightweight PTTs (< 80 g) in marine mammals, birds, or even small animals up to 300 g (Britten *et al*. 1999; Soutullo *et al*. 2007), have prompted new research into sources of GPS errors associated to wildlife telemetric tracking, especially when fix-loss rate is related to animal behaviour or habitat use. This study focuses on the biological, environmental, and technical factors affecting the fix-loss rate—either caused by GPS misconnections or battery undercharging—in Argos GPS PTTs. We considered specific biological traits of bearded vultures including sex, age, territorial and breeding status, and flight activity (derived from the monthly rates of fixes of perched and flying birds) as biological factors. Concurrently, we considered environmental variables including topographic altitude, surface solar radiation, and total precipitation, as well as technical factors considering the transmitter usage time and the duty cycle (i.e. fix recording scheduled regimes), as extrinsic factors. Afterwards, given the flying nature of our case study species and the effect that this kind of movement behaviour has showed over some technological characteristics of the GPS transmitters in previous studies (Silva *et al*. 2017), we explore the influence of these biological and environmental variables over the flight activity trying to better understand this behavioural parameter and consequently its effect on the FLR (see figure 1). Based on previous solar-powered GPS tracking studies (Kaczensky *et al*. 2010; Byrne *et al*. 2017; Silva *et al*. 2017; Hofman *et al*. 2019), our hypothesis was that both FLR and flight activity of birds are strongly influenced either by specific biological traits and/or extrinsic factors, especially those related to technical factors. We hypothesized that individuals with greater flight activity (higher rates of fix in flight, RFF—reasonably assumed to be non-territorial individuals, who usually travel larger distances (Margalida *et al*. 2016; García-Jiménez *et al*. 2018), would be more exposed to direct solar radiation, thus present increased battery charging,

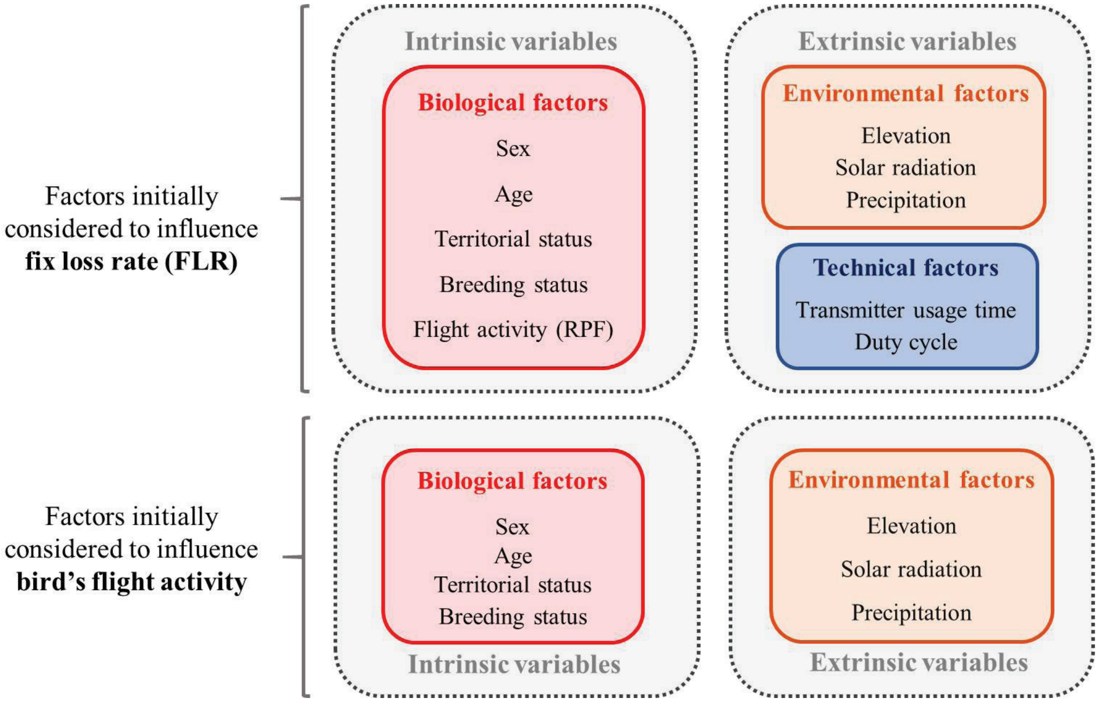

Figure 1 | Factors considered to influence Fix Loss Rate (FLR) and bird's flight activity (composed considering both monthly numbers of fix perched and fix in flight).

and a lower FLR compared to territorial individuals. Considering extrinsic factors, weather conditions will affect fix reception success because periods with more daylight hours (i.e. summer, presenting the highest surface solar radiation and lowest total precipitation) also favour thermal conditions for flight, in contrast to winter, promoting thus birds' flight activity. Topographic altitude will also probably affect FLR due to the challenging GPS connection in steep terrains. At the same time, it is expected that the transmitter usage time will negatively affect transmitter performance as a consequence of the decreasing battery and electronic system performance of the device.

MATERIAL AND METHODS

Study area

We assessed the GPS fix loss errors resulting from bearded vultures studied in the Pyrenees, a steep mountainous region with maximum altitudes of 3,400 m, located in the north of the Iberian Peninsula on the border between France and Spain. It includes three different bioclimatic areas (Montane, Sub-Alpine and Alpine) with average annual temperatures between 0 and 20 °C, and a four-season Mediterranean climate with seasonal weather conditions (Cuadrat *et al.* 2010).

Study species

The bearded vulture is a territorial, cliff-nesting vulture specialized in feeding on the bones of medium size ungulates (Margalida *et al*. 2009). In common with other avian scavengers it exploits thermal and orographic updrafts to use the least energy as possible when foraging. It is an endangered species now only found in certain mountainous areas of Europe, Asia, and Africa (del Hoyo *et al*. 1994; BirdLife International, 2017). In the Pyrenees, the spatial ecology of this species has been studied since the 1980s', originally using conventional VHF radio tracking (Sunyer 1991; Antor *et al*. 2007; Gil *et al*. 2014) and more recently with the solar-powered Argos or GSM data recovery system with GPS-PTTs Margalida *et al*. 2013; Margalida *et al*. 2016; García-Jiménez *et al*. 2018).

Tracking and data origin

Between 2006 and 2019, twenty bearded vultures were tagged with 17 different 70 g solar-powered Argos' satellite transmitters (PTT/GPS Microwave Telemetry, Inc. Columbia, MD, USA, all of the 2005–2008 logger generation)—three of which were reused on new individuals—attached to the bird's back with a breakaway thoracic junction stitched with cotton thread harness made of 0.64 cm Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA) (for further details see Margalida *et al*. 2016). The usage time of the transmitters was 5.34 ± 3.03 years (n = 14) on average. To compute this mean value for the three reused PTT, we summed the time usage of each peer of individuals using the same PTT, and for the rest of the PTTs, we excluded the records corresponding to the birds dead on the field (n = 3) since their transmitters could not be recovered and the reason for stopping fix recording was unlikely related with technical causes. We only considered the records of individuals whose PTTs stopped working properly, accounting times from the moment the PTTs were turned on until the moment we stopped receiving location data (see *Supplementary* table S1). All of the transmitters were programmed to report hourly GPS fixes between 04:00 and 22:00 UTC hours each day (manufacturer estimated error ± 18 m), except for two individuals whose PTTs transmitted every 2 h. Regarding the biological factors: (1) age of individuals were assigned to four different age classes according to plumage characteristics: juvenile (1 year old); immature (2–3 years old); subadult (4–5 years old); and adult (> 6 years old) (for details see Margalida *et al*. 2016; García-Jiménez *et al*. 2018); (2) sex was determined by molecular analysis of blood samples (PCR amplification of the CHD-W gene as described in Ellergren 1996); (3) territoriality was described as territorial or non-territorial individuals, depending on their breeding behaviour (García-Jiménez *et al*. 2018); (4) breeding season was defined either as breeding period (1st January to 31st July) or non-breeding period (1st August–31st December; Margalida *et al*. 2016); and (5) flight activity was defined according to Silva *et al.* (2017) by the complementary rates of perched fixes (RPF, calculated from monthly fixes with speeds slower than 1.39 m/s) and fix in flight (RFF, calculated from monthly fixes with speeds equal or faster than 1.39 m/s) (tables 1 and 2). Regarding the extrinsic factors: for technical variables, (1) we accounted for the device usage time and (2) duty cycle (as mentioned, of 1 or 2 h depending on the individual) and for environmental variables, (3) topographic altitudes were obtained using a Digital Elevation Model (ASTER Global DEM, 1 arc-second spatial resolution); and (4) surface solar radiation and (5) total precipitation were obtained from an interim full-daily at surface forecast (European Centre for Medium-Range Weather Forecasts, 0.75° each 3 h). Monthly means of all three parameters were calculated using the Movebank Env-DATA track data annotation service (Cruz *et al*. 2013; Dodge *et al*. 2013) (figure 1).

Data processing and statistical analysis

The fix-loss rate (FLR) used in this study was calculated as a monthly value for each individual consisting of the proportion of days per month on which no fixes were recorded. We evaluated the effects of both biological and extrinsic factors (including both technical and environmental variables) on the performance of the 17 transmitters represented by monthly FLRs computed as the number of days per month on which no data were collected, divided by the total number of days on which data were scheduled to be collected. We generated a data set of monthly observations (n = 889), each with its own FLR. Since we reused three of the 17 transmitters to track the movement pattern of 20 birds, we needed to distinguish between two different levels when computing mean FLRs: the PTT/transmitter level and the individual level. For instance, the PTT usage time depends directly on the transmitter but variables related with the biological traits depend uniquely on the individual.

At first, we examined the FLR with some non-parametric explorative analyses to evaluate possible differences among these two levels and to evaluate the influence of the month on the FLR yearly distribution. Secondly, we grouped all the predictor variables: (1) age, sex, breeding and territorial status, and RPF (this latter describing flight activity) as biological factors; (2) PTT usage time per month and duty cycle as the technical factors; and (3) monthly means of topographic altitude, surface solar radiation, and total precipitation as environmental factors (see figure 1).

Thirdly, we performed a deviance partitioning analysis (Cuscó *et al*. 2018) to evaluate the effect on FLR of the single and joint contributions of each of the three groups of variables comparing by basic algebra the percentage of the explained conditional R^2 of each of the best generalized linear mixed models (GLMMs; Nakagawa & Schielzeth, 2013) built including the aforementioned biological, technical and environmental factors as fixed factors (where applicable) and the individual as a random factor. Thus, we built seven separate GLMMs to evaluate: (1) the single contribution of the biological factors, (2) the single contribution of the technical factor; (3) the single contribution of the environmental factor; (4) the joint contribution of the biological and technical factors; (5) the joint contribution of the biological and environmental factors; (6) the joint contribution of the technical and environmental factors; and (7) the joint contribution of the biological, technical and environmental factors (see more details about how to perform a deviance partitioning analysis in Anadón *et al*. 2006). These analyses were computed using R statistical software (R Core

Team 2019) version 3.6.2. For the GLMMs, we applied the "glmer" function of the "lme4" R package (Bates *et al*. 2009) with a binomial error distribution and logit-link function. All the deviance explained by the different groups of variables was expressed in percentages when we referred to the deviance partitioning results.

Fourthly, to determinate the significant variables influencing the FLR, we constructed the full model with all of the biological, technical and environmental variables as fixed factors and the individual as a random factor considering again a binomial error distribution and logit-link function, made a model selection using Akaike's Information Criterion (AIC; Burnham & Anderson 2002), and chose the best models with a delta AIC < 2 (figure 1).

And fifthly, to better understand the individual flying behaviour and how it could affect FLR, we analysed the influence of all of the same biological and environmental factors on the flight activity of the birds. For this analysis, a weighted RPF (wRFP) was created combining the monthly number of perched fix and monthly number of fix in flight (see Zuur *et al.* 2009 for applying binomial generalized models for proportions). Thus, we modelled wRPF using a GLMM (binomial error distribution and logit-link function) with all the biological and environmental variables as fixed factors and the individual as a random factor, and then selected models giving delta AIC < 2 (figure 1). Technical factors were not included as predictors in this model because of their obvious absence of influence over the flight activity of the birds.

For all the mixed models built in this study, the relative contributions of the fixed and random factors to R^2 were estimated with the "r.squaredGLMM" function from the package "MuMIn" (Barton 2019). We also reviewed for the variance inflation factors (VIF) for all the predictor variables at the first stages of the GLMMs building using the "car" package (Fox & Weisberg 2018) to assess collinearity (accepted VIF values < 3). In fact, we firstly considered season (defined as yearly quarterly periods i.e.: winter, from January to March; spring, from April to June; summer, from July to September; and fall, from October to December) and month for all the GLMMs' analyses, but they were finally excluded because of their high correlation with breeding season and surface solar radiation. All continuous variables were standardized and centred before modelling using the "scale" R function and all of the nonparametric analyses were performed after checking for the absence of a normal distribution.

Tracking data are inherently auto-correlated, although if fixes are taken infrequently enough so as to be longer than the autocorrelation timescale of the data, data can be considered independent, especially for animals that move long distances in short periods of time (D'Eon 2003; Mitchell *et al.* 2019). This is the case for our study species in this study, which present minimum duty cycles of 1 h (see also Margalida *et al.* 2016).

Ethics statement

All the work was conducted in accordance with relevant national and international guidelines, and conforms to all legal requirements. Captures and blood sample collection were carried out in compliance with the Ethical Principles in Animal Research. Thus, protocols, amendments and other resources were conducted in accordance to the guidelines approved by the Catalan Autonomous Government (Generalitat de Catalunya) following the R.D.1201/2005 (10th October 2005, BOE 21st October 2005) of the Ministry of Presidency of Spain. All experimental protocols were approved by the Catalan Autonomous Government and MAGRAMA (References 15.546 and 25.306).

RESULTS

A total of 95,686 location results from 20 bearded vultures tracked with 17 transmitters in the Pyrenees were recorded from 2006 until January 2019. Of these records: 32.6% were from females and 67.4% from males; 83.8% were from adults and 11.0% from subadults; 4.6% were from immatures and 0.6% from juveniles; 35.6% were from territorial birds and 64.4% from non-territorial ones.

Fix-loss rate (FLR)

We found a substantial FLR variability showing significant differences between individual birds (Kruskal–Wallis, χ^2 = 278.13, df = 18, $p < 0.001$) and also between individual PTTs (χ^2 = 251.39, df = 15, $p < 0.001$). Five PTTs showed an FLR less than a 30%, seven showed FLRs of between 30 and 40%, one had an FLR of 48.2%, and the remaining five registered an FLR equal to or higher than 50% (table 1). The FLR was highly variable at the individual level: seven birds had an FLR less than 30%; another seven showed FLRs between 30 and 40%; two ranged from 40 to 50%; and four showed an FLR higher than 50% (table 1). However, FLR barely fluctuated between months, showing no significant differences over the year (Kruskal–Wallis, χ^2 = 10.92, df = 11, $p = 0.45$), ranging between mean values of 0.31 ± 0.24 in May to 0.37 ± 0.23 in October.

The total conditional R^2 obtained from the GLMM built to evaluate the joint contribution

Table 1 | Basic biological traits and individual measures of fix loss rate (FLR) during a set period of time; rate of fix in flight (RFF) and rate of perched fixes (RPF) (mean ± SD for the monthly FLR, RPF and RFF individual values) for 20 birds tagged with 17 70 g solar-powered Argos' satellite transmitters (PTT/GPS Microwave Telemetry, Inc. Columbia, MD, USA) all bought in 2005-2008. In bold indicate transmitters (platform transmitter terminal, PTT) that were used on two different birds and * indicates when FLRs were equal or higher than 50%. For the territorial status (T: territorial; NT: non-territorial) the years of the beginning and ending (if any before 2019) are shown. The PTT FLRs were the same as the individual values of FLRs showed in this table, excepting for the case of the three PTTs that were reused: PTT2 presented a mean monthly FLR = 0.17 ± 0.14; PTT4 presented a mean monthly FLR = 0.36 ± 0.21 and PTT8 presented a mean monthly FLR = 0.50 ± 0.30*.

Individuals	PTT	Sex	Age (years)	Territorial status	FLR	Time period	Usage time (years)	RPF	RFF
Adrian	PTT1	M	4	T (2012-2016)	0.30 ± 0.15	05/2009 - 01/2019	9.8	0.72 ± 0.26	0.28 ± 0.26
Andreia	**PTT2**	H	>7	T (2009)	0.29 ± 0.15	03/2009 - 09/2009	0.6	0.47 ± 0.32	0.52 ± 0.32
Pocholo	**PTT2**	M	>7	NT	0.16 ± 0.14	07/2011 - 01/2019	7.6	0.75 ± 0.23	0.25 ± 0.23
Batín	PTT3	M	>7	T (2008)	0.29 ± 0.15	05/2008 - 04/2015	7.0	0.50 ± 0.33	0.50 ± 0.33
Cabó	**PTT4**	H	>7	T (2007)	0.47 ± 0.15	11/2007 - 08/2008	0.7	0.53 ± 0.37	0.47 ± 0.37
Sofia	**PTT4**	H	>7	NT	0.34 ± 0.20	11/2008 - 05/2012	3.6	0.71 ± 0.29	0.29 ± 0.29
Dulantz	PTT5	M	6	NT	0.22 ± 0.19	04/2013 - 10/2014	1.5	0.64 ± 0.30	0.37 ± 0.30
Elisabeth	PTT6	H	18	NT	0.30 ± 0.21	03/2015 - 01/2018	2.9	0.77 ± 0.23	0.23 ± 0.23
Garrotxa	PTT7	H	5	T (2012)	0.40 ± 0.29	05/2008 - 06/2013	5.2	0.61 ± 0.31	0.38 ± 0.31
Gervàs	**PTT8**	H	>7	T (2007)	0.28 ± 0.19	05/2007 - 04/2009	1.9	0.69 ± 0.28	0.31 ± 0.28
Min	**PTT8**	M	5	NT	0.56 ± 0.30*	05/2009 - 08/2017	8.4	0.73 ± 0.27	0.27 ± 0.28
Isaac	PTT9	M	5	NT	0.19 ± 0.16	11/2010 - 01/2014	3.2	0.70 ± 0.26	0.29 ± 0.26
Jairo	PTT10	H	4	T (2014)	0.32 ± 0.17	11/2010 - 06/2016	5.6	0.76 ± 0.27	0.24 ± 0.27
Morreres	PTT11	M	1	NT	0.28 ± 0.15	11/2007 - 09/2012	4.9	0.62 ± 0.31	0.37 ± 0.31
Nicky	PTT12	M	5	T (2011)	0.64 ± 0.30*	06/2009 - 05/2017	8.0	0.53 ± 0.34	0.47 ± 0.34
Noah	PTT13	H	>7	NT	0.48 ± 0.13	04/2008 - 09/2008	0.5	0.84 ± 0.23	0.16 ± 0.23
Revilla	PTT14	H	5	NT	0.33 ± 0.17	04/2013 - 11/2013	0.6	0.87 ± 0.17	0.13 ± 0.17
Sasi	PTT15	M	1	NT	0.61 ± 0.24*	08/2007 - 06/2008	0.9	0.78 ± 0.24	0.22 ± 0.24
Subfli	PTT16	H	4	T (2012)	0.33 ± 0.17	05/2008 - 04/2012	4.0	0.72 ± 0.28	0.28 ± 0.28
Tossal	PTT17	H	>7	T	0.74 ± 0.27*	11/2006 - 12/2006	0.1	0.82 ± 0.22	0.18 ± 0.22

of the biological, technical and environmental factors to the FLR was 0.148 (0.093 of the marginal R^2 corresponding to the fixed effects + 0.055 of deviance corresponding to the random effects). The highest was provided by the sum of both technical factors (single effect of 1.5%) and biological traits (with the highest single retained effect of 5.8%) and its interactions with the other groups (− 0.6% shared between both groups, − 0.5% shared between technical factors and environmental factors, 3.3% shared between biological traits and environmental factors, and 13.1% resulting from the interaction of the three groups). Environmental factors retained a single effect of − 7.8% (figure 2).

Regarding the GLMMs results (table 2), we found two models from the total selection that met the delta AIC < 2 criterion. The parameters

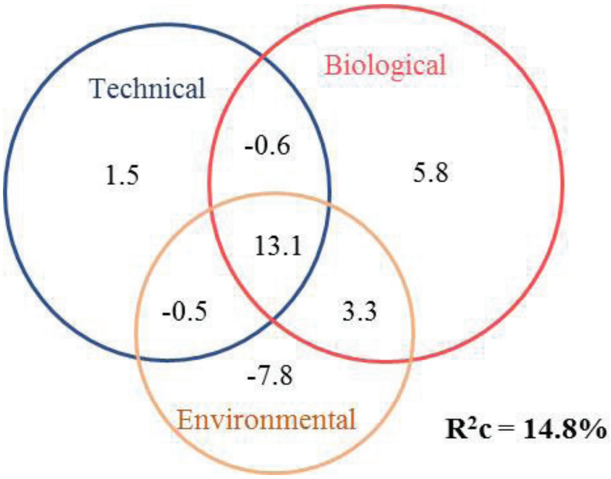

Figure 2 | Conditional R^2 partitions resulting from a partial regression analysis of 17 Microwave PTTs monthly fix-loss rates. Percentages of conditional R^2 (deviance explained by the entire model, including both fixed and random effects) explained by each group of variables: ***Technical*** (PTT's lifetime and duty cycle), ***Biological*** (rate of perched fixes, sex, age, territorial and breeding status), and ***Environmental*** (surface solar radiation, total precipitation, and topographic altitude) and by their interactions. The total conditional R^2 of the model is also shown.

Table 2 | Competing GLMMs to evaluate the influence of different biological traits and extrinsic factors (comprising both technical and environmental variables) on the fix loss rate (FLR). The individual (Indiv) was included as a random factor. We present the most parsimonious selected model with ΔAIC < 2. K: total number of parameters (explanatory terms + random term + residual deviance); AIC: corrected Akaike information criterion; ΔAIC: difference between the AIC value for that model and the best model; and W: Akaike weight. Biological traits included: flight activity measured through the rate of perched fixes (RPF), age (Age), territorial status (Territ), breeding season (Br_S) and sex (Sex). Technical variables were transmitter usage time (T_PTT) and duty cycle (Dcycle), and environmental variables were topographic altitude, surface solar radiation, and total precipitation

MODEL	FACTORS	K	AIC	ΔAIC	W
M1	T_PTT - RPF + Age + Sex + Territ + Br_S + (1|Indiv)	10	6929.6	0	0.725
M2	T_PTT -Dcycle - RPF + Age + Sex + Territ + Br_S + (1|Indiv)	11	6931.6	1.94	0.275

influencing the efficient performance of the transmitters included all of the biological and technical variables tested. Non-territorial birds, males, and breeding individuals showed a significantly lower FLR than females, territorial birds or non-breeding vultures. The rate of perched fixes (RPF) showed a negative relationship with the FLR, while the PTT usage time exerted the opposite effect, so that the higher the RPF and—in parallel—the smaller the PTT usage time, the lower the FLR becomes. Indeed, longer duty cycles provoked also lower FLR, although this variable was only selected for one of the two final models selected. Regarding age, adults and subadults showed significantly lower FLRs. None of the environmental variables were included in the significant GLMMs eventually built. The partial effects of all the explanatory variables included at least in one of the two final models selected are shown in *Supplementary* figure S1.

Flight activity

Considering all the data, we observed an average of 64.3 ± 20.0% rate of perched fixes (RPF) and 31.8 ± 16.5% rate of fixes in flight (RFF). Of the 20 bearded vultures tagged, 65.0% (n = 13) showed a quite homogeneous flight activity pattern, their mean RPF ranging between 87.4 and 68.8%. Three individuals showed rates of 61.3–63.5% and the other four showed perched fix rates lower than 52.8%. Even so, three of the birds exhibited a higher monthly RFF than RPF (table 1).

The RPFs ranged significantly between 70.4% in summer and 66.4% in winter (Kruskal–Wallis, $\chi^2 = 21.12$, df = 3, $p < 0.001$). The variables selected for the competing GLMMs influencing flight activity (table 3) were territoriality, breeding status, age, and sex (although, the last two were not always

Table 3 | Competing GLMMs for evaluating the influence of different biological traits and environmental variables on birds' flight activity (computed as a weighted rate of perched fix). The individual (Indiv) was included as a random factor. We present the most parsimonious selected models with ΔAIC < 2. K: total number of parameters (explanatory terms + random term + residual deviance) AIC: corrected Akaike Information Criterion; ΔAIC: difference between the AIC value for that model and the best model; and W: Akaike weights. Biological traits included: age (Age), territorial status (Territ), breeding season (Br_S), and sex (Sex). Environmental variables were topographic altitude, surface solar radiation, and total precipitation, but none was selected for the final models.

MODEL	FACTORS	K	AIC	ΔAIC	W
M1	Territ + Br_S + (1|Indiv)	4	7154.2	0.00	0.3
M2	Sex + Territ + Br_S + (1|Indiv)	5	7154.4	0.19	0.3
M3	Age + Sex + Territ + Br_S + (1|Indiv)	8	7155.1	0.90	0.2
M4	Age + Territ + Br_S + (1|Indiv)	7	7155.4	1.17	0.2

included in the final models). Territorial and breeding individuals showed significantly lower RPFs than non-breeding and non-territorial ones. The mean RPF and RFF were 50.2 ± 25% and 39.3 ± 22.6% for territorial individuals and 72 ± 10.5% and 27.6 ± 10% for non-territorial birds, respectively. The environmental variables were not included in the final models. The partial effects of all the explanatory variables included at least in one of the four final models selected are shown in *Supplementary* figure S2.

DISCUSSION

Studies of movement ecology often suffer from lost geolocation information due to: (1) technical glitches such as insufficient battery power; (2) environmental factors such as the roughness of the terrain (i.e. the conjunction of vegetation and topography; Aubrecht *et al.* 2010) or changing climatological parameters; and (3) intrinsic factors (i.e. biological traits) such as the behaviour of individuals (Frair *et al.* 2010; Silva *et al*. 2017). Our findings point out that a combination of technical variables and biological traits gave the best explanation of maximum deviance (22.6%), suggesting that these two groups of factors have a much greater influence on the monthly FLR than environmental factors. This was also one of the main conclusions achieved by Hofman *et al.* (2019), in a study where they gathered information of 167 projects deployed on 62 species in 142 study areas worldwide through some questionnaires with the aim of assessing the performance of satellite telemetry units (predominantly collars) tracking terrestrial wildlife. Concretely, they found out that the transmitter performance was strongly influenced by unit and species characteristics while environmental conditions increased the variability, influencing the transmitters' technique effectiveness. Concurrently, we propose that it could be that technical and biological variables already gather part of the deviance explained by the environmental factors. Such is the case for the breeding status, a parameter directly related to time of year, seasonality, solar radiation, and daylight duration in addition to its biological significance for the species. Another technical variable that affects the FLR, the transmitter battery level, is also related to solar energy availability, and hence to the time of year (through the seasonal variations in solar irradiance received by the device; Byrne *et al*. 2017; Silva *et al*. 2017). Battery power limits the time for the transmitter to search satellites to obtain a location and so influence in the number of satellites acquired for the process (Moen *et al*. 1996), however it is a parameter only available in the newer GPS models. In this respect, the logger generation, transmitters' manufacturers, and data receiving system—all of the three uniform parameters for our study case given that all the 17 devices were Microwave solar-powered Argos-GPS bought between 2005 and 2008—are also important technical variables that need to be considered when studying GPS accuracy and location errors (Frair *et al.* 2010; Silva *et al*. 2017; Péron *et al*. 2020). On the other hand, our results show that individual flight activity could be one of the most influential factors determining the fix performance of a device. Contrary to previous studies; Byrne *et al.* 2017; Silva *et al.* 2017) and our initial hypothesis, the greater the proportion of perched fixes, the lower is the resulting FLR. One possible explanation for this observation could be related to the difficulty of satellite acquisition while a bird is flying, as has been noted for moving animals in various mammal studies (Edenius 1997; Cargnelutti *et al*. 2007; Frair *et al.* 2010) perhaps because of changes in the position and orientation of the GPS transmitter. Our findings also confirmed that longer duty cycles (of 2 h compared with those of 1 h) produced lower FLR, probably associated with the fact that more intense duty cycles increase the transmitter energy consumption and consequently reduce the device usage time (Jurdak *et al.* 2010). In fact, Silva *et al.* (2017) suggested that FLR due to poor GDOP (when Geometric Dilution of Precision limits the transmitter to contact with enough satellites to produce a fix) increased when the birds moved. Nevertheless—considering that the time to obtain a fix increase in dynamic versus static conditions—longer duty cycles (of 2 h compared to 30 s and 15 min interval times) would produce higher fix loss rates while flying, but the opposite situation could happen while the birds are perched, when the length of the fix interval is not so relevant. In addition, as it was predicted, the FLR increases with transmitter usage (as happened in Gau *et al*. 2004; Hofman *et al*. 2019), a relevant information considering that the mean usage time for our PTTs was 5.34 ± 3.03 years (n = 14).

Given the number of studies which point to landscape structure as an important driver of the FLR (Girard *et al*. 2002; Cain *et al.* 2005) we expected the topographic altitude as a variable influencing FLR. However, our monthly-scale analysis could have diluted the effect of this environmental variable and a complementary shorter time-scale FLR study (e.g. daily or hourly) may show a higher influence of this specific variable on the fix loss errors. Notwithstanding these uncertainties, our analyses of the possible effects of bearded vulture biological traits on the FLR constitutes a novel approach to the better understanding of the treatment of PTT locations. All the biological variables tested in this study influenced the RPF and also significantly affected the fix reception success. Interestingly, non-territorial bearded vultures travel further and later in the daylight than territorial birds (García-Jiménez *et al*. 2018), but exhibit significantly higher RPFs (72 ± 10.5% for non-territorial individuals versus 50.2 ± 25% for territorial birds). At the same time, breeding and territorial adults showed lower FLRs even if they spent less time perched than non-breeding, non-territorial and younger and individuals. Probably their daily activity related to parental duties (nest-building, territorial defense, and foraging) results in increased flight activity and a higher proportion of their time spent flying, even if the distances covered are shorter than those of non-territorial birds (Krüger *et al.* 2014; Margalida *et al*. 2016; García-Jiménez *et al*. 2018).

Our results showed an overall monthly mean FLR of 34.5 ± 24.72% ranging between a minimum of 3% and maximum of 100% (n = 17). This is lower than the values found for analogous transmitters by Silva *et al.* (2017), used on the same Pyrenean and Cantabrian population of bearded vultures (FLR = 0.40 ± 0.12), and those recorded by Soutullo *et al*. (2007), for lightweight Argos GPS transmitters used on Golden Eagles *Aquila chrysaetos* in a rocky cliff area in Eastern Spain (FLR = 0.45). In this latter study, breeding season also influenced the FLR (probably through seasonal effects), as was the case in our study. Nevertheless, our findings show the importance of understanding that significant variations in FLR may be due either to variations in individual bird behaviour or to variations in technical glitches affecting each PTT performance. Therefore, it should be expected that both biological and technical factors play a fundamental role in the correct performance of the GPS fix programming.

The significant differences in FLR between male and female birds are not easily explained from a behavioural and ecological perspective (mean values of 0.32 for males cf. 0.39 for females), even if non-territorial males do indeed exploit larger areas and fly over longer distances, as it is the case of territorial females (Margalida *et al*. 2016; García-Jiménez *et al*. 2018). The specific relationships between the biological traits of this species and RPF or RFF are clear, but even if their influence on the FLR is also obvious, it is more difficult to explain the effect of certain biological variables such as territoriality or sex on FLR. The fix success rate results are most likely due to a synergy between complex interactions; for instance, between flight height and terrain roughness, or between the availability of environmentally optimal flight conditions (which are also favorable for solar battery charging) linked to the likelihood of flight activity and the resulting associated increase in transmitter movement. In any case, it is clear from this study that biological factors such as sex, age, breeding and territorial status have particular effects on

FLR and must be considered when studying fix error rates in other flying species (e.g. bird and bat species). Even considering the apparent limitations of working with a single species in a GPS fix loss error study, as it has been shown, our findings can be extrapolated to different medium and large-size animal populations and species. Moreover, technological improvements of materials and both hardware and software enhancements are leading to increasingly better transmitters' performance with improved location accuracy and reduced FLRs. However, there are still many transmitters in use (in addition to the quite a few already developed) that present scheduled location duty cycles, data receiving Argos-GPS system and device manufacturers similar to the ones evaluated in this study, so these findings obtained remain relevant for long-term conservation studies.

Every animal telemetry tracking study should include an error analysis before reaching any ecological conclusions or hypotheses regarding spatial utilization, since the results can vary substantially depending on extrinsic factors such as GPS transmitter model, retrieval data system, PTT usage time, season, etc., or biological factors such as those analysed in this study. All of these changing elements can influence the data collected and lead to errors in interpreting patterns of movement. Fortunately, these kinds of tracking error, together with accuracy biases in the horizontal plane (x and y coordinates) are being addressed and overcome as transmitter technology improves, thus reducing the potential influence of tracking device shortcomings on the recording and interpretation of basic parameters regarding the spatial ecology of a species Frair *et al.* 2010; Augustine *et al*. 2011; Douglas *et al*. 2012; Byrne *et al*. 2017; Péron *et al*. 2020).

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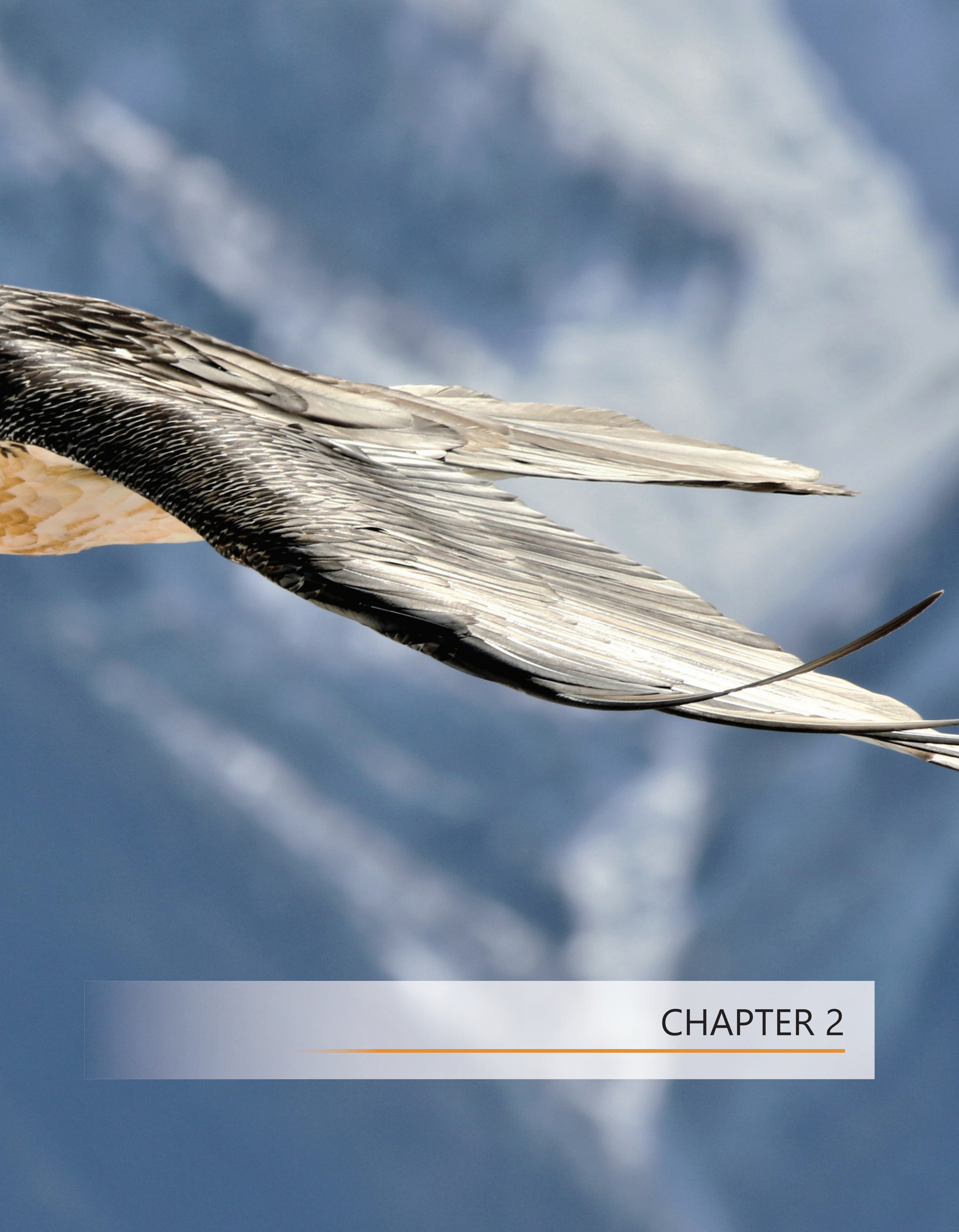

CHAPTER 2

Photo by Walter Bachmann.
A close-up of an adult bearded vulture (*Gypaetus barbatus barbatus*) in flight.

CHAPTER 2

Drivers of daily movement patterns affecting an endangered vulture flight activity

by

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ABSTRACT

The development of satellite tracking technology enables the gathering of huge amounts of accurate data on animal movements over measured time intervals, to reveal essential information about species' patterns of spatial use. This information is especially important in optimizing the design of conservation and management strategies for endangered species. In this study, we analysed the main drivers of daily patterns in the flight activity of the threatened Bearded Vulture *Gypaetus barbatus*. We studied 19 Bearded Vultures tagged with solar-powered GPS transmitters from 2006 to 2016 in the Pyrenees (Spain). We assessed the relative influence of external factors (season and daylight time) and internal factors (sex, breeding season and territorial status) on their daily activity behaviour by computing mean hourly distance travelled, maximum displacement and cumulative distance travelled per hour. Our findings showed a clear difference in all the estimators between territorial and non-territorial (floating) members of the population, showing that non-territorial individuals spent much longer in flight and travelled larger distances per day. We detected an important influence of daylight time and season on the daily rhythms of Bearded Vultures; flight activity increased during the last three quarters of daylight and was greatest in the spring. Breeding period and sex had also an effect on the maximum displacement and cumulative distance travelled. Individuals flew more during the breeding period and females tended to exhibit greater cumulative and maximum distances per hour than males regardless of breeding season. Pyrenean Bearded Vultures flight daily activity was strongly influenced by daylight time, season, and territorial status, while individual sex and breeding season showed a milder effect on the birds' movement behaviour. This study gives a novel insight into how external factors act as main drivers of the daily flight activity pattern of a long-lived avian scavenger.

Keywords

daily movements, daylight time, GPS, *Gypaetus barbatus*, season, Spain, territorial status

BACKGROUND

Interest in movement ecology has increased in recent years due to its key role in the design of more specific and efficient management and conservation strategies. The development of satellite tracking technology enables the gathering of huge amounts of accurate data on animal movement over measured time intervals, to provide essential information on species' patterns of spatial use (Rutz & Hays 2009; Bouten et al. 2013). Modern satellite transmitters can also record individual physiological parameters during flight (Vyssotski *et al.* 2006; Mandel *et al.* 2008). The activity decisions made by individuals influence overall population behaviour and so affect population viability as each individual decides its own specific demographic process, such as migration, feeding, and reproductive behaviour (Morales *et al.* 2010). The assessment of space use and territory occupancy patterns is particularly useful in bird community studies (e.g. Tracey *et al.* 2004; Holland *et al.* 2009; Gaidet *et al.* 2010). Beyond the direct information gathered on dispersal (Robinson *et al*. 2009; Margalida *et al*. 2013), roost site selection (Balbontín 2005), and foraging activity (Pinaud & Weimerskirch 2007; Monsarrat *et al.* 2013), study of movement ecology provides information indirectly related to an animal's behaviour in reaction to prevailing climatic conditions (Mandel *et al.* 2008; Wilson *et al.* 2008; Shepard & Lambertucci 2013), on the effects of food availability on the use of space and on population trends (Margalida & Colomer 2012; Margalida *et al.* 2017).

Avian scavengers provide human society with indispensable ecological services, recycling carrion biomass. through their removal of waste and preventing the accumulation of dead animal biomass, so reducing the spread of diseases and contributing to nutrient cycling (DeVault *et al.* 2003; DeVault *et al.* 2016). Due to the ephemeral occurrence and random distribution of carcasses, vultures have evolved adaptive traits to exploit carrion as effectively as possible (Kendal 2014; Moreno-Opo *et al.* 2015; Moreno-Opo *et al.* 2016). The balance between their maximization of food intake and minimization of energy expenditure has therefore developed to determine the daily foraging movements of scavenging species (Spiegel *et al*. 2013; Alarcón *et al.* 2017). To date, several internal and external factors have been suggested as drivers of the daily activity movement patterns of scavengers, acting either independently or in synergy. Intrinsic factors include biological and physiological parameters such as territorial status, sex, breeding season and level of hunger (Donázar *et al.* 1999; Spiegel *et al*. 2013; Krüger *et al.* 2014; Holland *et al*. 2017). External factors are mainly characterized by weather conditions and daylength —both of which generally change seasonally— (Mandel *et al.* 2008; Shepard *et al*. 2011), food availability (Kendal 2014), and intra- or interspecific interactions (Kendal 2014).

The Bearded Vulture *Gypaetus barbatus* is a long-lived territorial vulture inhabiting Old World mountain biomes with a diet consisting 70–90% of bones from wild and domestic ungulates, and therefore occupies a very specialized trophic niche (Houston & Copsey 1994; Margalida 2010; Moreno-Opo *et al.* 2016). Despite the increment of the Pyrenean population in the last 30 years, this positive tendency could be menaced by mortality factors such as the illegal use of poison baits, lead intoxication, food shortages, and anthropogenic habitat changes (Hernández & Margalida 2009; Margalida 2012; Margalida *et al*. 2014; Berny *et al*. 2015; Mateo *et al*. 2015). This situation highlights the need for an in-depth understanding of the potential threats, including mortality hotspots, the causes of breeding failure, and limitations on the species' use of space. For instance, information regarding their daily activity patterns is especially useful in planning reintroduction conservation programs and to enhance any future conservation or management action considering its habitat use and spatial behaviour. This study set out to assess the influence of internal and external factors on the daily activity patterns of Pyrenean Bearded Vulture flight activity. To this end, we analysed 38,248 data obtained from a population of 19 GPS-tracked Bearded Vultures in the Pyrenees (Spain) between 2006 and 2016, to examine the effect of internal factors such as sex, territorial status and breeding season, and of external factors such as daylight time and season.

METHODS

Study species

The habitat distribution of Bearded Vultures has been shrinking since the 1970s (with only 243 pairs remaining in the European Union in 2016). During the last 30 years a variety of management and conservation programs have been developed for this threatened species, achieving a substantial rise in the Pyrenean population, although, the overall distribution of Bearded Vulture has scarcely expanded (Margalida *et al.* 2008). This species is enlisted as near threatened by the IUCN Red List (BirdLife International 2015).

Study area

This study was conducted in Pyrenees, located in the border area between France and Spain, in the Eurosiberian region. In this area the

Bearded Vulture population comprises more than 70% of the European breeding population. The most important breeding areas lies on the southern slopes of the Pyrenees, with the highest nesting densities in steeply sloping areas over 1000 m height level, where human access is limited and orographic updraughts are more frequent (Margalida 2010).

Capture, tracking and data collection

Twenty Bearded Vultures were captured in the period 2006–2016 using radio-controlled bow-nets at supplementary feeding stations (n = 17), at nests (n = 1), or as injured individuals recovered at official wildlife recovery centers (n = 2), where birds are released following rehabilitation (for more details about these individuals' capture see (Margalida *et al.* 2016; Margalida *et al.* 2017). We monitored their movement patterns using 70 g solar-powered Argos satellite transmitters (PTT/GPS Microwave Telemetry, Inc. Columbia, MD, USA) attached by means of a breakaway harness with a 0.64 cm Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA). The transmitters were programmed to send a fix (manufacturer's estimated error ± 18 meters) each hour from 4:00 to 22:00 UTC, with the exception of two individuals, whose transmitters sent a GPS location every 2 h. Birds were aged into four different classes using plumage characteristics: juveniles (birds until the 1st year), immatures (2–3 years), sub-adults (4–5 years) and adults (6 years or over). Identification of gender was performed using blood samples by PCR amplification of the CHD-W gene (Ellergren 1996). We defined territorial Bearded Vultures when exhibited spatially aggressive defense, nestbuilding behaviour and sexual activity on a fixed area (Burt 1943; Böger *et al.* 2008; Margalida *et al.* 2016).

Data processing and statistical analysis

We analysed the daytime routine of Bearded Vultures by calculating three different estimators: maximum displacement, defined as the average Euclidean distance between the initial daily location and any position reached on the consecutive hours; hourly distance, approximated as the average straight-line distances covered in an hour and cumulative distance travelled, estimated as the sum of straight-line distances covered during each hour on a given day. To build a uniform and robust data base, we selected only data from days where at least seven consecutive GPS-locations were recorded during day with a maximum time lapse of 4 h between fixes. One of the tracked birds did not meet this minimum set of criteria for locations, so we exclude all its data from the analysis.

We studied differences in the daily movement parameters according to three internal factors: sex, breeding season, and territorial status; and two external factors: daylight time and season.

To evaluate the influence of sex on the daily movement of Pyrenean Bearded Vultures we considered only territorial individuals. For breeding season comparisons of daily activity patterns, we divided the data in the two breeding periods (*breeding period*, from 1st January to 31st July, and the *non-breeding period*, from 1st August to 31st December) based on Margalida *et al.* (2016). To study the possible influence of season on the daily pattern of flight activity we defined four seasons conforming to the Mediterranean climate: spring (from 21st March to 20th June); summer (from 21st June to 22nd September); fall (from 23rd September to 20th December); and winter (from 21st December to 20th March). We did not include age in the analysis because our previous studies showed it to be subordinate compared to territorial status (Margalida *et al.* 2016). Differences in maximum displacement, cumulative distance travelled and hourly distance travelled for different territorial status and breeding season were compared using the Wilcoxon Mann–Whitney tests. Sex related differences between territorial individuals were also tested for these three variables. We analysed each relationship independently.

To standardize the seasonal variation in daylight, we generated an index of daylight duration (hereinafter called daylight index) which denotes the daylight time considering the astronomical twilight as the start and the end of a daylight length setting sunrise —the astronomical dawn, the time when the geometric center of the Sun is 18 degrees below the horizon in the morning— (value 0) and sunset —the astronomical dusk, when the geometric center of the Sun is 18 degrees below the horizon preceding the night— (value 1) for each day. We included the three twilight periods before sunrise (astronomical, nautical and civil twilights; data obtained from www.timeanddate.com and summarised in *Additional file 1*) because several authors have suggested that they mark the beginning of the first daily peak of activity in bird's circadian pattern (Cuthill & Mcdonald 1990; Aschoff 1966; Liechti *et al.* 2013), as well as a short time after sunset during which birds were observed making the journey back to their roosting sites. We computed this daylight index as the division of daylight elapsed fix time by daylight length, where the numerator is the period of daylight spent until the fix transmission, and denominator is length of daylight hours within a given 24 h day.

To analyse and represent the data we grouped the daylight index ranges into an integer scale from 0 to 10 following the scale described above, but to a higher decimal order. We incorporated also some locations before and after the astronomical twilight (with index values − 1 and 11, consecutively) to evaluate the behaviour of the birds some dark hours previous to sunlight incidence (*Additional file 1*, *Additional file 2*: figure S1 and table S1).

To examine the relationship between movement parameters and biological (sex, breeding season, and territorial status) and external (daylight time and season) factors we used linear mixed models (LMM) with individual as a random factor (McCullagh & Searle 2000). We compared each model with the null case, including both the variables and the interactions. Model comparisons were carried out using Akaike information criteria (AICc; Burnham & Anderson 2003). We computed delta AICc to determine the strength of evidence, and AICc weights to represent the relative likelihood of each model (Burnham & Anderson 2003). Models with delta AICc > 4 were discarded. All analyses were conducted using R statistical software (v 2.3-2. R Development Core Team 2007, http://www.Rproject.org) with the lme4 package for LMM analyses. All tests were two-tailed and statistical significance was set at $\alpha \leq 0.05$. All results were shown as mean ± 1 SD.

RESULTS

We recorded 78,814 GPS locations from 20 Pyrenean Bearded Vultures, during November 2006 to December 2016. After filtering, we analysed 38,248 fixes from 19 individuals. The highest frequencies of locations were recorded from 9:00 to 16:00 UTC usually concurring with the hours with major sunlight availability (*Additional file 2*: figure S1, S2 and table S2). The records were —according to sex— 34.1% females and 65.9% males and —in terms of the age class and territorial status— 86.6% adults (of which 28.6% were locations from territorial birds), 11.3% were from subadults, 2.0% were from immatures, and 0.1% were from juveniles.

Territorial status and breeding season

The floating population (non-territorial birds) exhibited a significantly greater daily activity pattern compared to territorial birds. Significant differences were found in cumulative distance travelled (Wilcoxon test, $Z = 13.0$, $p < 0.001$), maximum displacement during the daylight ($Z = 40.2$, $p < 0.001$) and hourly distance travelled ($Z = -3.4$, $p < 0.001$) according to their territorial status. Non-territorial individuals exhibited the highest values for the three daily distance covered estimators during the breeding period (Figs. 1, 2 and 3). In nonterritorial individuals, the maximum mean cumulative distance travelled was c. 42 km, showing a marked rise during the two middle daylight quarters (from daylight index values of 2–8), while territorial individuals showed a gradual increase in this distance estimator throughout the daylight hours (figure 1), reaching maximum medium values of 20–22 km cumulative distance travelled. The same pattern was observed for the maximum daytime displacement in the non-territorial birds, although territorial vultures showed increasing mean values until the middle of the daylight period, followed by stabilization of these values (figure 2). Independently of territorial status, the longest average hourly distances were travelled during the middle of the daylight period, although the greatest distances were achieved by non-territorial individuals (6.75 ± 9.05 km), regardless of breeding season (figure 3). Furthermore, non-territorial individuals during the breeding period showed a range of maximum average displacements between 0.06 ± 0.11 and 20.77 ± 26.51 km, while non-breeding birds had a significantly lower mean maximum displacement range of between 0.14 ± 0.21 and 16.83 ± 21.01 km ($Z = -7.4$, $p = 0.01$). Breeding season also significantly affected territorial individuals: during the breeding period they exhibited a notably higher maximum distance from the nest 5.25 ± 13.56 km, and longer mean cumulative distance travelled of 22.07 ± 21.48 km, compared to the maximum daily displacement of 3.72 ± 8.41 km ($Z = -7.5$, $p < 0.001$) and daily covered distance of 20.02 ± 18.06 km ($Z = -5.7$, $p < 0.001$) observed during the non-breeding period. The territorial birds also showed significantly higher values of hourly displacement during the breeding period ($Z = -4.6$, $p < 0.001$; see figure 3).

The effect of sex in territorial Bearded Vultures

During the breeding period, females showed higher flight activity than males, performing maximum distances travelled per day of 14.31 ± 28.93 km, cumulative distances travelled of 37.38 ± 37.45 km, and hourly distances travelled of 5.22 ± 7.45 km, in contrast with males which travelled mean maximum day distances of 5.07 ± 6.76 km ($Z = 5.2$, $p < 0.001$), cumulative daily distances of 21.67 ± 17.53 km ($Z = 2.4$, $p = 0.02$) and hourly distances of 3.24 ± 4.27 km ($Z = 3.3$, $p = 0.001$). A similar trend was also observed within the non-breeding birds, where males achieved a maximum displacement of 3.20 ± 4.12 km and hourly distances of 3.04 ± 3.94 km at least 1 km significantly less than females, which achieved maximum distances covered per day of 6.96 ± 17.94 km ($Z = -2.6$, $p = 0.009$) and hourly movements of 4.42 ± 5.48 km ($Z = -3.0$, $p = 0.002$; see Figs. 4, 5 and 6).

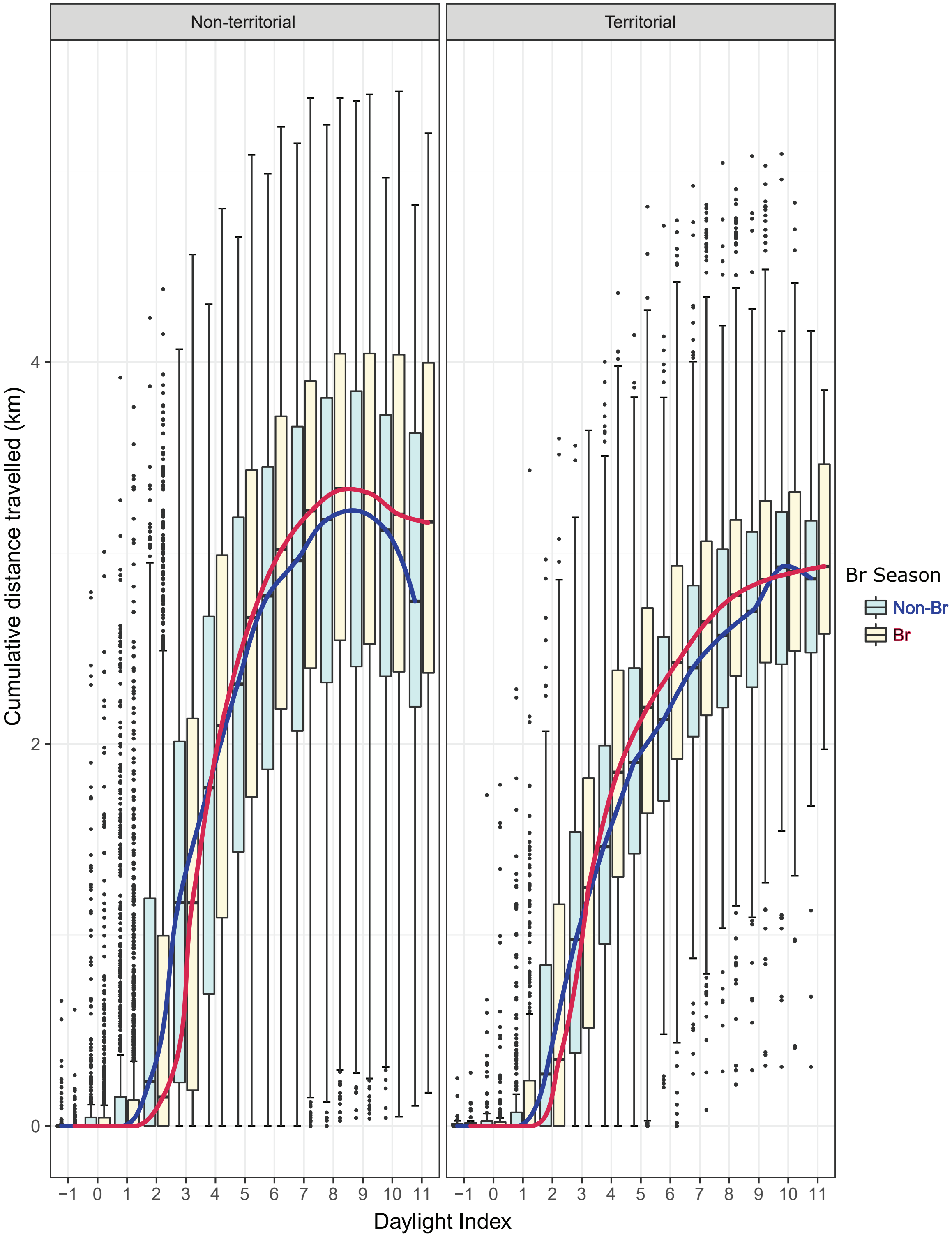

Figure 1 | Influence of territorial status (left: non-territorial, right: territorial) and breeding season (blue: non-breeding, red: breeding) on the cumulative distance travelled. The response variable, log (y + 1), has been transformed to represent the variation graphically

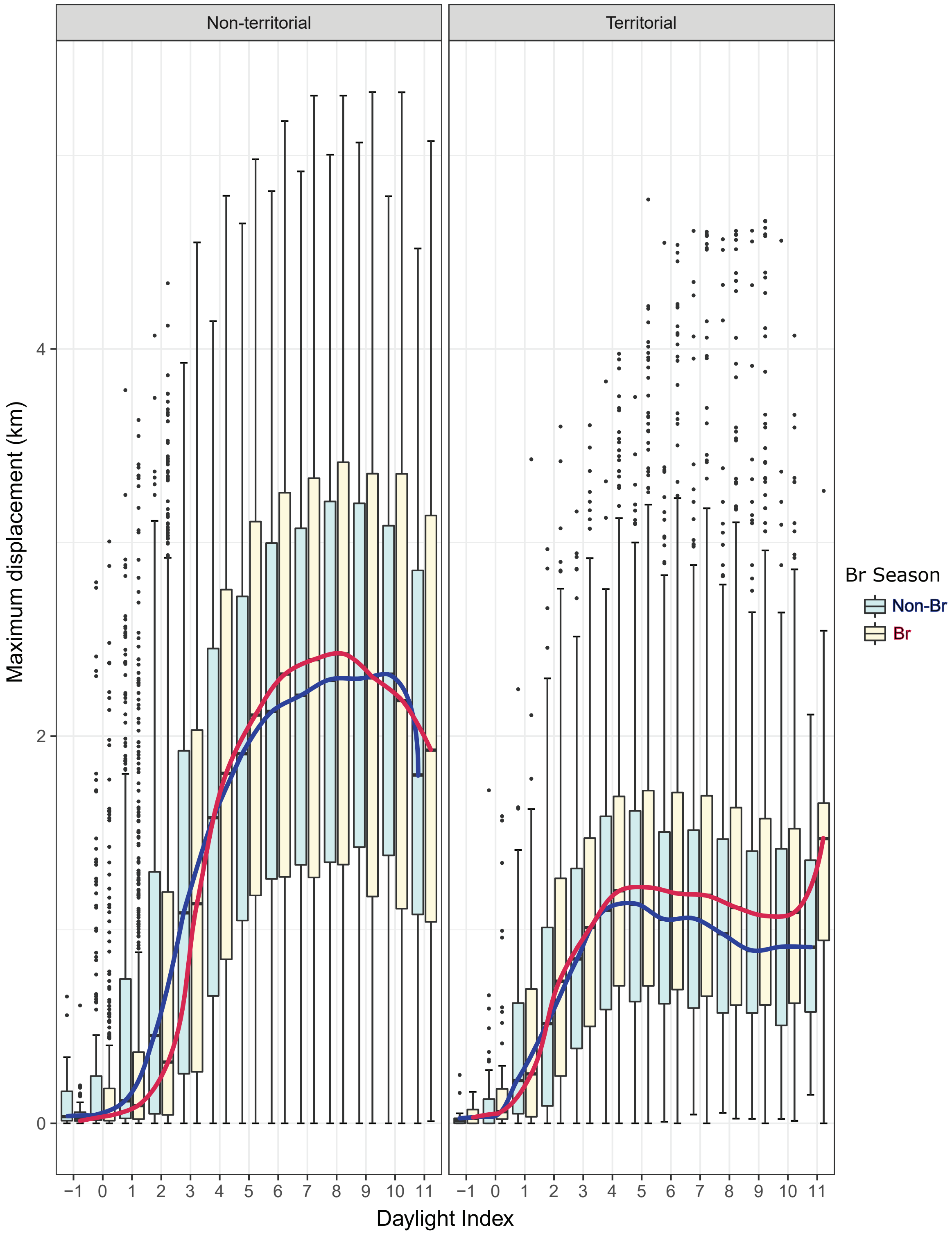

Figure 2 | Influence of territorial status (left: non-territorial, right: territorial) and breeding period (blue: non-breeding, red: breeding) on the maximum displacement travelled by adult territorial individuals.

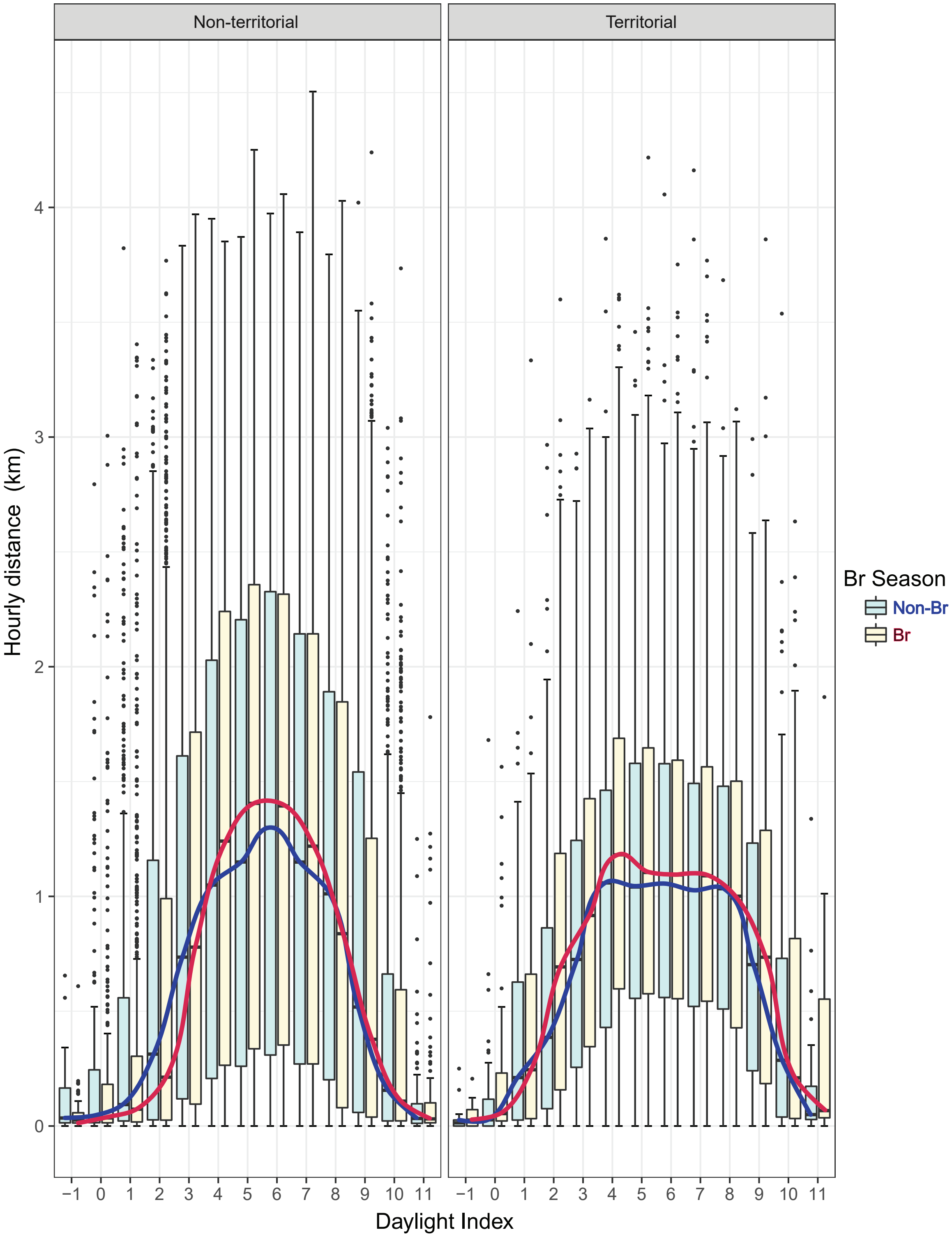

Figure 3 | Influence of territorial status (left: non-territorial, right: territorial) and breeding period (blue: non-breeding, red: breeding) on the hourly maximum displacement. The response variable, log (y + 1), had been transformed to represent the variation graphically

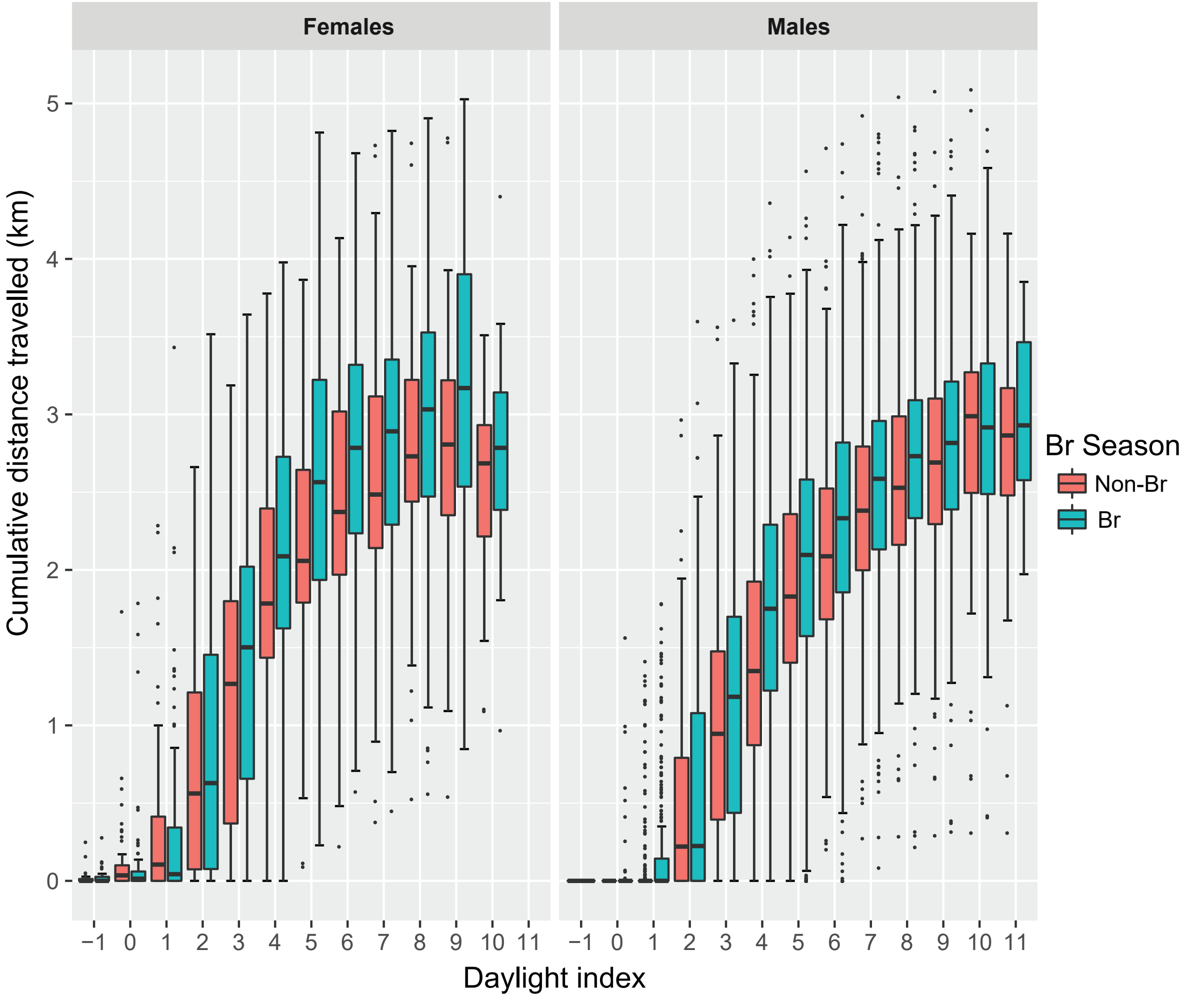

Figure 4 | Influence of sex and breeding period (red: non-breeding, blue: breeding) on the cumulative distance travelled by adult territorial individuals.

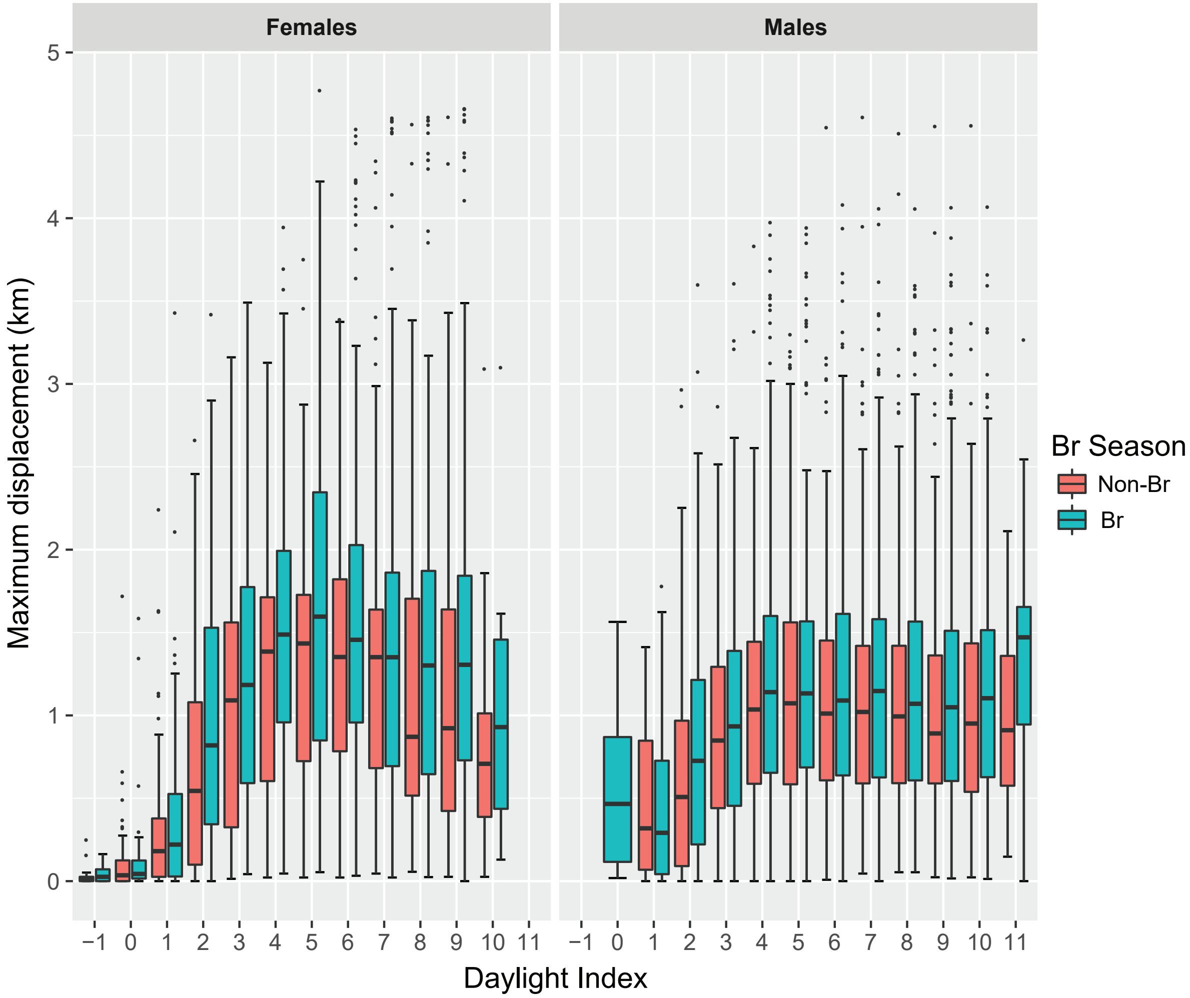

Figure 5 | Influence of sex and breeding period (red: non-breeding, blue: breeding) on the maximum displacement travelled by adult territorial individuals.

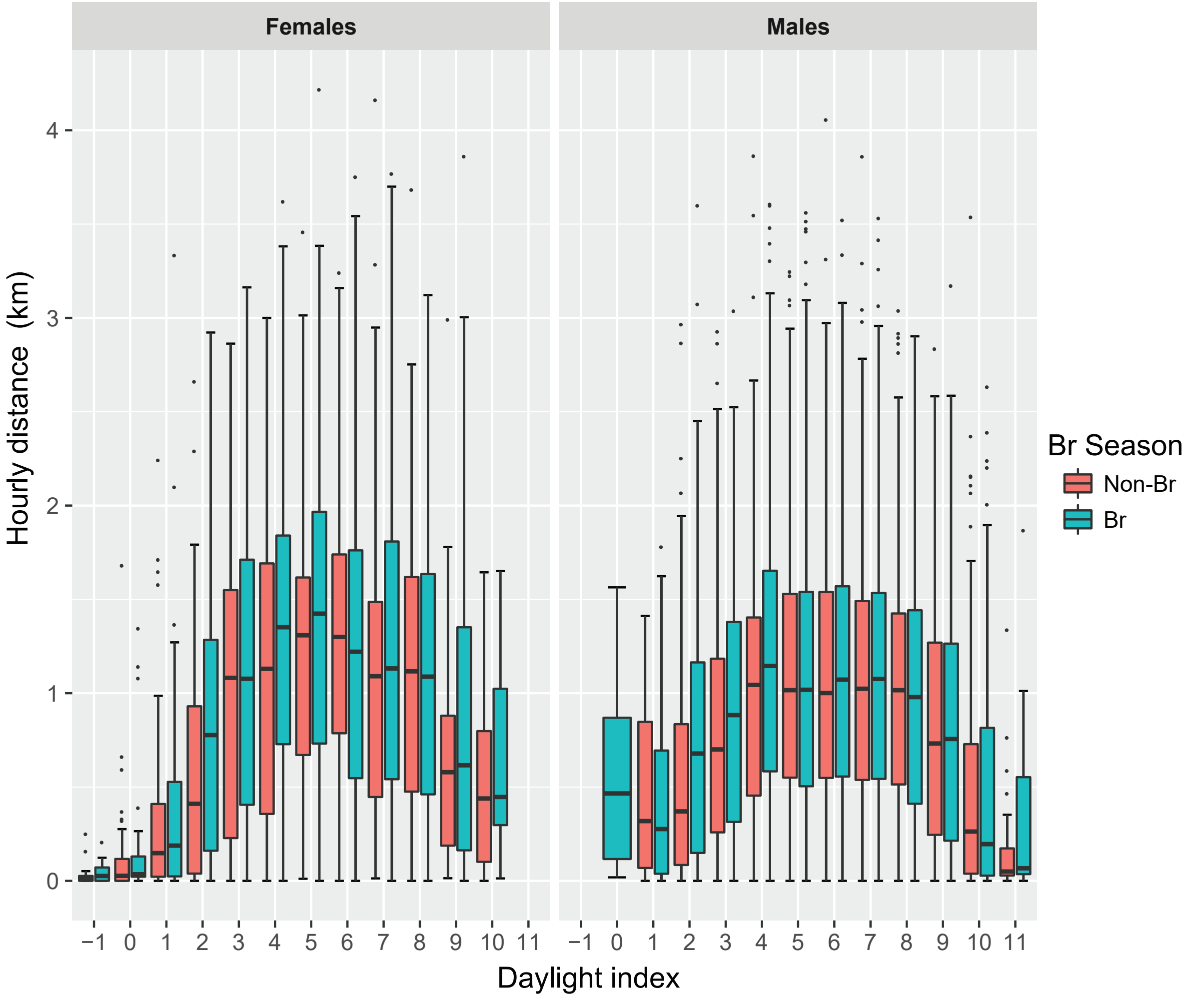

Figure 6 | Influence of sex and breeding period (red: non-breeding, blue: breeding) on the hourly mean distance travelled by adult territorial individuals.

Seasonal patterns

Based on the linear mixed models results, season is a highly significant factor leading to remarkable differences between the mean seasonal values of all three flight distance estimators (table 1).

Flight activity of non-territorial birds stands out in spring, when they reached the greatest maximum daytime displacement, cumulative distance travelled, and hourly distance. Nevertheless, a similar flight pattern was observed for non-territorial Bearded Vultures in every season, showing a growing trend for the daily maximum displacement and cumulative distance travelled from 8 h since 18 h (UTC), excepting fall, when the peak of activity was achieved a little before (around 16–17 h, UTC). In spring and summer (the two seasons with the highest daylight availability) the Bearded Vulture flight activity extended longer (until 22 h UTC). The second greatest maximum displacement and cumulative distance travelled was recorded in winter (figure 7).

Territorial Bearded Vultures presented an increased flight activity during spring and summer achieving the peak approximately at 18 h UTC. In fall and winter even though the flying activity decreased, the rise was interestingly detected at 19 h, coinciding with the hours around astronomical sunset. No data were registered after 20 h for territorial birds (figure 7).

Concerning hourly distance, all the individuals showed a uniform movement pattern during all the year, attaining the maximum values around 13 h UTC. During fall, individuals travelled the shortest distances (figure 7).

Table 1 | Linear mixed models to explore the factors influencing the distance covered estimators (maximum displacement, cumulative distance travelled and hourly distance).

Model	Factors	K	AICc	ΔAICc	W
Maximum displacement	**Territ*Sex+ Season + DI**	10	101320.8	0.00	0.99
Cumulative travelled distance	**Territ + Season + DI + Sex + Br_S**	10	107447.1	0.00	0.65
	Territ + Season + DI	8	107449.3	2.28	0.21
Hourly distance	**Territ + Season + DI**	8	89516.3	0.00	0.64
	Territ + Season + DI + Sex	9	89518.2	1.93	0.24
	Territ + Season + DI + Sex + Br_S	10	89519.6	3.29	0.12

Factors included were territorial status (*Territ*), daylight index (*DI*), climatic season (*Season*), breeding season (*Br_S*), and sex (*Sex*) and the simple interactions *Sex*Territ, Season*Territ* and *Br_S*Territ*. The model with the lowest AIC value (in bold) is the most parsimonious. K: total number of parameters (explanatory terms + random term + residual deviance); AICc: Corrected Akaike information criterion; ΔAICc: difference between the AICc value for that model and the best model; and, W: Akaike weights.

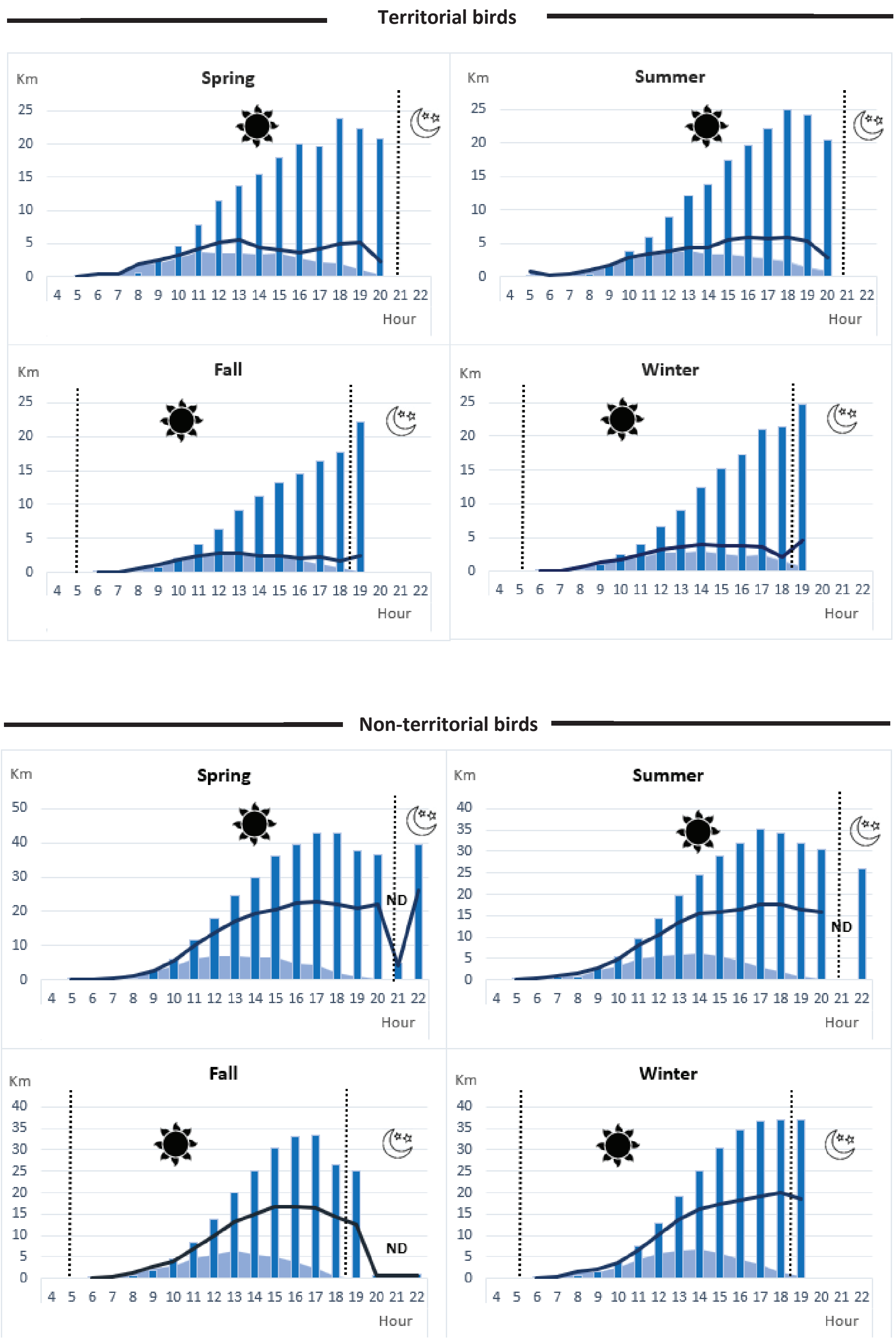

Figure 7 | Influence of season and territorial status on Bearded Vultures flight activity represented by three estimators: maximum displacement (line chart), cumulative distance travelled (bar chart) and hourly distance travelled (area chart). *ND* not enough data available at that level. Astronomical twilight is marked—if it is present—with a dashed line. The sun is placed at noon time.

Multifactorial model

The daylight index and seasonal factors were the most influential of all the parameters tested in every linear model since they were selected in each of the models built for the three distance covered estimators. Consecutively, territorial status had the next most noticeable effect on cumulative distance travelled and hourly displacement, followed by the effect of sex which only appeared in the cumulative distance travelled model. Breeding season was the factor with the weakest relationship with all of the three distance covered estimators.

The best explanatory model for maximum displacement involved the interaction between sex and territorial status, daylight index, and seasonal variables. In the hourly distance case, the model comprising territorial status, season and daylight index overcame the null model, while for the cumulative distance travelled estimator, the best model involved all of the variables tested (table 1, *Additional file 3*).

DISCUSSION

Our results on daily flight behaviour show an important spatial decoupling between the territorial and non-territorial individuals in the Pyrenees. Because non-territorial individuals are not central place foragers, they exhibited greater daily flight activity travelling longer distances, showing greater cumulative distances covered in an hour, higher maximum displacements, and greater hourly distance rate. These findings agree with the results regarding foraging movements obtained by Krüger *et al.* (2014) in South Africa and by Margalida *et al.* (2016) in the Pyrenees, in which territorial status influenced spatial distribution patterns of Bearded Vultures. In these studies, non-territorial individuals exhibited Kernel 90% home ranges of between 10,500–26,000 km2 in South Africa and 1800– 11,600 km2 in the Pyrenees, areas that are significantly larger than those covered by territorial individuals of 286 ± 361 km2 in South Africa and 63 ± 59.5 km2 in the Pyrenees. In addition, our results show a daily temporal dissociation according to the status of an individual (territorial vs non-territorial); non-territorial birds showed greater increments in maximum distance covered and the cumulative distance covered. The non-territorial status of these individuals allows them to travel farther and until later into the daylight period (i.e. during the last third of the daylight hours) compared with territorial individuals, who increased their maximum daily distance travelled until the period close to noon after which their daily maximum distance values stabilised (Figures 1, 2, 3, 4, 5, 6).

Our findings suggest that breeding period also has an influence over the daily flight activity, but lower than other internal factors. As with other obligate avian scavenger species, breeding Bearded Vultures experience an increased energy requirement due to parental effort. These reproductive tasks could explain the noticeable rise in the three different distance parameters measured during the last three quarters of the daylight period in the territorial birds. This accords with the significant seasonal effect detected in their daily activity patterns because the greatest distance of maximum displacement, cumulative distance and hourly distance travelled were observed in spring -especially for non-territorial birds -, coinciding with the peak of the breeding period, whilst the shortest were realized in fall during the non-breeding period (figure 7). However, our results only showed a significant effect of the breeding period on the cumulative distance travelled. Reproductive failure is a factor which should also be considered because it would allow the vultures to travel further afield, especially during March and April, when reproductive failure rates (hatching period and first days of the chick) are at their highest.

The influence of season has been generally evident in other studies of the circadian rhythm of birds (Liedvogel *et al*. 2009, Helm & Visser 2010; Alarcón *et al*. 2017), because variations in the quantity and intensity of solar radiation throughout the year determinate the timing of a bird's circadian behaviour (Hiraldo & Donázar 1990), and conditioning intrinsic factors such as the speed of migration (Shamoun-Baranes *et al*. 2003). Seasonal effects can also influence external factors such as variation in carrion food availability due to seasonal transhumance of livestock (Margalida *et al.* 2017), thus shaping vultures' daily activity patterns, and biasing the performance of solar powered GPS transmitters (Silva *et al.* 2017). We detected a seasonal influence on the values of the distance covered estimators, the longest distances being recorded in spring. Flight activity pattern seems to increase similarly on every season during the same daylight time (at the last third of the daylight) differentiating between the two territorial status. An elevated flight activity is maintained by non-territorial individuals some hours after astronomical sunset for every season, whilst territorial birds seem to sustain or even augment their activity pattern after dusk particularly in winter (but not in spring or summer), probably related with the reproductive period (figure 7). In addition, the flying fixes ratio registered in winter (37%) was higher than all of the other seasons (the lowest was logged in summer (32.5%), considering flying fixes > 1.39 m/s following Silva *et al*. 2017). This supports our aforementioned hypothesis that the energetic requirements of Bearded Vultures rise during the breeding period (winter and spring) combined with the decrease in of food availability in this time of year (Margalida *et al.* 2017) which forces them to fly for longer periods and over longer distances. However, despite this, we did not observe a clear seasonal variation in the daily activity patterns of the territorial Bearded Vulture flight behaviour.

While timing of sunrise and sunset determines the daily start and end of aerial activity in most obligate scavengers (Xirouchakis 2007), Bearded Vulture is able to continue flying after the sunset. In fact, maximum air temperature and wind speed in temperate climate ecosystems, and thus the best wind uplift conditions for large avian scavenger flight, occur in summer during the hours around noon (Hiraldo & Donázar 1990; Ephrath 1996). So, even while the greatest chances of finding profitable carcasses are in the early morning hours because ungulate mortality peaks during the night (Kendal 2014; Alarcón *et al.* 2017), the highest displacements of Pyrenean Bearded Vultures are recorded during the second half of the daylight, regardless of season, by virtue of their energy-efficient foraging flight and reduced wing loading in comparison with other vulture species (Shepard & Lambertucci 2013; Cramp & Simmons 1977; Hiraldo & Donázar 1990). This allows Bearded Vultures to profit the later daylight hours of convective updraughts to return to the nest or to search for a roosting site (Shepard & Lambertucci 2013). Moreover, the specific diet of this vulture —based mainly on the exploitation of bone remains, a resource which is preserved long time after a carcass has died— (Houston & Copsey 1994; Margalida & Villalba 2017) releases it from interspecific competitive pressures, reasonably diminishing the impact of the optimal time to exploit carrion in the species daily feeding habits (Moreno-Opo *et al.* 2016). All these physiognomical and ecological attributes enable Bearded Vultures to solve the trade-off between the ideal feeding time and the availability of wind resource performing the furthest travelling distances during the afternoon, even though the greatest hourly distances travelled are achieved at mid-day.

The sex of an individual influenced the longest distances covered in a day and our results showed intrasexual, but not inter-sexual, differences for this estimator. Concretely, both adult non-territorial females and males travelled significantly farther in a day than territorial individuals. However, an unexpected asymmetry was detected between the sexes for the cumulative distance travelled. Females covered significantly more kilometers than males during a day, consistent with the trend in spatial use already described for the same Pyrenean Bearded Vulture population (Margalida *et al.* 2016). Several studies of avian species underpin this inter-sexual spatial pattern discordance relating to the behavioural differences in reproductive roles between the sexes (Gray & Hamer 2001, Lewis *et al*. 2002) as well as individual or even sex-size variations (Shaffer *et al.* 2001; Lewis *et al.* 2005; Alarcón *et al*. 2017). However, the Bearded Vulture is a monomorphic species and parental care is divided equally between the male and female (Margalida & Bertran 2000), and therefore we would predict similar energy requirements for both sexes. A possible explanation of this sexual difference in daily distance covered during the breeding period could be due to the raised female energy demand resulting from the egg biosynthesis and the reproductive jeopardy if this is not met. In spite of the differences in daily spatial behaviour between the sexes, there are no differences in the temporal daily flight patterns between them.

According to our findings, the daytime flight behaviour of the Bearded Vulture does not follow a random pattern. The external factors studied (daylight index and season) strongly regulate the daily flight activity, while internal factors such territorial status, sex, and breeding period mould its flight dynamic. The synergy between both categories of factors enables the Bearded Vulture to confront the trade-off between travel costs—mostly constrained by weather conditions—and energy requirements. In addition, territorial status was, predictably, the most influential of all the internal factors studied. Other interesting drivers of flight behaviour have come to light, such as the relationship between territoriality and breeding season and the influence of sex in this monomorphic species, suggesting that these synergistic and intrinsic factors may play a currently unexplored role in this species' flight patterns.

Understanding the daily movement ecology of the Bearded Vulture is essential for predicting its future dispersal, foraging and reproductive patterns. These data are interesting for developing future conservation strategies (such as those related to the management of supplementary feeding sites) both in the Pyrenean region and other ecosystems with distinct climatological conditions or food availability. Indeed, given the variety of mortality risks faced by this species and its high adult mortality rate (Carrete *et al.* 2006; Margalida *et al*. 2008; Margalida 2012), information on the daily distances travelled by juveniles during their early dispersal stages might help to improve the design of future conservation measures.

CONCLUSIONS

This study is the first detailed daily activity analysis developed on the Bearded Vulture improving our knowledge on the movement ecology of this threatened species trough a finer spatio-temporal information about the daytime flight routine of the species. Our findings show that the main drivers of the Bearded Vulture daily flight activity are daylight time, season, and territorial status of the individual. This agrees with several authors' hypothesis supporting the daylight time as the most influential factor of all of the external factors determining circadian behaviours (Daan & Aschoff 1975). Pyrenean Bearded Vultures covered the furthest travelling distances during the afternoon. Moreover, internal factors as territorial status had a remarkable effect on the daily activity patterns of the vulture. Non-territorial Bearded Vultures presented the greatest daily flight patterns. Both individual's sex and breeding period mildly shaped the flight activity resulting in the females and breeding individuals travelling further afield than males and non-breeding individuals.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

The study was conducted in full compliance with Spanish laws and regulations. Captures and blood sample collection were carried out in compliance with the Ethical Principles in Animal Research. All experimental protocols were approved by the Catalan Autonomous Government and the Spanish Ministry of Agriculture and Fisheries, Food and Environment (References 15546 and 25.306).

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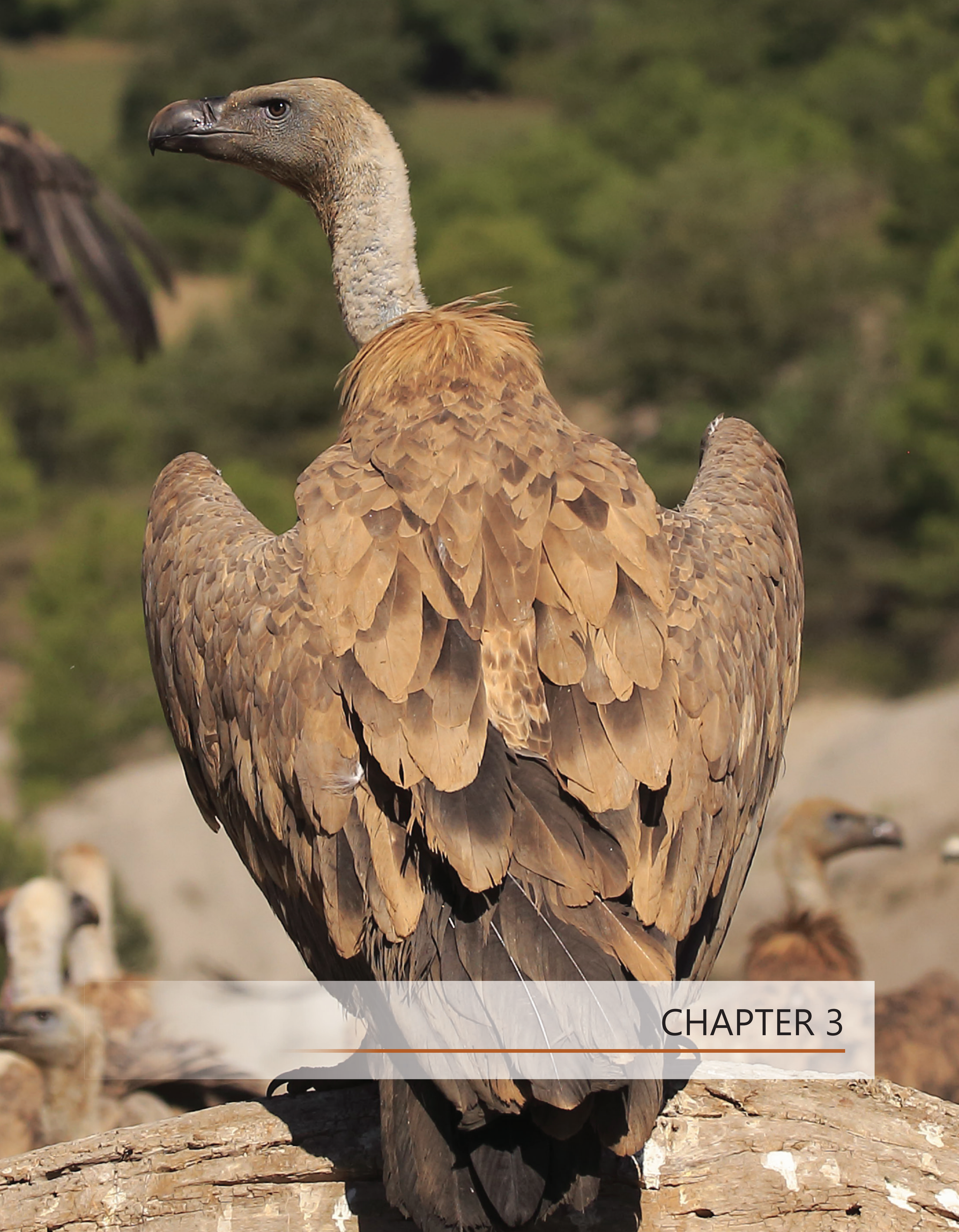
ECOSYSTEM SERVICES



CHAPTER 3

Photo credits:

Ecosystem services
Photo by David Izquierdo Acebes.
A foggy dawn in the Maestrazgo's landscape —where the hacking for the bearded vulture reintroduction project in the region is located— somewhere in the Tinença de Benifassà Natural Park (Castellón).

Chapter 3
Photo by Miguel Ángel Díaz Guillén.
A wake of griffon vultures waiting for the perfect moment to feed.

CHAPTER 3

Economic valuation of non-material contributions to people provided by avian scavengers: Harmonizing conservation and wildlife-based tourism

by

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ABSTRACT

Nature's contributions to people (NCP) are fundamental to human well-being. In particular, non-material NCP, defined as effects on personal perspectives which enhance people's quality of life, are currently the most abstract and least well-defined NCP. Avian scavengers are a globally threatened guild that plays a key role in our society but currently only valued for their NCP of disease control and carcass removal. We describe the first economic valuation of the recreational and educational experiences brought by avian scavenger-based tourism in Spain, concretely, at vulture supplementary feeding sites (SFS) in the Pyrenees and their important contribution to the incomes of the local human population. Between February 2018 and January 2020, we collected information on the management and characteristics of 53 (c. 80%) of the Pyrenean SFS using telephone interviews and questionnaires. We estimated that photography and avian scavenger-watching at SFS produce an average of US $4.90 ± 2.67 million annually, including US $2.53 ± 1.36 million in direct economic benefits to the local population. Using a conservative economic approach, this study is one of only a few to value some of the important non-material contribution provided by avian scavengers to our society. Our study also suggests that further research on non-material NCP provided by avian scavengers at SFS is needed. Finally, we discuss the delicate balance between recreational experiences arising from wildlife-based tourism and biodiversity conservation, contrasting the contribution of SFS to the income of local human populations against the problems they raise for vulture conservation.

Keywords

conservation economics, cultural ecosystem services, ecotourism
vulture restaurant, vultures

INTRODUCTION

Ecosystem services are the direct and indirect benefits that humans obtain from ecosystems and therefore play an essential role in human well-being. They have received increasing attention over the last 20 years, especially since the term was popularized by the Millennium Ecosystem Assessment in 2005 (MA 2005; Costanza *et al.* 2017). However, in 2017, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) introduced a new and closely related concept, Nature's Contributions to People (NCP) (Christie *et al.* 2019). NCP have been defined as all the contributions of living nature to people's quality of life, including both the positive (i.e. beneficial) and negative (i.e. detrimental) inputs that people obtain from the ecosystems (Díaz *et al.* 2018). Each specific cultural setting would condition their classification through three partially overlapping groups: material (actual goods provided by nature, such as food, energy, or medicinal products; e.g. Bondé *et al.* 2020), non-material (the effect of nature on the subjective or psychological aspects supporting people's quality of life such as recreational, aesthetic, learning, and inspirational experiences; Chan *et al.* 2011), and regulating NCP (functional and structural aspects of organisms, ecosystems and biodiversity that contribute to society's well-being by changing the environmental conditions which affect humans and regulate the other two kinds of NCP; e. g. Martín-López *et al.* 2019) (Díaz *et al.* 2018).

Only during the last two decades have non-material NCP (i.e. cultural services) been socially recognized. They are very difficult to assess, especially because they appear intangible and usually manifest as indirect benefits (Hernández-Morcillo *et al.* 2013; Milcu *et al.* 2013). Consequently, they have been given little or no scientific, social, or economic value, leading to some conservation decisions (e.g. ignoring local knowledge, and/or people perceptions) with serious negative consequences for our environment and society (Butler & Oluoch-Kosura 2006; Zografos & Howarth 2010; Barua *et al.* 2013). Since the end of the 20th century, one of the most common methods for trying to place a true value on these non-material NCP have been economic evaluations of recreational activities (Martín-López *et al.* 2009; Everard & Kataria 2011; Milcu *et al.* 2013). Although the published information on NCP valuation is increasing, some important species or specialized guilds are frequently ignored by the general public and undervalued by scientific educationalists and the specific stakeholders directly related to them. Such is the case of the vertebrate scavengers (Moleón & Sánchez-Zapata, 2015; Cailly Arnulphi *et al.* 2017), a guild with a fundamental role in many ecological processes, functions, and ecosystem services (Moleón *et al.* 2014; DeVault *et al.* 2016).

Humans and vertebrate scavengers, including obligate scavengers (such as vultures, whose food comes exclusively from scavenging) and facultative scavengers (such as raptors, corvids, or mammalian carnivores), have been directly interdependent since the Late Pliocene, when our ancestors started to eat meat. Indeed, the NCP provided by this guild have benefited our species from the very first biped hominids (Moleón *et al.* 2014; Morelli *et al.* 2015). For example, humans have obtained different ornamental resources, such as feathers, from scavengers (a material NCP) (Finlayson *et al.* 2012). Regarding regulating NCP, scavengers' ability to dispose of waste and organic matter preventing disease transmission to humans (e.g. brucellosis, tuberculosis, or anthrax) and their role in the nutrient cycle in processing carcasses have been widely recognized as providing substantial benefits to human health (Swan *et al.* 2006; Markandya *et al.* 2008; Ogada *et al.* 2012a; O'Bryan *et al.* 2018), contribute to the long-term maintenance of soil structure (Wilson & Wolkovich 2011; Beasley *et al.* 2015) and reduce environmental pollution (Markandya *et al.* 2008; Morales-Reyes *et al.* 2015). However, very few studies have highlighted the importance of scavengers in the provision of non-material NCP, for example where scavengers form the basis for spiritual experiences (rituals and celebrations), wildlife-based tourism (recreational experiences) or supporting personal identity (the satisfaction derived from knowing that a particular species exists) (see e.g. Becker *et al.* 2005; Morelli *et al.* 2015; Aguilera-Alcalá *et al.* 2020). Indeed, these cultural values are widespread in human societies and intertwined, connecting all NCP with each other.

Terrestrial vertebrate scavengers (especially obligate scavengers and large mammalian scavengers) have been declared one of the world's most endangered guilds in recent decades (Hoffmann *et al.* 2010; Ogada *et al.* 2012b; Ripple *et al.* 2014). Old World vultures and condors are the most globally threatened avian functional guild due to the recently suffered severe declines in many of their populations across the globe (Buechley & Şekercioğlu 2016; Safford *et al.* 2019). To mitigate these sharp population declines, many conservation and population rescue plans have emerged (Astore *et al.* 2017; Botha *et al.* 2017). Among other remedial initiatives, supplementary feeding sites (SFS, also known as “feeding stations” or “vulture restaurants”) have been established. Feeding stations provided a conservation tool to: fight illegal poisoning and reduce lead or pharmacological toxic risks (the main threats to vulture mortality); encourage species dispersion into new areas; improve breeding success and survival; remedy population declines; and to compensate for decreases in carcass availability resulting from sanitary policies developed to reduce bovine spongiform encephalopathy (Houston 2006; Donázar *et al.* 2009). The balance of pros and cons of the specific management and uses of this conservation tool has been broadly discussed (Piper 2005; Donázar *et al.* 2009; Cortés-Avizanda *et al.* 2016). For instance, the initial conservation reason for constructing an SFS has recently been corrupted by the increasingly popular tendency to build SFS strictly to serve tourist interests (e.g. birdwatching, wildlife photography) with the consequent economic benefits. In fact, the wildlife-based touristic value of vulture breeding areas and SFS has become a notorious source of income for many local economies (Anderson & Anthony, 2005; Piper, 2005; Ferrari *et al.* 2009). Perhaps surprisingly, the scale of the economic benefits of these non-material contributions that vultures provide at SFS has not been quantified before.

Spain is one of the most popular European countries for ornithological tourism specifically to see scavengers, particularly vultures, since it hosts most of the European vulture population (Margalida *et al.* 2010). Concretely, there are more than 90% of the European breeding populations of cinereous, 90% of the Eurasian griffon, 47% of the Egyptian, and 63% of the European bearded vultures (Margalida *et al.* 2010; del Moral 2017; del Moral & Molina 2018a; del Moral & Molina 2018b; Margalida & Martínez 2020). Spain has also established a large network of SFS since the 1980s, most being built initially as management-conservation tools recurrently applied by administrations (Moreno-Opo *et al.* 2015). We based our study in the Spanish Pyrenees, taking advantage of the fact that it is inhabited by all four European vulture species and also has a wide network of SFS, and where efforts have been made to try to harmonize the conservation purposes of SFS with recreational experiences and environmental educative activities through wildlife-based tourism.

The main goal of this study was to evaluate the economic benefit of non-material NCP provided by the European avian scavengers through recreational and educational activities (i.e. wildlife-based tourism) at the SFS in the Pyrenees. In addition, we discuss the sensitive trade-off between recreational experiences associated with wildlife-based tourism and conservation in a situation in which, on the one hand, SFS provide important contributions to local human population's incomes and, on the other, must ensure the conservation of European avian scavengers.

MATERIAL AND METHODS

Study area

The Pyrenees is a > 400 km long mountain range located on the border between southern France and northeastern Spain. There are currently at least 67 working SFS in the Pyrenean and Pre-Pyrenean area (seven in France and 60 in Spain) each with very different spatial and temporal feeding routines. Of these, 29.85% (*n* = 20) located in the eastern Spanish Pyrenees (Aragon and Catalonia autonomous communities) receive visitors (people who visit a hide or viewpoint specifically linked to an SFS normally under the guidance of the organization in charge of the SFS). Only the entrance of the field technicians directly to the SFS is allowed. Hides built, managed, and exclusively intended for photography were not included either in this study or in the descriptive statistics. All SFS considered here had been created for the principal purpose of scavenger conservation.

Data collection

Data were gathered between February 2018 and January 2020. Data collection was systematically divided into two main stages. First, basic information on the management and structural characteristics of each SFS was collected through telephone interviews with the managers of 53 (79.1%) of the Pyrenean SFS, 18 of which were part of the 20 SFS that formally receive visitors. The information obtained included the mean number of people visiting each SFS each year and the price, if any, of entrance and/or the main recreational activity offered (birdwatching, photography and/or educational activities). Of those SFS accessible to the public, 35% (*n* = 7) were inside a protected area (national or natural parks). Of these, we could only find data on the actual number of visits for two of them, so we did not include the other five (marked as "not considered" in table A in the *Appendix A*) in the economic analysis. This was because, unlike the other 15 SFS receiving visitors, we could not assume that the main reason for all public visits to the parks (some of which receive up to 561,000 visitors per year; GenCat 2019) was mainly to enjoy watching avian scavengers (tables 1 and A).

Second, 94 survey questionnaires (either in English or Spanish) were randomly distributed among 9 of the 15 SFS to gather information

Table 1 | Information obtained from telephone interviews with SFS managers and from the SFS visitors surveyed (questions included in the questionnaires are shown). The last column shows the possible answers to the multiple-choice questions.

Source of information	Type of information	Specific question	Close-ended questions
SFS managers	Management characteristics of the SFS	Main activity offered	Birdwatching
			Educational
			Photography
		Mean number of annual visitors	–
		Entrance cost (in €)	–
SFS visitors	Trip characterization	Where did you start your trip? (city and country)	–
		Trip duration, including travelling time (in days)	–
		Accommodation	Hotel
			Hostel
			Apartment
			Camping
			Rural house
			Relatives' or friends' house
			Own house
		Meals usually eaten outside accommodation	Breakfast
			Lunch
			Dinner
		How many people are travelling with you?	–
		Are there any children travelling with you?	Yes / No
		If yes, how many?	–
	Socio-economic status	Average monthly income	< 1000€
			1000 - 2000€
			> 2000€

on the travel, subsistence (food, lodging), and opportunity costs (see the *Economic valuation* in *Material and methods* section) incurred by each visitor (i.e. the trip characterization). Given the diverse management dynamic of the SFS (only two of the SFS surveyed offered scheduled visits), the questionnaires could not be made face-to-face. At each SFS, a hard copy of the questionnaires randomly distributed to each visitor at the end of the recreational and/or educational activities and they were fulfilled by each visitor. Questions covered information about where people came from, the duration of the entire trip (travel time / time spent at the SFS / time in the general area), the place (s) where they were lodging, the meals they were eating away from their accommodation, whether they came alone or with their children (how many), and their socio-economic status (monthly income) (see table 1). We met the ethical standards governing social surveys by informing respondents in writing at the beginning of the questionnaire that their participation was voluntary and that their anonymity would be ensured.

Economic valuation

First, we used the descriptive nonparametric Wilcoxon and Mann-Whitney U tests ($\alpha = 0.05$) to explore if there were significant differences in the mean trip expenses and specific trip parameters such as distance travelled (distance by road in km) between the trip departure point and the SFS visited and trip duration (see table 1) between visitors who started their trip from anywhere in Spain (national visitors) and those with departure points outside the country (international visitors). We used the Kruskal-Wallis test ($\alpha = 0.05$) to determine whether there were substantial differences in trip expenses depending on the SFS visited.

Second, we calculated the specific costs of each trip parameter:

(1) *Travel costs*. For national visitors and those coming from southern France, we calculated the travelling costs considering the distance by road (km) between the departure point and the specific destination (the SFS visited). For international visitors and those from the Spanish Islands (considered national visitors in the non-parametric tests), we first calculated the distance by road (km) from their home to the closest city with an airport and then estimated the mean cost of a plane ticket from that airport to Barcelona. Then we calculated the distance by road (km) from Barcelona to the destination SFS and added the cost of renting a car (estimated mean US $17.4 per day after consulting the prices on several car renting websites in the Barcelona airport area). We calculated the cost of a round trip in all cases and used US $0.22 /km (0.19 €/km) as the cost of car travel expenses according to Spanish income tax claim guidelines (Orden EHA/3771/2005) and assumed the shortest route by road taking into account any necessary road tolls.

(2) *SFS entrance cost*. We collected data on the specific entrance price, if any, of the different SFS.

(3) *Accommodation costs*. We calculated a mean price for each type of accommodation for all the SFS surveyed by averaging the prices of three in the same category, for the high and low seasons separately, to arrive at a mean price per night for each type of accommodation. The overall mean price of US \$33.7/adult and US \$10.5/child per night was applied to those people who did not indicate their accommodation in the questionnaire (n = 5) (table B in *Appendix A*).

(4) *Food costs.* We asked which of the three main daily meals the visitors were eating away from their accommodation, and then used that information combined with some approximate prices per meal in Spain (table C in *Appendix A*). Children's costs were always estimated separately from adults' costs both for the accommodation and cost of meals.

(5) *Opportunity costs.* We included the opportunity cost of the time spent on the entire trip, taking four hours for the arrival and departure days and eight hours for each other day spent away. The opportunity cost is usually measured as the monetary value of what an individual could have been doing with their time instead of the activity they are on, generally calculated as 25% of the income of a working hour, at the given individual's salary (McKean *et al.* 1995; Becker *et al.* 2005). Working hours were assumed to be 40 h/week, as they would be in a normal full-time job in Spain. Children were omitted from the opportunity cost estimates.

We did not include the estimated cost of birdwatching and photographic equipment per visitor in the economic expenditure because we could not assume that the equipment had been acquired solely for scavenger-watching activities (especially for the cases where cameras were used).

Finally, we summed all these specific costs of each trip parameter for the entire trip to calculate the visitors' trip expenses and then computed a mean trip expenses/visitor value, as follows:

$$\text{Visitors'trip expenses} = T+(\mathbf{SFSe}+\mathbf{A}+\mathbf{F}+O)\times\text{trip duration.}$$

(Children's rates, shown **in bold**, were added if the visitor declared having made the SFS visit with accompanying children)

$$\text{Mean visitors'trip expenses} = \Sigma\text{Visitors'trip expenses}/n$$

where: travel costs (*T*); SFS entrance (*SFSe*, which depended on the trip duration only for SFS offering a photographic activity, but not for the SFS offering birdwatching and educational activities, where we considered it as a fixed cost independent from the trip duration); accommodation costs (*A*); food costs (*F*); and opportunity costs (*O*). Costs were calculated in € and then translated into US $ (table D in *Appendix A*), trip duration in days, and *n* represents the total number of visitors for which a visitor trip expense could be estimated ($n = 91$). Of these 91 visitors, four people did not respond to the trip duration question, so we assumed a minimum trip duration of two days based on the rest of the answers given in the questionnaire.

Based on the mean trip expenses per visitor and the mean annual number of visitors per SFS, we were able to estimate the annual expenses associated with the non-material NCP (recreational and educational experiences) provided by vultures at the Pyrenean SFS for which visits were allowed. We summed the total economic benefits estimated for the nine SFS surveyed and the estimated economic benefits for the other six, differentiating between the expenses resulting from visits made by nationals and international visitors to arrive at an average expense per person.

RESULTS

SFS, visitors and trip characterization

We obtained a mean of 10 ± 4 completed questionnaires per SFS surveyed (range 3–17, table A), whereas usable responses varied depending on the question, ranging from 76.6% ($n = 72$) answers giving monthly incomes to 98.9% ($n = 93$) answers giving the number of people who they were visiting the SFS with.

Of the respondents, 86.96% ($n = 80$ out of 92) were national visitors, coming mostly from the closest regions (Aragon and Catalonia, $n = 27$ and $n = 25$, respectively) within approximately 200 km of the SFS. However, national visitors came from all over Spain, 2500 km being the maximum distance travelled from the trip departure point (Canary Islands) to the SFS. The other 13.04% of respondents were international visitors starting their trip in a European country including Belgium, Denmark, France, Germany, Netherland, Hungary, Portugal, and the United Kingdom. The mean distance travelled by national visitors (mean ± SD: 543.57 ± 564.12 km) was significantly lower compared with that travelled by international visitors (2805.08 ± 933.07 km; Mann-Whitney *U* test, $U = 17$, $p < 0.001$; see table E in *Appendix A* for median and range values).

The SFS entrance price ranged between US $0 and US $209 per day per person, depending on the specific SFS and the duration of the visit. Normally, the entrance price of an SFS offering a photographic recreational activity varies depending on the number of days spent visiting. The longer the stay is, the more economical the price per day becomes. The SFS offering birdwatching only frequently charge no entrance fee. Those promoting an educational activity have the most variable fees because are either linked to a museum with a nominal entrance price, managed by a nature conservation NGO which only accepts donations, or offer a paying guided environmental education activity.

Most visitors, 40.45% (*n* = 36) incurred no accommodation expenses because they stayed in their own homes or with friends. These options were almost entirely chosen by national visitors (*n* = 35; 97.22%). The other 59.55% of the respondents were nearly equally distributed between all the different types of accommodation, except rural houses (only one person chose this option) (table B).

Visitors ate an average of 1.20 ± 0.79 meals away from their accommodation, lunch being the most frequent meal eaten outside; 74.39% (*n* = 61) of the visitors had lunch away from their accommodation, compared with 28.05% (*n* = 23) for breakfast or dinner.

We found significant differences in trip duration depending on the point of trip departure (national: 2.33 ± 1.67 days, *n* = 76 vs international visitors: 4 ± 2.27 days, *n* = 11) (Mann-Whitney U test, U = 218, $p = 0.008$; see table E). Overall, 65.52% of the visitors (*n* = 57) spent only one or two days on their visit, most of them staying in their own home or with friends or relatives (57.89%; *n* = 33).

Economic valuation

We calculated the trip expenses of 91 visitors. The overall average expense per person per trip (i.e. mean visitor's trip expenses) was US $441.74 ± 372.70. However, there were significant differences depending on which SFS was being visited (Kruskal-Wallis test, $\chi 2 = 51.38$, df = 8, $p < 0.001$) ranging from US $46.09 ± 14.23 to US $791.13 ± 524.86 and depending on the departure point of the trip (Wilcoxon test, W = 88.5, $p < 0.001$). The trip expense was quite variable among visitors (figure A in the *Appendix A*), but on average it was higher for international (US $956.85 ± 425.33) than for national visitors (US $363.50 ± 353.40) (tables D and E). Accordingly, the higher mean visitor trip expenses were spent in the SFS receiving higher proportions of international visitors.

The mean number of visitors was 812 ± 1,816 people per year per SFS (range 4–6,829 people depending on the SFS). The SFS receiving most visitors per year were those dedicated to educational activities, such as group guided visits around the SFS whose main focus was the vultures, or those linked to a nature conservation museum specializing in scavengers. In fact, when we excluded those SFS mainly promoting educational activities and look at those focusing on birdwatching and avian scavenger photography, we obtained a mean of 113 ± 137 visitors per year per SFS. The total number of people visiting the studied SFS in the Pyrenees in 2019 were 12,668 (*n* = 20, table A).

We found an annual expense estimated at US $4,900,930.20 ± 2,629,779.10 accruing from the non-material NCP provided by European avian scavengers through recreational and educational wildlife-based activities at the SFS in the Pyrenees, comprising 32.13% in travel expenses, 22.93% in SFS entrance fees, 10.78% in accommodation expenses, 17.92% in food expenses, and 16.24% in opportunity costs (figure 1). This means that, in the region overall, at least US $2,530,350.26 ± 1,357,754.95 (51.63% of total annual economic profits; i.e. SFS entrance cost + accommodation expenses + food expenses) are injected annually

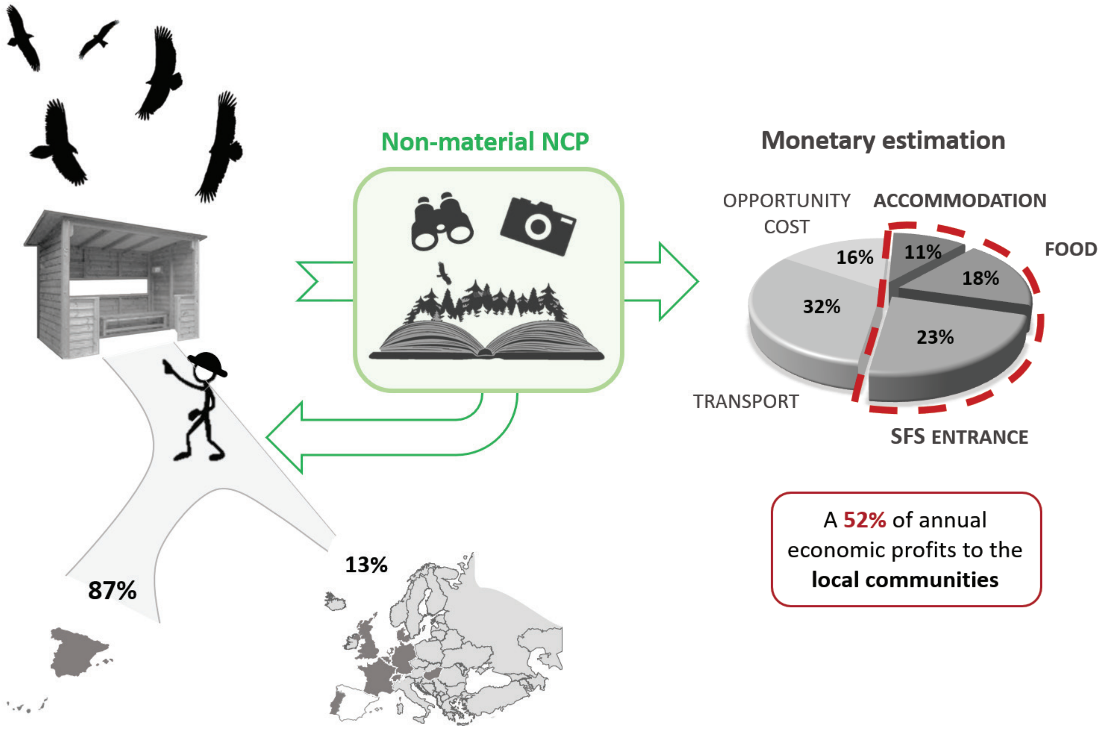

Figure 1 | Schematic representation of the economic valuation of the non-material contributions to people (non-material NCP) provided by avian scavengers through recreational and educational activities (i.e. wildlife-based tourism) at Supplementary Feeding Sites (SFS) receiving visitors in the Spanish Pyrenees. The main activities were birdwatching, photography and/or environmental education focused on scavengers. All these non-material NCP not only bring significant economic benefits to local communities, but also have an important effect on people's well-being in today's societies.

into local Pyrenean communities thanks to recreational and educational experiences based on avian scavenger-focused tourism at SFS alone (table D).

DISCUSSION

The relevance of the economic valuation of NCP provided by avian scavengers

Our findings showed that the non-material NCP provided by European avian scavengers through recreational and educational activities (i.e. scavenger-based tourism) at SFS produces a relevant economic income to the Pyrenean community. On average, we estimated an annual economic value of US $4.90 ± 2.67 million; including US $2.53 million ±1.36 million of direct economic benefits to the local community (see table D for results in Euros). It is important to note that this economic assessment is probably an underestimate because of our conservative approach to estimation of the individual trip expense parameters (e.g. car rental and food costs). In addition, accounting for the median trip durations of the national (two days) and international visitors (three-four days) estimated in our study (table E) and the difficult access to the SFS (only available by road and not always waymarked), we assumed that the main reason of the visitors for doing the trip was to watch avian scavengers. Indeed, interestingly national visitors were willing to cross over half of the country (i.e. mean of 544 km) to arrive to the SFS just for a weekend visit, and, on the other hand, international visitors were willing to travel almost across the whole European continent (i.e. mean of 2800 km) to watch and enjoy avian scavengers at SFS (table E). This is an interesting result in the case of Europe, where the distances between different countries is tiny compared with other continents (e.g. Africa or America), and also specifically in the case of the Pyrenees, a border area where visitors could be registered as "international", but come mainly from the South of France, having travelled only a few hundreds of kilometers. Moreover, this economic assessment is strongly dependent on the number of SFS visitors and, as it is a factor highly variable over time (on a yearly scale), even if we worked with yearly means of visitors, extrapolations to the future economic benefits obtained though scavenger-based tourism at SFS must account for this variability.

Because of an innate bird enthusiasm and the consequent investment that birdwatchers are willing to pay to practice this activity, birding is becoming "the fastest-growing and most environmentally conscious segment of ecotourism and the best economic hope for many beleaguered natural areas" (Salzman

1995). Nevertheless, currently, there are very few studies that empirically assess the recreational (Becker *et al.* 2005, 2009, 2010), sanitary (Markandya *et al.* 2008) or environmental economic value (Margalida & Colomer, 2012; Morales-Reyes *et al.* 2015) provided by vultures. Thus, to our knowledge, this is the first economic valuation of recreational and educational experiences through avian scavenger-based tourism in a European country. Becker *et al.* (2005) estimated that 85% of the visitors to a nature reserve in Israel (i.e. Gamla) came specifically to view threatened Eurasian griffon vultures, and that this activity produced a potential annual value of US $1.1–1.2 million. Then, also Becker *et al.* (2009) estimated through the travel cost method (TCM) an economic benefit of US $2.4 million and of US $2.94 million per year at two different nature reserves in Israel (i.e. Hai-Bar and Gamla, respectively) for the enjoyment of visiting the areas fitted with griffon vultures and a willingness to pay (WTP) for protecting this species of US $0.98 million at Hai-Bar and US $2.70 million at Gamla. Some of these sums resemble the benefits that we found were injected annually into local communities in the Pyrenees (US $2.35 million), which were generated uniquely through specific recreational/educational wildlife-based activities associated with the non-material NCP provided by the European avian scavengers. And that is only considering the SFS scavenger-based tourism of the region, leaving out of account specific avian scavenger festivals or guided photographic tours around the Pyrenean area, or even visitors looking for nature enjoyment beyond avian scavengers watching (further on detailed in the section bellow of the *Discussion*). This is a significant amount, especially if we consider that, according to a Spanish Environmental Ministry report of 2017, the estimated national economic revenue of direct expenses derived from nature-based tourism (i.e. a tourism mainly motivated by the development of recreational, leisure, interpretive, educational and sport activities in nature) was on average 9 million € (i.e. US $10.47 million) (SGAPC & MAPAMA, 2017).

Markandya *et al.* (2008) calculated the human health cost of medicines, doctor remuneration, and work compensation associated with human rabies transmitted by feral dog bites in India at an estimated annual mean of US $2.43 billion. Such rabies transmission increased alarmingly almost three decades ago following the dramatic decline of vultures in India. This drastic and sudden vulture decline resulted in an increase of facultative scavenger populations (e.g. feral dogs), which led to an increase in dog bites, and consequently rabies cases in humans. On the other hand, the monetary value of regulating NCP is undeniably relevant considering that, in Spain, vulture populations have been estimated to dispose of an average of > 8,000 metric tons of animal biomass annually, saving the country an estimated US $1.6 million each year (Margalida & Colomer 2012). Likewise, Morales-Reyes *et al.* (2015) estimated that natural removal of extensive livestock carcasses by scavengers would yearly save Spain 77,344 metric tons of CO2 eq. emissions produced by the artificial collection and transport of this rotting matter to authorized plants and US $50 million yearly in payouts to insurance companies. Studies like these (including this present one) clearly demonstrate the important social and economic benefits that avian scavengers provide to humans.

Our results showed the need to do more analyses of this type –and not only from an economic perspective– to improve appreciation of the societal value of both the avian scavenger guild, and the individual scavenger species. Economic valuations, such as the presented here, provide interesting perspectives on the important roles played by the scavenger guild and ornithological tourism in Spanish society today. They can help to reveal the as yet often hidden benefits for human well-being arising from the non-material NCP provided by scavengers.

Given the relevant potential to improve the financial and environmental well-being of local communities that birdwatching tourism has demonstrated (Şekercioğlu 2003), highlighting the revenue and financial savings provided by vultures' NCP could help to promote the conservation of these globally threatened species. However, the economic outcome should not be taken as the sole reference to valuate NCP, since it is largely determined by the prevailing temporal and socio-institutional contexts, which means that this value is neither universal nor invariable across time or cultures (Kallis *et al.* 2013). Economic valuation needs to be complemented by other innovative NCP evaluation and analysis methodologies, such as social multi-criteria analysis (Munda *et al.* 1994; De Marchi *et al.* 2000), or deliberative valuation (Howarth & Wilson, 2006; Kelemen *et al.* 2013; Kenter *et al.* 2016).

Some recent complementary studies have emphasized the conservation values of the non-material NCP provided by vultures, highlighting their importance in addition to the purely economic benefits (Cortés-Avizanda *et al.* 2016; DeVault *et al.* 2016; Echeverri *et al.* 2020; Aguilera-Alcalá *et al.* 2020). In this context, further research is needed to evaluate also other non-material NCP provided by avian scavengers at SFS such as their contributions to aesthetic and learning values, sense of place, or spiritual awareness.

Characterizing avian scavenger-based tourism

We have evaluated a form of wildlife-based tourism aimed at a specific stakeholder group interested in enjoying a birdwatching, photographic, or educational activity focused specifically on the avian scavenger guild. However, we should not forget the interests not covered by our study. Non-specialist visitors to the region surrounding the study area and other national and natural parks also make an economic contribution: hunters and sportspeople, or those with a more generalist interest in nature and landscape-based leisure activities. They do not travel to protected regions specifically to see avian scavengers, but enjoy the general psychological, physical, and social benefits of being in contact with nature (Velarde *et al.* 2007; Abraham *et al.* 2010; Hausmann *et al.* 2020). That said, such visitors would likely profit from some of the direct and indirect non-material contributions provided by avian scavengers and appreciate their positive added value.

The recreational and educational experiences linked to SFS mainly promote domestic tourism, since 87% of the people visiting the SFS described here were national visitors (departing from somewhere inside Spain), while only 13% were international visitors coming from multiple European countries. National visitors came from all over Spain (travelling an average 544 km), although most were from areas surrounding the SFS; 87% of the national visitors came from a 200 km radius. The proximity of these visitors to SFS (mostly staying at their home or with friends) enabled an average stay in the study area of only two days. In contrast, international visitors, whose average journey was five-fold longer, spent twice as much time in the area. Interestingly, a study by Puhakka *et al.* (2016) in Finnish protected areas demonstrated that increasing length of stay, and especially the number of nights spent in the protected region, was positively correlated with an increase in the perceived well-being benefit felt by visitors, and the same is probably true for people visiting Pyrenean SFS. This relationship is probably linked to the feeling of escape from everyday routine that is one of the most common motivations in tourism (Iso-Ahola 1982), and is probably an important subjacent reason for spending more than one day visiting an SFS, where the recreational and/or educational activities proposed (i.e. birdwatching, educational, or photography) could be easily done in a single day.

A longer stay also meant that international visitors spent significantly more on their trip expenses than national visitors. The most common plan for up to 65.52% of visitors was to sleep at a friend's or relative's house (an option generally preferred by national visitors) and to eat only one meal away from their accommodation each day. As many as 74.39% of the visitors ate lunch away from their accommodation during their visit, while fewer than half took breakfast or dinner out. This meant that restaurants and food markets earned almost double the money taken by landlords and hotels as a result of visiting tourists.

Our findings also indicate that the SFS promoting educational activities (more likely to be visited by families) received higher incomes each year than those only offering photographic activities (usually specifically aimed at keen photographers, foreign visitors, or those with greater purchasing power). This is because SFS with an educational agenda generally get more visitors and therefore obtain greater annual incomes despite their lower entrance fees. Beyond solely recreational experiences, some SFS also play an important role in providing non-material learning and inspiration NCP, values that start to be assessed in vertebrate scavengers by some scientists (Aguilera-Alcalá *et al.* 2020). Regardless of the recreational and educational offer, SFS can offer professional training opportunities for field technicians and provide valuable resources for population censuses, demographic studies, and tagging of avian scavengers for scientific population monitoring (e.g. Margalida *et al.* 2020). Some studies analyzing these specific non-material NCP have already been published (e.g. Brink *et al.* 2020), but more studies should be designed to quantify and evaluate the impacts of these cultural contributions. In any case, we should never lose sight of the fact that scavengers are the NCP providers and the SFS only some platforms (although not the unique ones) that allow us to enjoy and benefit from these non-material NCP.

Conservation value and economic balance of SFS

Previous research in two nature reserves in Israel performed a cost-benefit analysis of the conservation efforts to preserve the endangered Eurasian griffon vultures (Becker *et al.* 2009), showing that to be economically efficient, SFS should help increase the vulture population by an average of 0.24–2.20 individuals per year. In addition, Donázar *et al.* (2009) estimated the cost of building a new SFS, either in France or Spain, at between US $21,900 and US $54,700, plus US $21,900 each year for its maintenance costs. If we project this data to the 67 SFS currently operating in the Pyrenees, it results in approximately US $1.47 million to US $3.66 million in building expenses and US $1.47 million in annual maintenance costs. Therefore, even taking into consideration the highest SFS estimated expenditures, a simple monetary balance shows that the mean annual economic benefit indirectly accruing to the Pyrenean human community from SFS avian scavengers-based tourism represents almost half of this initial building investment. Considering our conservative approach, at least US $2.53 million are recovered annually from visitor expenditure on accommodation, food, and SFS entrance costs. This is an interesting reflection especially if we take on board that most of the investment to build and maintain SFS originated with a conservation purpose are publicly funded in Spain.

Leaving aside the simple economics of SFS, their sensitive contribution to conservation strategies must also be considered (Brink *et al.* 2020; Cortés-Avizanda *et al.* 2016). While their potential benefits for wild fauna conservation and reintroduction are clear, a number of recent studies have shown that SFS are only useful conservation tools in specific contexts (i.e. when food availability is low, or there are risks from illegal poisoning) and during limited periods of time (i.e. critical breeding periods such as when chick are hatching and during their first days of life). Indeed, some studies have shown that the aggregating effect of SFS on the Pyrenean population of bearded vultures may cause reduced geographical expansion, declining breeding output, and the loss of habitat quality due to a conspecific attraction/aggregation and consequent shrinkage of territories and increase in intra-specific competition (Carrete *et al.* 2006; Margalida *et al.* 2016). SFS have been shown to cause monopolization of resources by certain species or individual age classes (Cortés-Avizanda *et al.* 2012; Duriez *et al.* 2012; Moreno-Opo *et al.* 2020), and can also act as sources of pharmaceutical rich residues in carcass debris from domestic livestock or promote the spread of pathogens from livestock to wildlife and the existence of multi-drug resistant pathogens (e.g. Plaza *et al.* 2020).

Therefore, even if SFS do act as a significant economic engine through nature-related sustainable tourism, we must not forget their original purpose of avian scavenger conservation. SFS are conservation feeding structures that may offer some exceptional times (i.e. only 30% of Pyrenean SFS) recreational and educational activities. Thus, SFS are not designed for tourism, but because of a conservation necessity. Consequently, they are ruled by conservation principles and when they are no longer needed, they stop working. In this sense, the scavenger-based tourism promoted by SFS could be considered such as the one linked to some no massed wildlife watching trips used to the population census, or environmental conservation projects that are partially funded and supported by volunteering work (Ellis 2003; Wearing 2004; Hughes *et al.* 2014), where the conservation practices would be equally developed even in the absence of tourists/volunteers and the main priority is the ecosystem preservation.

On balance, we need to ensure that potential cultural added value and economic and social benefits of SFS in fostering recreational activities (birdwatching, educational, or photographic opportunities) add to, rather than detract from, their conservation aims. To do so, a scientific lead is required to determine conservation priorities such as specific species needs, increasing carrying capacity in relation to food availability and expansion of scavenger species' geographic range (e.g. Margalida *et al.* 2020). Future management of SFS should therefore determine the priorities of the existing SFS and how best to harmonize conservation with recreational activities. Scientist should apply their professional expertise to supervising periodic monitoring of the continuing conservation value of SFS. This would be the only strategy to prevent at all times the possibility that this kind of wildlife-based tourism provoke short- or long-term behavioural disorders in the local wildlife (as it has already happened, for example, with sharks, marine mammals, polar bears, turtles, and birds in wildlife tourism experiences, e.g. Corkeron 2004; Dyck & Baydack 2004; Arcangeli *et al.* 2009; Landry & Taggart 2010; McFadden *et al.* 2017; Cisneros-Montemayor *et al.* 2020).

CONCLUSIONS

In a society where the scavenger guild is frequently neglected regardless of its fundamental role in a multitude of ecological processes and key role in human well-being (Moleón *et al.* 2014; DeVault *et al.* 2016), there is an urgent need to make the NCP provided by these species known and put them in value. Our findings contribute to highlighting the important role of avian scavengers in providing non-material NCP through recreational/educational activities at SFS. To this end, this study supports last years' call to better integrate scavenger conservation into the IPBES (Martín-López *et al.* 2018 and improve our understanding of the link between the today's human society and the scavenger guild. Nowadays, wildlife-based tourism is an important source of income for many local communities. Touristic activities associated with SFS have been discussed by Anderson and Anthony 2005; Piper 2005; and Ferrari *et al.* 2009, which frequently point out that the necessary harmonization between nature conservation and economic development is all too often forgotten. While recognizing that SFS construction should always follow conservation needs, and that scientific monitoring is necessary to constantly evaluate their usefulness as management tools, multiple cultural experiences based on the non-material NCP of avian scavengers can be promoted as means of increasing people's quality of life and generating local revenue. Birdwatching, educational, or photographic activities enrich the recreational experience of visitors to SFS, provide added cultural value to the regional landscape, and make a real contribution to the income of local communities. Future research in this area should seek to discover more about the potential value of SFS and the social value of iconic species as providers of non-material NCP, including the role they play in shaping visitors' perceptions of the scavenging fauna.

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CHAPTER 4

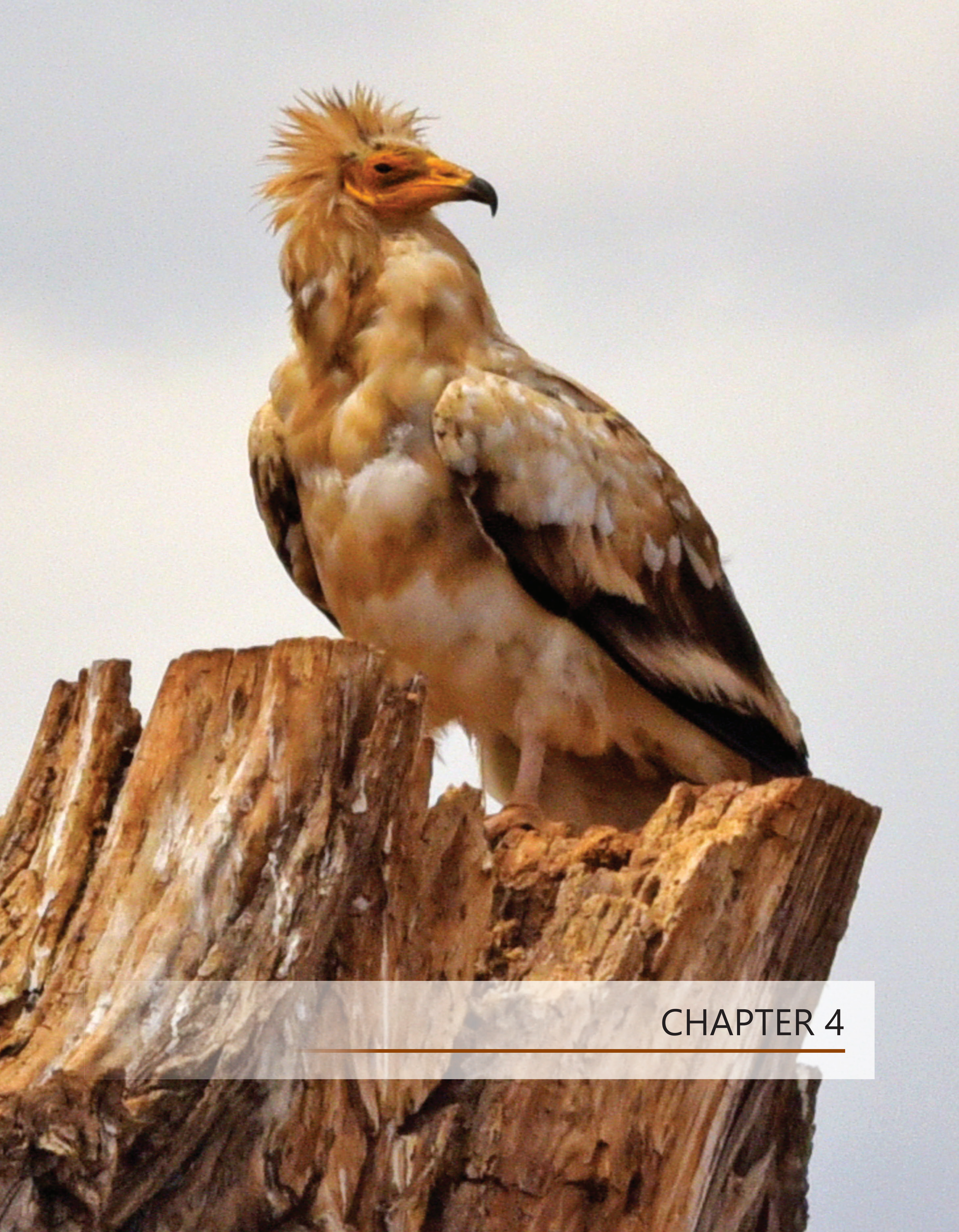

Photo by Marta Gila María.
An imperfect adult and an adult Egyptian vultures perched on their roosting tree (Madrid).

CHAPTER 4

Avian scavengers' contributions to people: the cultural dimension of wildlife-based tourism

by

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This chapter is under review:

García-Jiménez, R., Pérez-García, J.M., Margalida, A., & Morales-Reyes, Z. Avian scavengers' contributions to people: the cultural dimension of wildlife-based tourism (under review).

ABSTRACT

Scavengers provide significant nature's contributions to people (NCP), including disease control through carcass removal, but their non-material NCP are rarely considered. For the first time, we assess the extent and value of the NCP provided by European avian scavengers through a scavenger-based tourism at Pyrenean supplementary feeding sites (SFS). Using a two-step cluster analysis, two different types of visitor were identified (specialist avian scavenger-watchers and generalist nature-lovers) at those SFS offering recreational experiences (n=20, i.e. birdwatching, educational, or photographic activities). Most visitors (85%) perceived avian scavengers as beneficial NCP providers, associating this guild with non-material NCP (mostly supporting identities), followed by regulating and maintenance of options NCP (<1%). Our findings help to characterize the type of people who participate in scavenger related recreation and to identify and value their perceptions of avian scavengers. There has not been much previous research on positive human-wildlife interactions, even though ignoring people emotional bonds with nature can be perilous for biodiversity conservation.

Keywords

Cultural ecosystem services, ecosystem disservices, ecotourism, people's quality of life, raptors, social perceptions, vulture restaurant

INTRODUCTION

Nature is inherently imbricated with the existence of any living being. Humans have long tried to understand this involvement by delimiting the inflows that nature provides to our species. Many of the fundamental terms in the nature-people relationship were conceptualized during the late 20th century as interest in the subject blossomed. One such was the concept of ecosystem services (Costanza *et al.* 2017), the definition of which was consolidated in the 2005 Millennium Ecosystem Assessment (MEA 2005). Ecosystem services were defined as the benefits provided by ecosystems functioning to human society. Recently, a more accurate term —Nature's Contributions to People (NCP)— has been coined by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (Díaz *et al.* 2018) to include all of the detrimental and beneficial effects that living nature can exert on people's quality of life. This concept assumes culture to be the matrix where all the different NCP are developed and proposes a classification based on three partially overlapping groups: material, non-material and regulating NCP (Díaz *et al.* 2018). Material NCP are finite physically consumed goods such as water, energy, or building and ornamental materials; non-material NCP are those sustaining individual and collective well-being and psychology, such as aesthetic, experiential, recreational, intellectual and spiritual contributions; and regulating NCP are functions and structural features and ecosystems processes that regulate material and non-material NCP or influence environmental conditions which affect humans.

Due to their subjective nature, non-material NCP (i.e. cultural services) have always been the most abstract and least well-identified of the NCP (Milcu *et al.* 2013). These contributions to our culture which support learning and inspiring values, or create a sense of place or spiritual awareness, have not been given sufficient attention until recently (Hernández-Morcillo *et al.* 2013). However, non-material NCP are both critical in promoting nature conservation and enabling sustainable economic development (Eagles 2004). Understanding people's emotional bonds with nature is key to involving society in any nature conservation strategy (Bennett 2016). During the last two decades, the means of making non-material NCP visible have usually been based on financial assessments and determining socio-cultural preferences through interviews, surveys, or personal information posted on social media (Milcu *et al.* 2013, e.g. Vollmer *et al.* 2015; Oteros-Rozas *et al.* 2018).

Ecotourism and recreational wildlife-based activities are booming worldwide (Reynolds & Braithwaite 2001; Balmford *et al.* 2015). In particular, birdwatching is now one of the most popular wildlife-based hobbies around the world (e.g. Şekercioğlu 2002; Ma *et al.* 2013), and it has been estimated that in the United States alone, birdwatchers spend more than $30 billion annually on travel and equipment and would be willing to pay $35 to $134 per day on birdwatching activities (LaRouche 2003). One would therefore expect for a generally high social awareness of, and knowledge about the value of birds. But birds have not traditionally been recognized as ecological actors and providers of NCP (Şekercioğlu 2006). Indeed, scientific studies of NCP provided by birds remain biased, omitting certain guilds such as avian scavengers (Şekercioğlu, 2006; DeVault *et al.* 2016). Despite being a worryingly endangered guild (Buechley & Şekercioğlu 2016) playing an essential role in human well-being (DeVault *et al.* 2016), avian scavengers continue to be oblivious to society, or even seen as a threat (Lambertucci *et al.* 2021). There are very few studies on avian scavenger-based tourism, even though it currently provides a livelihood for many local communities (Ferrari *et al.* 2009). The slight attention given to this recreational experience has typically focused on its economic contribution to human society (e.g. Becker *et al.* 2005; García-Jiménez *et al.* 2021); hardly any studies have focused on the cultural value provided by scavenger-based tourism or the other diverse non-material NCP provided by avian scavengers (Morelli *et al.* 2015; Echeverri *et al.* 2020; Aguilera-Alcalá *et al.* 2020).

Supplementary feeding sites (SFS, also called “feeding stations” or “vulture restaurants”) have been one of the most popular conservation tools supporting the feeding of scavengers during spatial or temporal carcass shortages. However, this management-conservation tool has pros and cons, with some potential benefits but also ecological constraints when SFS are used to manage scavengers’ populations and distribution (Cortés-Avizanda *et al.* 2016). SFS can also be employed to raise social awareness in landowners, farmers, and the general public, while being used for recreational activities (i.e. ecotourism) (DeVault *et al.* 2016). However, various studies have shown that SFS cannot be used as permanent solutions because they can impact population fecundity (Carrete *et al.* 2006; Cortés-Avizanda *et al.* 2016), reduce the dispersion of sub-adult individuals (Margalida *et al.* 2013) and increase pathogen transmission (Marin *et al.* 2019). Consequently, SFS must not be created or sustained purely to appeal to tourists (Newsome and Rodger, 2008). Conservation requirements must dictate SFS management, even at the cost of potentially important economic opportunities for local communities (García-Jiménez *et al.* 2021).

Old World vulture populations suffered a sharp decline in the late 20th century (Buechley & Şekercioğlu, 2016). SFS were widely established to reverse this trend by reducing the potential impact of non-natural mortality due to habitat transformation, food shortages, and illegal poisoning (Donázar *et al.* 2009). Currently, Spain is one of the best European countries in which to view obligate (i.e. vultures) and facultative avian scavengers (e.g. eagles, kites, corvids, etc.). More than 90% of the European vulture population live in Spain (Margalida *et al.* 2010) as well as numerous species of facultative avian scavengers, including some endangered species, such as the endemic Spanish imperial eagle *Aquila adalberti* or the red kite *Milvus milvus*. Notwithstanding, Spain still maintains a broad network of operational SFS, the first being built more than 50 years ago (Donázar *et al.* 2009).

Our goal was to identify and value the NCP provided by avian scavengers through recreational and educational activities (i.e. wildlife-based tourism) at the SFS in the Pyrenees. Specifically, we aimed to: (i) characterize visitor profile at SFS and (ii) examine the perceptions, interest in, and knowledge base of SFS visitors regarding European avian scavengers.

MATERIAL AND METHODS

Study area

Our study was conducted in the Pyrenees, a mountain range of 50,000 km^2 located in southwest Europe on the border between France and Spain. All four European vulture species (cinereous *Aegypius monachus*, griffon *Gyps fulvus*, Egyptian *Neophron percnopterus*, and bearded vulture *Gypaetus barbatus*) occur there as well as a diverse community of facultative scavengers (e.g. red kites, black kites *Milvus migrans*, ravens *Corvus corax*, and golden eagles *Aquila chrysaetos*), all of which regularly visit the SFS network (Moreno-Opo *et al.* 2016). Currently, at least 67 SFS operate in the Pyrenees and adjoining Pre-Pyrenean area (seven in France and 60 in Spain). All of the SFS considered in this study were created principally for scavenger conservation (i.e. hides built, managed, and exclusively intended for photography were not included), and are managed either by public or private operators. Currently, at least 20 Pyrenean SFS are open to visitors (García-Jiménez *et al.* 2021), providing wildlife-based tourism and/or environmental educational activities in addition to serving conservation purposes.

Data collection

SFS characteristics

Between February 2018 and January 2020, 53 (79.1%) of the Pyrenean SFS managers were interviewed by telephone to gather basic information on the management and characteristics of each SFS, including whether the access to the general public was allowed. We interviewed 90% of the 20 Pyrenean SFS receiving visitors, all located in the eastern Spanish Pyrenees (Aragon and Catalonia regions). The information obtained included the activities offered beyond supplementary feeding of avian scavengers and showed that those SFS with recreational activities (n = 20 out of 67 Pyrenean SFS) provided at least one of the following: (i) *birdwatching* (30%); (ii) *education* (20%); (iii) *photography* (25%); and *education and photography* (25%).

Visitor information

To characterize the SFS visitor profiles enjoying the recreational and educational activities on offer and identify their perceptions of the avian scavenger guild, we carried out individual surveys in the same two-year period (February 2018–January 2020). We only considered 15 of the publicly accessible 20 SFS to survey the visitors. Five SFS were discarded because they were inside a protected area, and we could not assume that watching avian scavengers was the main reason for peoples' visits (see García-Jiménez *et al.* 2021 for details). We met the ethical standards for social surveys by informing respondents in writing, at the beginning of the questionnaire, about the nature of their voluntary participation and their guaranteed anonymity.

A total of 94 survey questionnaires (either in English or Spanish) were randomly distributed among nine of the 15 SFS considered. The questionnaire comprised 14 questions, divided into two sections: (1) a general section, with questions about visitors' personal interest in, perceptions of, and knowledge of the NCP provided by scavengers; and (2) questions characterizing their socio-economic status (see table S1 in Supplementary Information1). As part of the questionnaire, we provided visitors with colour images of 14 species of obligate and facultative avian scavengers generally present in the Pyrenees (the four European vultures, six birds of prey and four corvids; see table S2 in Supplementary Information1) and asked if they could visually identify and name the species. The only species absent in the Pyrenees is the Spanish imperial eagle, an important avifaunal icon of the Iberian Peninsula —thus, culturally representative— and easy to identify visually. It was included in the questionnaire in order to present two *Aquila* spp., allowing us to evaluate the visual identification and cultural recognition (i.e., species recognised but which could not be named) skills of the visitors.

We obtained an average of 10 ± 4 completed questionnaires per SFS surveyed (range 3–17). Given the diverse dynamics of the SFS (only two presented scheduled visits), the questionnaires were self-answered by each visitor, so usable responses varied from 66% (n = 62 answers, Q13) to 100% (n = 94 answers, Q2; table S1) depending on the question.

Data analyses

SFS visitor profiles

Based on visitors' knowledge, perception and interest in the avian scavenger guild, and their socio-economic status, we built a two-step cluster analysis (Norusis 2003) to evaluate a possible structuring of the SFS visitors into distinct "groups". This is a probabilistic model proper to include mixed variables and provides the distance between two clusters through the decrease in the log-likelihood function resulting from merging. We used five categorical variables: (i) the reason for their visit; (ii) the extent of their previous experiences with birds; (iii) the relationship between their occupation and birds, (iv) their educational level and (v) their average monthly income. The seven numerical variables were: (i) the material brought to the SFS (e.g. bird guides, binoculars, camera; see table S3 in Supplementary Information1); (ii) the visitor's self-rated interest in the avifauna; and (iii) the number of birdwatching excursions per year, plus four indices devised to determine the knowledge and perceptions of visitors regarding the avian scavenger guild: (iv) *species identification index* (ability to recognise and name a species); (v) *species recognition index* (ability to recognise a species, but not name it); (vi) *positive perception index*; and (vii) *less positive perception index* (see table S1 and Supplementary Information2). The Schwarz Bayesian criterion (BIC) for each cluster within a specified range was used to estimate the number of clusters. This estimate was then refined by finding the largest increase in distance between the two closest clusters at each hierarchical clustering stage. Background noise was screened out. The questions unanswered by the visitors were considered as non-available data (7.3% out of 1,580), but included in this specific ordination analysis as estimated values computed by the mean (of the numerical variables) and the mode (of the categorical variables).

After this cluster analysis, we studied the distribution of the different groups of SFS visitors among SFS offering three different types of recreational activities: educational, photographic, or both. Birdwatching was not included in these analyses because no questionnaires were completed in any of the SFS offering birdwatching exclusively.

SFS visitor knowledge and perceptions regarding avian scavengers

In order to evaluate visitors' knowledge regarding the avian scavengers, we considered two separate variables individually per visitor: (1) *visual species identification* (i.e. percentage of species correctly identified visually, n = 74 answers) and (2) *cultural species recognition* (i.e. percentage of species correctly culturally recognized, n = 77 answers). Mean ± SD values were then estimated for both variables.

To analyze SFS visitors' perceptions of avian scavengers and the NCP provided by them, we computed descriptive statistical analyses using two indexes: (1) an *NCP perception index* (i.e. a written reasoned comment expressing why a visitor gave a more or less positive value to each species); and (2) an *NCP valuation index* (i.e. a numerical valuation of each species as a provider of NCP using a five-point scale from least positive (1) to most positive (5)). Only reasoned comments mentioning beneficial or detrimental NCP were considered to compute this index. Combining both types of valuation methods (*NCP perception index* and *NCP valuation index*), we were able to understand and analyze the reasons for people enjoyment of avian scavengers through recreational activities, and to identify the scavenger species perceived as NCP providers and whether they were perceived more or less positively.

We transformed visitors reasoned comments into an *NCP perception index* as follows. First, we divided visitors' comments into usable or unusable (the latter comprising: unanswered questions, unsubstantiated like/dislike answers, and comments mentioning biological and/or behavioural traits which we could not relate to an NCP (e.g. reference to red kite as a facultative scavenger or raven as a thief). We identified 557 usable comments, but in some cases people included more than one argument in an answer, so these answers could be associated with more than one NCP, resulting in a total of 631 different perceptions. Second, we classified these perceptions into four types: abundance, intrinsic value, detrimental NCP, and beneficial NCP (see tables 1, and S4 and S5 in Supplementary Information1). NCP were classified according to the IPBES framework (Díaz *et al.* 2018).

Finally, we constructed the *NCP valuation index*, by classifying visitor numerical valuations as either less positive (from 1 to 2), neutral (3), and positive (from 4 to 5) (see details of the questionnaire in table S1).

Table 1 | Beneficial NCP related to the 14 European avian scavengers studied as perceived by SFS visitors. Examples of the original reasoned comments are given. Classification of beneficial NCP based on Díaz *et al.* (2018).

NCP group	NCP category	Examples
Material	—	—
Non-material	Learning and inspiration	• It informs me about eagles' presence
		• It warns the other species in the woods
	Physical and psychological experiences	• Appearance (e.g. beauty, color of the plumage, silhouette, size, elegance)
		• It is nice to watch while flying (agility)
		• Pleasant/unpleasant squawk
		• A species rarely photographed
		• It is boring
	Supporting identities	• Singularity, peculiarity
		• Nature icon, an ecology symbol
		• They play their role, they are necessary, they are all important
		• Intelligence
		• Threat level
		• I see it in my village, close to my home
Regulating	Regulation of detrimental organisms and biological processes	• It is a hunting/scavenger/super-predator species
		• They have a cleaning role in the nature
		• Facultative scavengers cover those tasks that larger scavengers cannot
		• It has an essential role in the food chain
		• Sanitary role
		• It maintains the balance
Maintenance of options	—	• It is a conservation thermometer

[a] This is a summary table. For an extended version with the corresponding numerical valuations and more examples of the reasoned comments see table S5.

RESULTS

SFS visitor characterization

Visitors to SFS were normally Spanish adult (87% from Spain; 13% from other European countries) 47 years old on average, 81.7% in couples, and 72.6% parents with children. There was a high gender bias (only 29.9% were female). About 68.2% of visitors had taken higher education, and most were middle or high economic earners (54.2% and 31.9%, respectively) (see table S6 in Supplementary Information1).

Cluster analyses indicated that the best model identified two cluster-groups of visitors: (1) specialist avian scavenger-watchers; and (2) generalist nature-lovers (table 2). These two clusters were unevenly distributed among the SFS offering different types of recreational activities (figure S1 in Supplementary Information1). Generalist nature-lovers predominantly visited SFS providing educational activities (66.7%), while specialist avian scavenger-watchers preferred those offering photographic facilities (75%). SFS offering both educational and photographic experiences simultaneously received a more equitable proportion of visitors from both groups, i.e.: 63.2% specialist avian scavenger-watchers vs. 36.8% generalist nature-lovers.

Table 2 | Classification of SFS visitors from a two-step cluster analysis. Eeach characteristic is assigned to its originating question in the questionnaire, in parentheses. See table S1 for a detailed description of the variables included in the analysis and Supplementary Information2 for details on the indexes used. Variables marked * showed a relative importance on the predictor between 0.2 and 0.4; all the rest had higher values. The number of species identified and recognized are out of all 14 included in this study (listed in table S2).

Characteristics	**Visitors to SFS (%)**	
	Specialist avian scavenger-watchers 60.6% (57)	**Generalist nature-lovers** 39.4% (37)
Photography as one of the main reasons for visiting the SFS (Q1)	Yes	No
Material (Q2)*	A material combination that includes **binoculars** (and probably **photographic camera** and/or **bird guides**)	A material combination that includes a **photographic camera** (and possibly also **bird guides**)
Previous experience with birds (Q3)	High	Some
Self-rated interest in the avifauna (Q4)	9.4 ± 0.9	7.7 ± 1.8
Times per year going to birdwatching (Q7)*	64.9 ± 76.0	10.8 ± 15.6
Species visually identified (Q6)	12 ± 2 species	7 ± 4 species
Species culturally recognized (Q8)	13 ± 1 species	9 ± 4 species
Species positively perceived (Q8)*	11 ± 3 species	7 ± 4 species

SFS visitor knowledge and perceptions of avian scavengers

Visitor knowledge of avian scavengers

All species comprising the avian scavenger guild were better culturally recognized than visually identified. Corvids were much better visually identified by SFS visitors than birds of prey (72.3 ± 12% vs 58.1 ± 11.9%), but cultural species recognition was almost the same for both groups (78.6 ± 9.8% and 77.3 ± 7.2%, respectively) (figure 1).

Seventy seven percent of the visitors correctly visually identified the four European vulture species at the same time and 84.4% simultaneously recognized them culturally. Overall, obligate scavengers were better visually identified than facultative scavengers (89.9 ± 5.7% *vs.* 63.5 ± 13.4%) and likewise cultural recognition of the two groups (92.9 ± 4.8% *vs.* 77.8 ± 7.8%). Among all the avian scavenger species tested, the bearded vulture had the best visual identification and cultural recognition scores (97.3% and 98.7% respectively), whilst the Western marsh harrier *Circus aeruginosus* and common buzzard *Buteo buteo* were least frequently identified species (47.3% and 48.7%, respectively). The Western marsh harrier was also the least culturally recognized (66.2%) (see figure 1).

Visitor perceptions of and interest in avian scavengers

According to the *NCP perception index* (n = 631 SFS visitors' reasoned comments), most visitors perceived avian scavengers as providers of beneficial NCP (84.9%), followed by visitors who valued avian scavengers because of their abundance and ease of observation (12%), or their intrinsic value (2.2%), whereas only 0.8% of SFS visitors considered avian scavengers to be providers of detrimental NCP. Among the beneficial categories of NCP, non-material NCP were the most often mentioned (87.5%), followed by regulating NCP (12.1%), and maintenance of options (0.4%) (figure 2a).

At the functional level, abundance comments for facultative scavengers (14.3%) were twice that of obligate scavengers (7.3%), although the beneficial NCP were greater for obligate than facultative scavengers (90.7% vs. 82.2%, respectively) (figure 2b). At the taxonomic level, corvids received the highest proportion of reasoned comments related with the abundance (22.3%), contrasting with vultures (7.3%). In contrast, more respondents recognized the beneficial NCP of vultures (90.7%) compared with birds of prey (86.8%), or corvids (71.5%). The intrinsic value of a

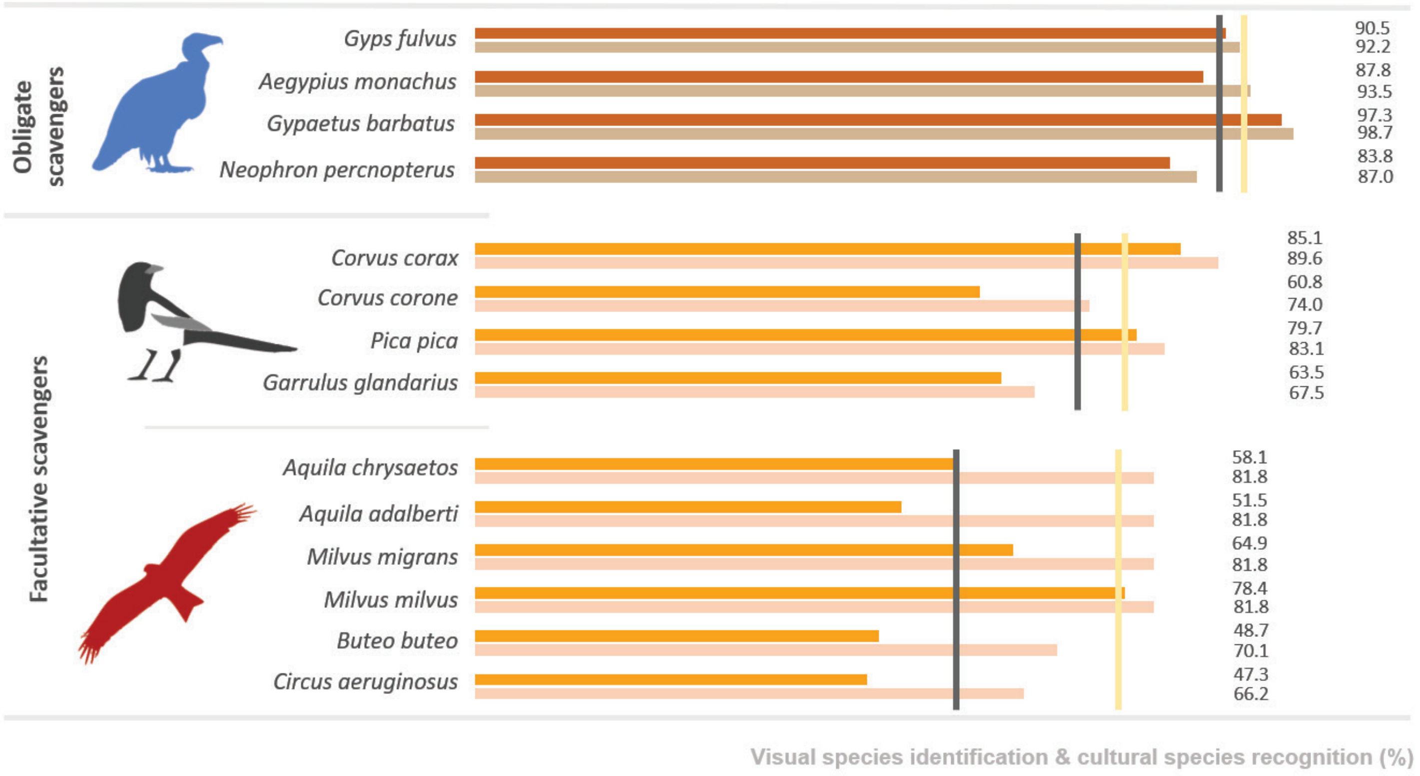

Figure 1 | SFS visitor knowledge of avian scavenger species. *Visual species identification* by visitors (%; n = 74 answers; dark top bar for each species) and *cultural species recognition* (%; n = 77 answers, light bottom bar for each species). Vertical bars show mean values of visual species identification (black; vultures 89.9%, corvids 72.3%, and birds of prey 58.1%) and cultural species recognition (yellow; vultures 92.9%, corvids 78.6%, and birds of prey 77.3%) within each taxonomic group. Species were grouped by functional groups (bar color): obligate (browns) and facultative scavengers (oranges); and taxonomic groups (colored silhouette): vultures (blue), corvids (black) and birds of prey (red).

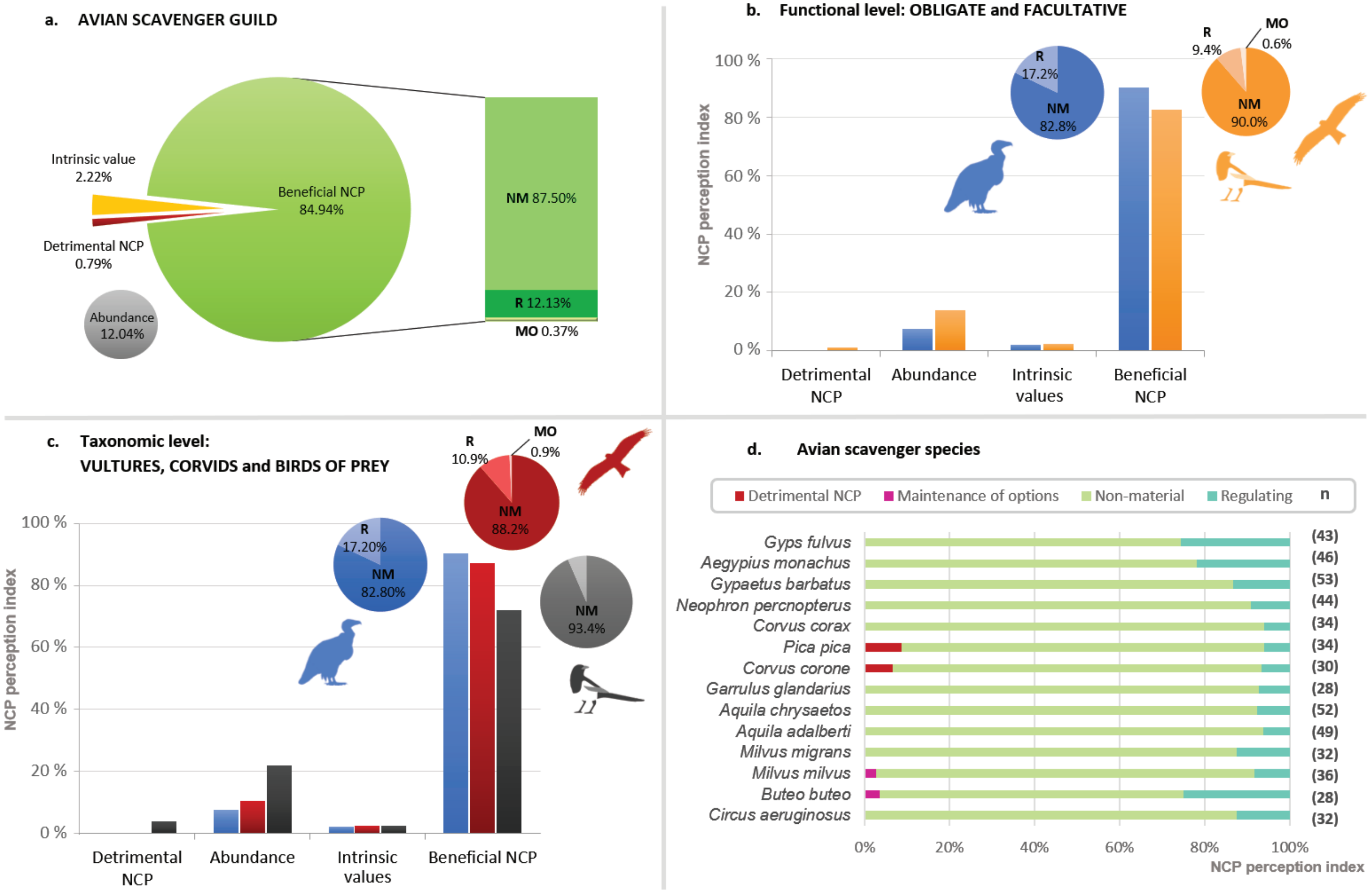

Figure 2 | SFS visitor perceptions of avian scavengers (*NCP perception index*): (a) at the avian scavenger guild level (all species together) (n = 615 reasoned comments); (b) at the functional level – obligate (blue) and facultative scavengers (orange) (n = 615); (c) at the taxonomic level – vultures (blue), corvids (black), and birds of prey (red) (n = 615); and (d) at the species level (n shown in brackets). Beneficial NCP include: non-material (*NM*), regulating (*R*), and maintenance of options (*MO*). In figure 2b and c, bar diagrams show the proportion (%) of reasoned comments grouped by abundance, intrinsic values, detrimental, and beneficial NCP (i.e. *NCP perception index*) and pie charts show the proportion (%) of reasoned comments classified by beneficial NCP groups (i.e. NM, R, and MO). Note that in figure 2d, abundance and intrinsic values were not included.

species was equally, though only rarely, noted for all taxonomic groups and species, while detrimental NCP were only recorded for corvid species (figures 2c and d).

Non-material NCP were the most mentioned NCP category, ranging from 82.8% of comments for vultures to 93.4% for corvids. Regulating NCP were associated mainly with obligate scavengers (17.2%), but were only mentioned in 9.43% of the beneficial NCP comments for facultative scavengers, concretely 10.9% for birds of prey and 6.6% for corvids (figure 2b and c). Maintenance of options was only mentioned by one visitor, who recognized the future benefits for biodiversity associated with the presence of red kite and common buzzard (figure 2d). In contrast, regarding detrimental NCP, SFS visitors mentioned the damage to animal biodiversity caused by two species: common magpies *Pica pica* and carrion crows *Corvus corone* (see figure 2d and table S4).

SFS visitors mentioned beneficial NCP in 536 reasoned comments, of which 98.9% could be classified into different categories (figure 3). Among non-material NCP, *supporting identities* was by far the most common non-material NCP mentioned in valuing scavenger species, ranging between 73% (n = 255) for birds of prey and 75.5% for vultures (n = 183). *Physical and psychological experiences* were slightly more associated with birds of prey (26.6%, n = 255) than vultures (23.2%, n = 183), or corvids (22.1%, n = 92). *Learning and inspiration* were the least frequently mentioned and were associated with particular species. They were mentioned once each for griffon and cinereous vultures, carrion crow and Eurasian jay *Garrulus glandarius*. Within the regulating NCP, only the category of “regulating of detrimental organisms and biological processes” was mentioned, although it was linked to all species (figure 3). Examples of the reasoned comments of SFS visitors classified as beneficial NCP provided by avian scavengers (i.e. *NCP perception index*) and the associated numerical valuations of avian scavengers (i.e. *NCP valuation index*) are presented in table S5.

Regarding the *NCP valuation index* (n = 77 answers), 71.4% of the 14 species received more than 50% positive numerical valuations (i.e. *NCP valuation index* = 4 or 5) and these 10 species presented less than 10% of the less positive ones (i.e. *NCP valuation index* = 1 or 2). Vultures were perceived by SFS visitors as the most beneficial functional group, followed by birds of prey and corvids. The bearded vulture received the most positive valuations

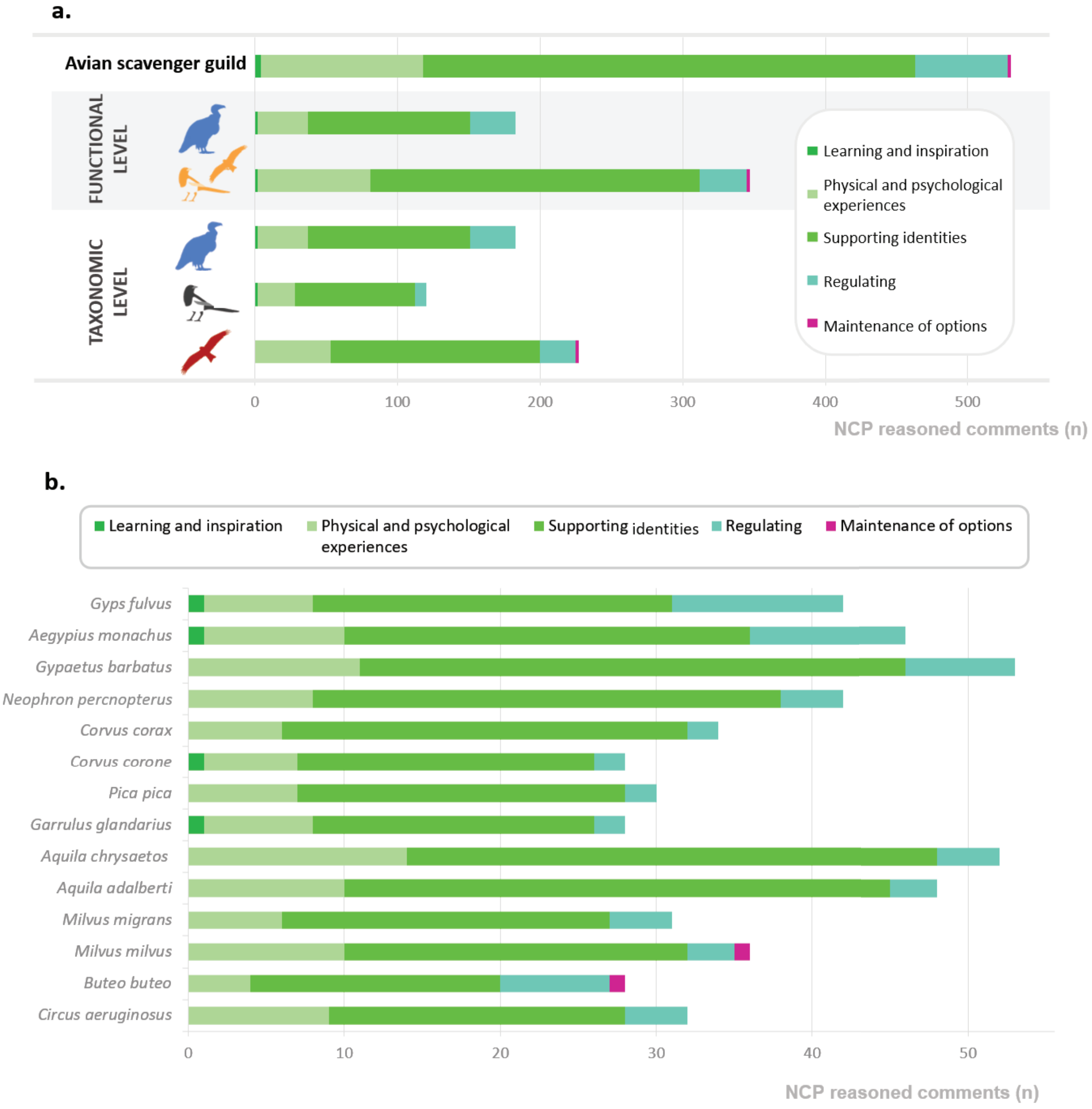

Figure 3 | Classification of the beneficial NCP provided by avian scavengers mentioned by SFS visitors (*NCP perception index*; n = 530 reasoned comments). NCP were grouped into: non-material (divided into the categories: *learning and inspiration*, *physical and psychological experiences*, and *supporting identities*; green bars), *regulating* (blue bar), and maintenance of options (i.e. future benefits; fuchsia bar). (a) For the avian scavenger guild (all species together) at the functional level obligate –blue–, and facultative scavengers –orange–, and at the taxonomic level vultures –blue–, corvids –black–, and birds of prey –red–; and (b) at the species level.

(89.6% with scores of 5 and 6.5% with scores of 4), but the only vulture not receiving less positive valuations was the Egyptian vulture. The only other species that did not receive less positive valuations was the golden eagle. In contrast, the raven (5.2% with scores of 1 and 13.0% with scores of 2) and the common magpie (7.8% with scores of 1 and 11.7% with scores of 2) were the species whose NCP were valued lowest (figure 4).

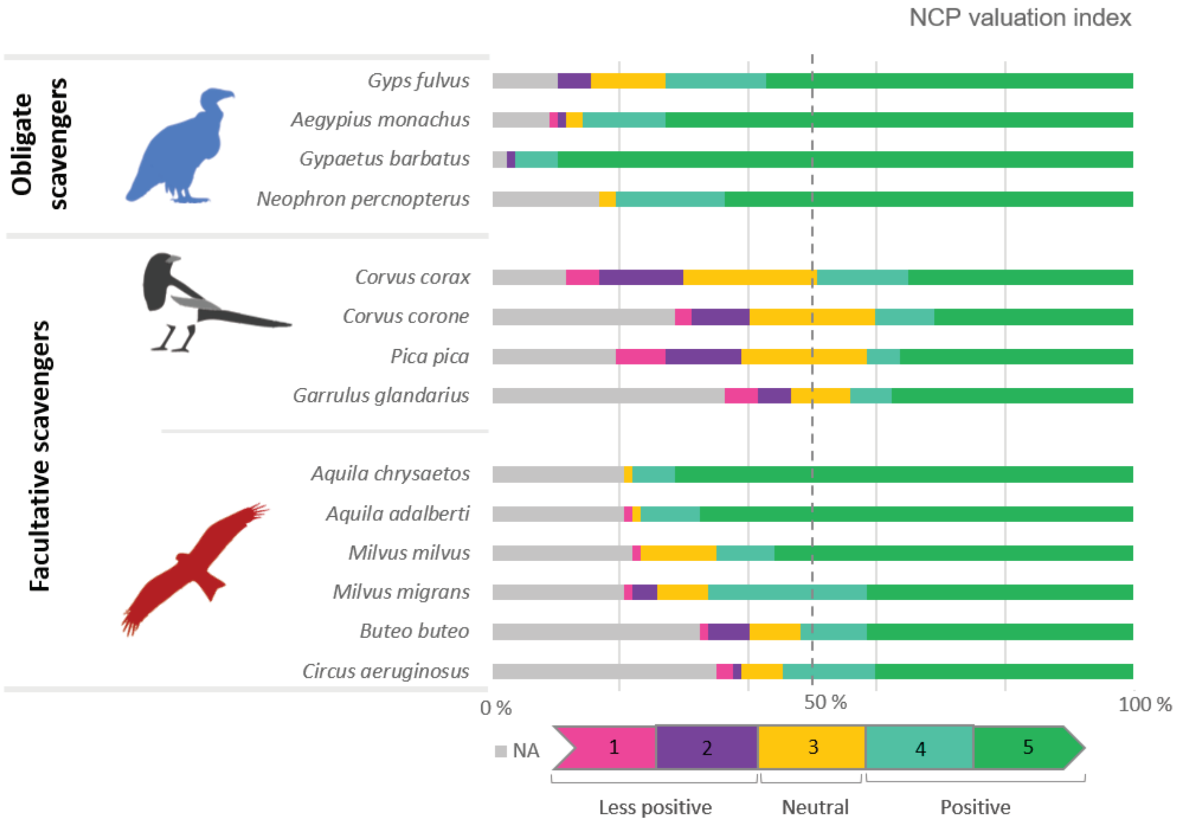

Figure 4 | SFS visitor perceptions of avian scavengers as providers of NCP by species (*NCP valuation index*; n = 77 answers). Each bar shows the percentage of the numerical valuations of avian scavenger species as providers of NCP on a five-point scale from less positive (pink) to more positive (green) values by SFS visitors. Non-available data (grey) were also included. For example, considering n = 77 answers, the griffon vulture shows 10.4% of NA data (grey), 0% of which have a score of 1 (pink), 5.2% have a score of 2 (purple), 11.7% have a score of 3 (yellow), 15.6% have a score of 4 (turquoise), and 57.1% have a score of 5 (green), showing that this species was perceived as a very positive NCP provider by SFS visitors.

DISCUSSION

This study is the first to identify and value, from a non-economic perspective, the NCP provided by European avian scavengers through scavenger-based tourism at the SFS and analyze the profile of Pyrenean SFS visitors. We identified and measured the perceptions of people who enjoy scavenger-related activities, a social group consistently overlooked in both the scavenging and the ecotourism worlds. The study showed that SFS visitors generally perceive avian scavengers as providers of beneficial NCP, especially appreciating their non-material NCP, particularly the supporting identities value. In general, SFS visitors were found to be a knowledgeable and positive regarding of scavengers, although to varying degrees depending on the species.

SFS visitor characterization

Many factors have been reported as shaping the perception of wildlife (e.g. Hough 2014; Shwartz *et al.* 2014). Regarding birds, some research has shown that species knowledge (including perceived diversity, spatial distribution, and abundance), past nature-related experiences, and surrounding cultural context (e.g. religion, stories, and films) can all influence human awareness and perception of an avifauna (Cox & Gaston, 2015; García-Alfonso *et al.* 2019; Leong *et al.* 2020). This study corroborated that the knowledge base of visitors to SFS (measured as the ability to visually identified and culturally recognize avian scavenger species), self-rated interest in birdlife, and avifauna relatedness (defined as the number of bird-related experiences of a visitor prior to the SFS visit) were some of the most influential factors characterizing different visitors' profiles. Species knowledge and awareness (both closely linked to human-nature relatedness and individual interest in nature and biodiversity) were recently shown to influence farmers' perceptions and local ecological knowledge about ecosystem services provided by scavengers (Morales-Reyes *et al.* 2018; García-Alfonso *et al.* 2019) and to positively influence multiple stakeholders' perceptions regarding these species (e.g. Cortés-Avizanda *et al.* 2018).

Photography was one of the primary motivational triggers for someone to visit an SFS and is also a representative factor in defining a visitors' profile, while the material brought, the frequency of self-guided birding explorations, and the positive perception of a species were less influential, but also relevant factors. Therefore, contrary studies indicating a homogeneous birdwatcher profile (Şekercioğlu 2002; 2003), and in line with those showing the heterogeneity of birdwatchers' as a group (e.g. Scott & Thigpen, 2003; Kim *et al.* 2010), we identified two well-differentiated types of SFS visitor: *specialist avian scavenger-watchers* and *generalist nature-lovers* (table 2). Photographic opportunities were among the main reasons for an SFS visit by a specialist avian scavenger-watcher, explaining the observed tendency of this type of SFS visitor to prefer visits to SFS offering photographic activities. Photographing scavengers in the wild has previously been associated with certain physical and psychological experiences, particularly those regarding aesthetic and supporting identity values (Aguilera-Alcalá *et al.* 2020). However, both types of visitors went to SFS offering all kinds of recreational activities and interestingly, generalist nature-lovers mostly visited SFS with educational activities, showing their interest in increasing their lesser knowledge of avian scavenger species.

As for USA and UK birders, our results showed that the average SFS visitor was an older adult man (around 47 years old), in a couple, with a high level of education, and of medium to high economic status (LaRouche 2003; Cooper & Smith 2010; Carver 2013; Shwartz *et al.* 2014; Belaire *et al.* 2015). However, none of these studies, or economic status predicted the determining factors defining the SFS visitor types found in our study, as is usual when the demographic parameters of birdwatchers were previously evaluated (Şekercioğlu 2002). In contrast, and in agreement with De Salvo *et al.* (2020), SFS visitor knowledge regarding avian scavengers, and their commitment and behaviour (i.e. material brought, self-rated interest in birdlife, and personal relationship to birds) had high relative importance in defining the two SFS visitor groups. Also consistent with the data reported by LaRouche (2003) and Carver (2013) regarding USA birdwatchers, most of the SFS visitors (85%) were nationals. The European Commission reported in 2015 that Spanish people were one of the European cultures most concerned about human responsibility for nature conservation (European Commission 2015). It is precisely this tendency for regional tourism what makes possible to plan community-based avian scavenger conservation strategies (Roe *et al.* 2009; Störmer *et al.* 2019), at least in Spain. Thus, SFS visitors could provide a link between avian scavengers and general public perceptions to facilitate an increasing positive awareness of the NCP value of scavengers to society and to promote avian scavenger conservation.

SFS visitor perceptions of avian scavengers

Even though bird-based tourism is increasing worldwide (Şekercioğlu 2003), the appreciation by birdwatchers of the NCP provided by birds has not often been considered in the literature (e.g. Belaire *et al.* 2015; Leong *et al.* 2020), particularly in relation to the avian scavenger guild. According to Methorst *et al.* (2020), among vertebrates, birds' contributions to people have not received extensive scientific attention, yet birds was the only taxon in which beneficial NCP were predominantly reported. Our findings showed that a majority of SFS visitors perceived avian scavengers as beneficial NCP providers (85% of the comments analysed, figure 2a), being their perceptions mainly related to the appreciation of non-material NCP, followed by regulating NCP, and maintenance of options NCP (figure 3 and table S5). Interestingly, these perceptions of SFS visitors to avian scavengers contrast with those of farmers, who mostly appreciate their scavenging service (Morales-Reyes *et al.*

2018). In a world where scientific research has traditionally focused on the detrimental NCP arising from human-wildlife conflicts (Peterson *et al.* 2010), this study highlights the positives in human perception of wildlife. Thus, vultures and eagles were positively perceived as significant providers of NCP in the Pyrenees, followed to a lesser extent by kites and other birds of prey. In contrast, corvids were little valued as NCP providers (figure 4), although only some corvid species were specifically mentioned as providers of detrimental NCP and only by a few SFS visitors (figure 4 and table S4). These conclusions are similar to those of Morales-Reyes *et al.* (2018) in their analysis of Spanish farmers' perceptions of the scavenger guild, but contra to the perceptions observed in farmers in Argentinian Patagonia, who perceive avian scavengers as harmful to livestock (Ballejo *et al.* 2020).

While regulating NCP have often been associated with scavengers (e.g. disease control, or recycling of organic matter through carcass removal, Whelan *et al.* 2008), and the material NCP of scavengers are widely tradable in Africa (Buij *et al.* 2016), non- material NCP have rarely been considered, much less evaluated. This knowledge gap arises in part because non-material NCP are intangible and abstract in nature and have generally been the least studied of the NCP (Chan *et al.* 2012) being assumed to have no marketable value. However, many recent studies showing the positive relationship between birds and human psychological well-being have been perfomed over the last two decades (Luck *et al.* 2011; Cox & Gaston, 2015). Although often focused on green spaces in urban environments, these studies have related bird species richness, behaviour and/or abundance with improved mental health (Wheeler *et al.* 2015; Cox *et al.* 2017), and lower psychological stress (Medvedev *et al.* 2015), eventually increasing personal and neighborhood well-being (Luck *et al.* 2011). Bird species richness has even been associated with life-satisfaction at a whole-continent level, being probably as relevant as income or access to green space for Europeans (Methorst *et al.* 2021). Still, even though previous research has shown the positive effects on people of enjoying watching and interacting with birds (Belaire *et al.* 2015), fewer studies have evaluated the non-material NCP provided by birds in the wider environment (MacKerron and Mourato, 2013), and only a few have studied it for avian scavengers (Becker *et al.* 2005; Echeverri *et al.* 2020; Aguilera-Alcalá *et al.* 2020).

This study introduces an interesting evaluation of the mindset of a previously unexplored social actor (i.e. SFS visitors) and analyzes the perspective of people who enjoy wild avian scavengers at both the regional and international scales. Our findings demonstrate that non-material NCP are those most highly valued by SFS visitors (88% of the comments among beneficial NCP perceived, figure 2a), similar to finding for other groups who enjoy bird-based leisure activities (especially in urban environments; e.g. Cox & Gaston 2015; Wheeler *et al.* 2015). We show that the non-material NCP mostly perceived in avian scavengers were those linked to the supporting identities NCP, while those related to physical and psychological experiences were less frequently mentioned, but also present for all the species examined (figure 3b). Interestingly, learning and inspirational values were positively perceived for vultures (griffon and cinereous) and corvids (carrion crows and Eurasian jays) (see figure 3 and table S5), although Aguilera-Alcalá *et al.* (2020) felt that this kind of non-material NCP within the scavenger guild was normally predominantly focus on mesocarnivores.

The maintenance of options NCP, which includes all the processes which support ecosystem resilience and underpin all current and future NCP, has previously been observed in evaluations of human-wildlife interactions (Störmer *et al.* 2019). Here, we confirm this NCP observation for the first time in the analysis of perceptions of the scavenger guild, particularly for black kites and common buzzards. Because the maintenance of options NCP spans all of the material, regulating, and non-material NCP groups, its presence in local people's perceptions of scavengers is a strong argument in support of the conservation of these species and the encouragement of more inclusive social attitudes toward management plans and conservation strategies to increase their effectiveness and social acceptance (Bennett 2016).

CONCLUSION

All the NCP analyzed in this study are generally non-tradable in traditional markets but are frequently perceived as public "cost-free" goods with and one and the same value to all beneficiaries (Wenny *et al.* 2011). In consequence, they are usually overlooked by society and therefore undervalued, and lack methodologies to evaluate them holistically (Milcu *et al.* 2013). By revealing the general mindset of people interested in scavenger-based tourism, this study contributes to closing a noteworthy knowledge gap regarding the non-material NCP provided by vertebrate scavengers. Our findings support the potential for growth of a flourishing scavenger-based recreational tourism, reflecting a powerful emerging interest in, and appreciation of, the non-material NCP provided by European avian scavengers. This study also reinforces recent calls made by the IPBES to conserve the threatened populations of avian scavengers (Martín-López *et al.* 2018). Further multidisciplinary analysis, including multiple social actors, is needed to provide a more integrated and holistic perspective on the social role of avian scavengers in society.

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GENERAL DISCUSSION

Photo by Juan Carlos García Gómez.
A golden eagle feeding.

General discussion

Classical food webs have traditionally been theorized ignoring the meaningful role of scavengers (e.g. DeAngelis *et al.* 1989 and see revies in Beasley *et al.* 2015; Moleón & Sánchez-Zapata, 2015). Human aversion to death as well as rotten matter, difficulties in identifying scavenged versus depredated materials (including limitations to quantify scavenged intakes in diet studies), and the fact that most species feed opportunistically on carrion have led to an underestimation of the importance of scavenging in food web research (DeVault *et al.* 2003). Indeed, scavenging has long been perceived as an anecdotal and random process (e.g. Wilson and Wolkovich estimated in 2011 that scavenging links are underrepresented in food-web research 16-fold). Despite the recent recognition of the relevance of detritus presence and its implication in food webs (Moore *et al*. 2004; Wilson & Wolkovich 2011; McCann 2012), vertebrate scavengers continue to be undervalued. Considering this social context, the lack of basic biological knowledge and quantitative measures of vertebrate scavenging behaviour is not surprising. However, technology improvements and an increasing awareness of the ecological, environmental, sanitary and economic importance of scavenging by vertebrates (e.g. Markandya *et al*. 2008; Bump *et al*. 2009; Margalida & Colomer 2012; Ogada *et al*. 2012b; Barton *et al.* 2013; Beasley *et al.* 2015; Morales-Reyes *et al*. 2015; Ćirović *et al*. 2016) have sparked an abundance of research on the scavenger guild during the past two decades. The studies presented in this thesis help to advance our understanding of both the main biological and behavioural traits as well as the significance of avian scavengers, from individual species to the avian scavenger guild, in the current socio-ecological context.

Understanding the spatial ecology of an obligate avian scavenger

One of the greatest advances in technology has taken place in the movement ecology discipline. From its most archaic beginning, vultures and condors served as model species due to their large bodies and the long distances covered across terrestrial ecosystems in the implementation of animal-attached devices which were initially large and heavy (Cooke *et al*. 2004; Alarcón & Lambertucci 2018). Currently, the sensitive conservation status of many vulture species is a pressing reason to understand their movement patterns. Among vertebrate animals, vultures show some of the most affected populations, certain species reaching global population declines of up to 99% (Hoffmann *et al*. 2010). At present, 16 out of 23 vulture species worldwide (i.e. 70%) face a certain degree of conservation threat (see figure 2), all the ecological, economic, health and cultural contributions that they provide also being at risk (Ogada *et al*. 2012b; Moleón *et al*. 2014b; DeVault *et al*. 2016). Thus, the study of the movement ecology of vultures is fundamental to advance with their biology knowledge and, with it, streamline conservation strategies.

Nowadays, the main tools used in movement studies are transmitter devices that combine a Global Positioning System (GPS) to obtain location data and a satellite telemetry system for data transmission (e.g. Cooke *et al*. 2004; Ropert-Coudert & Wilson 2005; Alarcón & Lambertucci 2018). Current technological improvements allow, for example, satellite telemetry transmitters (such as solar-powered GPS devices) to emit and self-record animals' movement data, at the same time as measuring and recording individual physiological parameters in diverse environments, even while flying (Vyssotski *et al.* 2006; Mandel *et al.* 2008; Duriez *et al.* 2014). However, the performance of these transmitter devices is not uniform. External factors —characterized by environmental and technical parameters, such as orography, climatic conditions, or transmitter duty cycle— and internal factors of individuals tracked (e.g. sex, age, territorial status, or flight activity) have been shown to shape the correct functioning of the devices (see review in Hofman *et al.* 2019). Thus, simultaneously to movement ecology studies, analyses of the errors and bias in transmitter devices' performance, such as the one presented in *Chapter 1*, are required to avoid drawing incorrect conclusions and making the wrong management recommendations (Krejcar

2011; Thomas *et al.* 2011; Hofman *et al.* 2019). These tracking problems are especially relevant for threatened species, as is the case of many vulture species, where reliable information is particularly important for reintroduction projects and conservation plans.

As set out in this thesis, the bearded vulture is a good model species to explore the flight patterns of a vulture species. Some studies by Krüger *et al*. (2014), Margalida *et al*. (2013, 2016), and Subedi *et al.* (2020) have estimated the spatial behaviour of the bearded vulture, showing a clear influence of the territorial status. In these studies, non-territorial individuals exhibited home ranges at kernel 90% of from 10,500–26,000 km^2 in South Africa, an average of 23,930.8 ± 32,366.2 km^2 (estimated for immatures) in the Himalayas of Nepal, and between 1,800–11,600 km^2 in the Pyrenees, areas. These home ranges are significantly larger than those (also at kernel 90%) covered by territorial individuals of 286 ± 361 km^2 in South Africa, 63 ± 59.5 km^2 in the Pyrenees, and 150.3 ± 135.8 km^2 in the Himalayas of Nepal. In addition, this PhD dissertation's findings showed that, on average, the Pyrenean bearded vultures spent more time perched than in flight (showing monthly rates of perched and in-flight fixes of 64.3 ± 20.0% *vs* 31.8 ± 16.5%, respectively; *Chapter 1*).

Nevertheless, no studies about the daily activity of this species had previously been developed (*Chapter 2*). The findings of this thesis confirm that both external and internal factors influence daily flight activity of the bearded vulture, as well as the correct operation of the transmitter with which they were tracked (*Chapters 2 and 1*, respectively). In particular, Pyrenean bearded vultures' daily flight activity was strongly influenced by daylight time, season, and territorial status, while individual sex and breeding season showed a milder effect on the birds' movement behaviour. At the same time, internal biological factors (such as territoriality and breeding status, but also to a lesser extent age and sex) were shown to significantly influence birds' flight activity (*Chapter 1*). Interestingly, although non-territorial bearded vultures presented the greatest daily flight patterns, territorial and breeding birds seemed to spend significantly more time flying than non-territorial individuals. In parallel, the fix success rate of the birds transmitted was apparently due to the interactions between a series of factors (*Chapter 1*). Additionally, a complementary study describing for the first time the nocturnal flight activity of this same species' population has been developed in the last year (García-Jiménez *et al.* 2020; this study can be found at the end of this thesis in *Appendix II*). In this work, it is shown that adult bearded vultures also present some sporadic nocturnal flights, although they are certainly not related with the feeding behaviour of the species.

The Pyrenean bearded vulture population is considered as the cornerstone of the Western Palearctic bearded vulture population; therefore, its conservation is crucial to achieve a viable self-sustaining European metapopulation of the endangered vulture (Margalida 2010). Understanding the daily movement ecology of the bearded vulture is essential for predicting its future dispersal, foraging and reproductive patterns. These are indispensable data for developing future conservation strategies (including reintroduction programmes and the use of SFS as conservation tools) both in the Pyrenean region and other ecosystems with distinct climatological conditions or food availability. Indeed, given the variety of mortality risks faced by this species and its high adult mortality rate (Margalida *et al*. 2008; Margalida 2012), information on the daily distances travelled by juveniles during their early dispersal stages might help to improve the design of future conservation measures. For instance, information on the space use of other large raptor species (e.g. eagles and Eurasian griffons) have already helped to shape some guidelines to minimize avian scavenger mortality from power lines and wind farms (Lehman *et al.* 2007; Guil *et al.* 2011; Carrete *et al.* 2012; Marques *et al.* 2014), to assess the effectiveness of the "Protection areas for the feeding of necrophagous species of European interest" (PAFs) network in the improvement of scavenger conservation in Spain (Morales-Reyes *et al.* 2017), or to avoid scavenger-human detrimental interactions such as large soaring birds' collisions with airplanes (Hauptfleisch *et al*. 2020; Arrondo *et al*. 2021).

In addition, the current anthropogenic pressures leading climate change are altering species' distribution ranges. Direct and indirect consequences of climate change for species distribution, disease prevalence and predator abundance will certainly result in spatial and temporal changes of carrion availability in ecosystems (Wilmers & Post 2006; Wilmers *et al.* 2006; Wilson & Wolcovich 2011), just like non-natural measures such as the implementation of controversial sanitary regulations (Donázar *et al.* 2009b; Margalida *et al.* 2010; Arrondo *et al.* 2018) and anthropogenic food subsidies (Oro *et al.* 2013; Mateo-Tomás *et al.* 2015; Fluhr *et al.* 2017). All these factors are altering the food resources of the environment and consequently influencing the behaviour and survival of multiple species of the ecosystem, including the scavenger guild (e.g. Butman *et al.* 1995, Pain *et al.* 2003, Chamberlain *et al.* 2005; Martín-Vega & Baz 2011; Cortés-Avizanda *et al*. 2012; Margalida & Colomer 2012; Ogada *et al.* 2012a; Margalida *et al.* 2017; Arrondo *et al*. 2020). In this context, movement ecology studies are essential to encourage the conservation of key scavenger species such as vultures and large predators, which are in serious jeopardy worldwide (Hoffmann *et al.* 2010; Buechley & Şekercioğlu 2016). This is an urgent need that it will be extremely difficult to meet unless there is broad recognition of their crucial ecological role, including their provision of ecosystem services to our society (Moleón *et al.* 2014b).

A shifting gaze on scavengers: integrating the cultural dimension

Since the early hominids, humans have been linked to scavengers. This guild has played a key role in our evolution, providing multiple beneficial contributions (i.e. ecosystem services) to our lineage (Moleón *et al*. 2014b; Morelli *et al*. 2015). Hence, humans have traditionally lived in harmony with vertebrate scavengers, identifying them as allies in an ecosystem where traditional agro-pastoral practices dominated. Large populations of these species have historically existed in Europe (Boitani & Linnell 2015; Cortés-Avizanda *et al.* 2015), avian scavengers being abundant throughout the Mediterranean Basin (Donázar 1993). Nevertheless, this equilibrium was disrupted in the modern era, when hunting and scientific collecting became a trend in Europe (see e.g. Chapman & Buck 1893, 1910; Hiraldo *et al.* 1979), as it also did in many regions of North America and Australia (Bijleveld 1974; Newton 1979; Olsen 2006). Birds of prey were intensively persecuted and many of their populations worryingly decreased, including those of avian scavengers. However, from the late 20th century to today, the legal protection of many of these species was progressively implemented and many populations of birds of prey have notably recovered in Europe (Deinet *et al.* 2013). On this continent, we can now find some of the most representative and healthiest populations of vultures and other Old-World avian scavengers, compared to Africa or Asia (where vulture populations have been massively decimated; Buechley & Şekercioğlu 2016; Safford *et al.* 2019). This change has clearly resulted from the cessation of direct killing as well as the progressive correction of other mortality factors. Some of the most helpful actions have been the legal prohibition of certain pollutants, the modification of intrusive power lines, the increase in habitat protection, and the establishment of species-specific conservation measures (Newton 1979; Donald *et al*. 2007; Williams *et al*. 2012; Kolecek *et al*. 2014). These corrective actions have been developed within recovery and conservation plans shaped by the scientific research devoted over the last few years to showcasing the relevance of scavenger existence and their fundamental role in our well-being through the scientific (tending also toward social and political) recognition of their NCP. Despite this positive social tendency, certain stakeholders are still distrustful of scavenger species. Thus, the millenarian relationship between humans and scavengers has been affected in recent years by increasing negative perceptions resulting from human-vulture conflicts (i.e. apparently vulture "attacks"), especially among farmers. Unfortunately, this conflict has produced a viral spread of partial and biased information through the social media despite its limited empirical support (Margalida *et al.* 2014; Duriez *et al.* 2019; Margalida & Donázar 2020; Ballejo *et al.* 2020; Lambertucci *et al.* 2021), conditioning certain people's knowledge and perception of vultures.

Bearing in mind this scenario, it seems clear that sustainable biodiversity conservation should also include the social-ecological approach (Liu *et al.* 2007; Ban *et al.* 2013; Martín-López & Montes 2015; Bennett 2016; Bennett *et al.* 2017). Indeed, the human dimension is already being considered through awareness, perceptions, personal values (existence, religious, etc.), beliefs, attitudes and knowledge of nature, but only in certain specific areas of conservation biology (e.g. natural protected areas, volunteering, etc., see Halpenny & Caissie 2003; Palomo *et al*. 2014). Yet, in spite of the latest research advances identifying the scavengers' contributions to improve our quality of life, as well as the anthropic pressures on scavenger conservation, the social perception of avian scavengers is still unattended (see a few very recent examples in Cailly Arnulphi *et al.* 2017 and Cortés-Avizanda *et al*., 2018, focused on one single species, or multi-species evaluations in Morales-Reyes *et al*., 2018; Henriques *et al.*, 2018; and the ones mentioned below). Some studies have emerged in the last ten years including people perception to address human-avian scavenger conflicts (Santangeli *et al.* 2016; Hauptfleisch & Avenant 2016), including famers' and shepherds' perceptions of this guild (e.g. Pfeiffer *et al.* 2015; Morales-Reyes *et al.* 2018, 2019; Ballejo *et al.* 2020). However, scarce research explores the positive non-material NCP provided by avian scavengers (e.g. Becker *et al.* 2005, 2009, 2010; George *et al*. 2016; Aguilera-Alcalá *et al.* 2020; Echeverri *et al.* 2020) —even if positive NCP have been the ones most reported for birds among all vertebrate animals in the literature (see review in Methorst *et al*. 2020)— or the perception that the different stakeholders of society (other than farmers) hold toward avian scavengers, either as a guild or the individual species.

This thesis shows, for the first time, the NCP provided by avian scavengers through a scavenger-based touristic activity from a combined socio-ecological and economic approach (*Chapters 4 and 3*, respectively). Even if bird-based tourism (i.e. all occasional recreational activities and organized touristic tours motivated by birdwatching) is increasingly worldwide (Şekercioğlu 2003 and see examples in Jones & Buckley 2001; Şekercioğlu 2002; Lee *et al.* 2010; Ma *et al.* 2013; Bisht & Joshi 2017), the NCP perception of the birdlife from people who enjoy this resource (i.e. birders and birdwatchers; e.g. Belaire *et al.* 2015; Leong *et al.* 2020) or the local social impact of the activities that they usually practise (e.g. Şekercioğlu 2002; Carver 2013) has not frequently been considered, not least when related to avian scavengers.

In this context, Becker *et al.* (2005) were pioneers, first evaluating the economic value of a recreational activity based on a vulture species. They estimated that 85% of visitors to a nature reserve in Israel (i.e. Gamla) came specifically to view threatened griffon vultures, and that this activity produced a potential annual value of US $1.1–1.2 million. Then, also Becker *et al*. (2009) estimated through the travel cost method (TCM) an economic benefit of US $2.4 million and of US $2.94 million per year at two different nature reserves in Israel (i.e. Hai-Bar and Gamla, respectively) for the enjoyment of visiting the areas in which griffon vultures were located and a willingness to pay (WTP) for protecting this species of US $0.98 million at Hai-Bar and US $2.70 million at Gamla.

Following this main idea of using an economic approach to value and showcase non-material NCP provided by an obligate scavenger, in this thesis (*Chapter 3*) it has been estimated the economic value of the non-material NCP provided by European avian scavengers through recreational and educational activities (i.e. scavenger-based tourism) at Pyrenean SFS. On average, an annual economic value of €4.21 ± 2.26 million (US $4.90 ± 2.67 million); including €2.18 ± 1.17 million (US $2.53 ± 1.36 million) of direct economic benefits to the local community was estimated. Moreover, the methodology followed in this study was more exhaustive than the one applied by Becker *et al*. in 2005 (i.e. the TCM), given that we considered the food and accommodation costs in our computations besides the trip and opportunity costs considered in the TCM. Indeed, together the food and accommodations costs represented the highest contribution to local revenue (see figure 1 in *Chapter 3*).

At the same time, we evaluated and identified the NCP provided by avian scavengers through this same scavenger-based touristic activity at Pyrenean SFS beyond the economic contribution to society (*Chapter 4*). This thesis results reveal how people who enjoy avian scavengers by visiting SFS mostly perceived the beneficial NCP provided by these species. SFS visitors focused on non-material NCP (as general birdwatchers also do), particularly appreciating the supporting identity value of the avian scavenger species (i.e. its peculiarity, intelligence, conservation threat level, and more examples of values perceived by SFS visitors in table 1 of *Chapter 4*). These findings confirm some of the results presented by Cortés-Avizanda *et al*. (2018) about the perceptions shown for the Egyptian vulture in a protected area in northern Spain. In this study, they determined the social perceptions about the Egyptian vulture of different stakeholders (i.e. hunters, livestock keepers, tourists, and farmers together with other locals) and stated that tourists were not as aware as other stakeholders of the regulating NCP (i.e. regulating ecosystem services) provided by the endangered vulture. However, no more information was explored about the tourist perception, knowledge, or the factors conditioning their perspective about this single scavenger species. In this respect, this study brings out an interesting evaluation of the mindset of a previously unexplored social actor (i.e. SFS visitors), analysing the perspective of people who enjoy wild avian scavengers at an international regional scale (i.e. the Pyrenees), interpreting their perception of 14 avian scavenger species.

Since the perception of avian scavengers by other stakeholders (such as farmers and shepherds) has been a subject addressed to some extent in the literature (e.g. Santangeli *et al.* 2016; Henriques *et al.* 2018; Morales-Reyes *et al.* 2018, 2019), a future comparative study encompassing all social actors' perceptions of avian scavengers (e.g. scientists, farmers, shepherds, conservation managers, local communities, tourists, and conservationists) would be necessary to have a representative global human perception of this guild in present-day society. Some of these social actors have already been independently studied (e.g. *Chapter 4*; Cailly Arnulphi *et al.* 2017; Brink *et al.* 2020; Morales-Reyes *et al.* 2018; Henriques *et al.* 2018), but rarely treated as a whole (but see Cortés-Avizanda *et al.* 2018 and Aguilera-Alcalá *et al.* 2020).

Exploring conservation biology strategies for avian scavengers: community-based conservation and ecotourism

Over the past three decades, the literature has focused on understanding the key role of local human communities in the implementation of conservation measures (Western & Wright 1994; Adams & Hulme 2001; Hackel 2001; Hajjar & Molnar 2015; Wali *et al.* 2017). These studies generally argue that conservation intervention should not be pursued against the interest and wishes of local people if it is meant to be successful in the long term. Moreover, to ensure the inclusion of locals' wishes throughout the conservation process, researchers have proposed involving local people as an integral part of a wildlife conservation policy, a concept called *community-based conservation* (CBC; Western & Wright 1994). Even if the practical implementation of this inclusive conservation strategy is still being refined (Barrow & Fabricius 2002; Shackleton *et al.* 2002; Berkes 2004), it is known that at least two main requirements have to be fulfilled: (1) the participation of local communities in the planning and management of the conservation strategies and (2) to provide some economic benefits (frequently resulting from local capacity-building processes) in a sustainable ecological context that help with the local communities' subsistence (Hackel 2001; Brooks *et al.* 2006; Brooks *et al.* 2012).

One way to develop this CBC strategy is through ecotourism (e.g. Amat & Abdullah 2004; Hoole 2009). The International Ecotourism Society defines ecotourism as "responsible travel to natural areas that conserves the environment and improves the well-being of local people". Ideally, ecological tourism should then create local incentives for conserving natural areas, by generating income through sustainable, low-impact, low-investment, and locally-owned operations (Boo 1990; Goodwin 1996; King & Stewart 1996). Unfortunately, the real cases that could exemplify the correct implementation of this ideal are scarce and infrequently durable (Isaacs 2000; e.g. certain natural protected areas; Eagles & McCool 2002). Nowadays, wildlife-based tourism is an important source of income for many local communities (Reynolds & Braithwaite 2001; Balmford *et al.* 2015). In particular, birdwatching is one of the most popular wildlife-based hobbies around the world (e.g. Jones & Buckley 2001; Şekercioğlu 2002; Lee *et al.* 2010; Ma *et al.* 2013; Bisht & Joshi 2017). However, promoting ecotourism could make us fall in the commodification of wildlife or the NCP provided by ecosystems (Boo 1990; King & Stewart 1996; Gómez-Baggethun & Ruiz-Pérez 2011). To develop a proper ecotourism practice, it is crucial to have a deep understanding of the basic characteristics and interactions of the biological and social spheres involved in the process always respecting the human-nature harmony, including environmental limitations and carrying capacity (Eagles & McCool 2002). Ecotourism must be used as a tool to link sciences with educational and conservation practices at different scales, but never as an economic resource isolated from conservative and environmental principles (Sander 2012; Fernández-Llamazares *et al*. 2020; Tauro *et al*. 2021; e.g. Jacobson & Robles 1992). There is much to be gained if sound ecotourism is conducted, as it proposes a win-win scenario for the socio-ecological systems within which we live, protecting natural areas and benefiting local communities at the same time (Weaver 1998).

According to the results of the studies contained in this thesis (*Chapters 3 and 4*), recreational activities based on avian scavenger tourism (such as environmental education, birdwatching or controlled photography) developed in a scientifically monitored environment could comply with the aims of both the CBC strategy and ecotourism. Moreover, these recreational activities seem to be a potential tool to showcase non-material contributions of avian scavengers to the general public. Previous studies, such as the one by Cailly Arnulphi *et al.* (2007), have evinced how negative perceptions of the Andean condor (*Vultur gryphus*) as a predator of livestock could be reversed through education highlighting its major ecological role as a scavenger. In accordance with this statement, in the study developed in *Chapter 4*, it was shown how the group of visitors to the Pyrenean SFS with greater knowledge of the avian scavenger species (i.e. "avian scavenger-watchers", who successfully identified and recognized more avian scavenger species) valued more species positively than the visitors that presented a lower level of knowledge of the species (i.e. "nature enjoyers"). Unfortunately, a study by Moleón and Sánchez-Zapata (2015) highlighted the existence of an important mismatch between present scientific evidence of the ecological significance of scavenging and the absence of relevance given to this guild in ecology textbooks. Therefore, the value placed on the non-material NCP provided by avian scavengers that results from the combined socio-ecological and economic approach that we used in *Chapters 4 and 3* (respectively), together with the study of people's perception of avian scavengers (*Chapter 4*) and knowledge acquisition about their basic behavioural traits (*Chapters 1 and 2*) are fundamental mainstays if a positive and holistic integration of avian scavengers in our society is to be achieved.

In the present context of a vulture crisis, where a renewed recognition of the NCP that scavengers may provide to society is emerging (e.g. *Chapters 3 and 4*; Deygout *et al.* 2009; Wilson & Wolkovich 2011; Dupont *et al.* 2012; Margalida & Colomer 2012; Morales-Reyes *et al.* 2015; Aguilera-Alcalá *et al*. 2020), the inclusion of the socio-cultural dimension linked to the species' space use information in the conservation strategies is imperative. Since on-site use can be considered one of the most effective ways to understand the relative importance of biodiversity (Kniivilä 2006), the existence of environments where people can profit from non-material NCP provided by scavengers is important to bring the general public closer to this guild and the particular scavenger species that compose it. This kind of interaction would increase people's awareness and popular and ecological knowledge of the species, therefore promoting a favourable mindset toward scavengers. In this respect, knowing the space use that different avian scavengers make of their surrounding environment is essential to predict where (spatially precise) these species are going to provide their NCP. However, to set up this ambience of socio-ecological value exchange between humans and avian scavengers, conservation biology values should never be overlooked (see some examples of the consequences of ignoring conservation biology values for birds of prey in Martínez-Abraín *et al.* 2010). Further, the establishment of these structures and dynamics through which these socio-ecological interactions would take place should always follow conservation needs and be subject to a meticulous scientific monitoring that constantly evaluates their usefulness as management tools.

The loss of scavengers from the current ecosystems would mean deep and irreversible changes to nature (Beasley *et al*. 2015; DeVault *et al*. 2016) that we are not ready to confront. It is our moral responsibility to find the most feasible way to harmonize human existence in a healthy and balanced global ecosystem, which includes the presence of solid scavenger populations.

Future perspectives

Movement ecology has revolutionised animal research, including vertebrate scavengers, mostly through technological improvements in tracking devices showing increasing accuracy and spatio-temporal resolution. This has made it possible to provide a detailed spatial context to multiple ecology and conservation biology questions so far unanswered for scavenger vertebrates, some of them related with the renewed recognition and evaluation of the ecological role of scavengers in recent years. In this thesis I have attempted to fill some of the movement ecology information gaps of an emblematic and threatened avian scavenger species, such as the bearded vulture. Still, there always are new ecological questions opening up for this guild that should be addressed in future research.

For instance, an interesting study to improve current management and conservation actions would be the analysis of the SFS influence in avian scavenger species foraging routine along their different age classes, considering the amount of carrion distributed, feeding periodicity and location of these vultures' restaurants. A recent and innovative study of Fluhr *et al.* (2017) already evaluated the degree of routine movement behaviour in a population of Eurasian griffons, but no more similar studies are developed for any other avian scavenger species. Additionally, to my knowledge, there is no longitudinal research measuring the SFS effect in individual avian scavenger foraging behaviour (i.e. long-term studies that consider avian scavenger SFS use along all age classes from the same individual birds).

Also, given the technological advances in modern transmitter devices that allow to record not only accelerometry data, but also individual physiological parameters during flight, more research should be developed combining this intrinsic information with movement ecology data. In this way, we would be able to understand intrinsic factors leading birds' movement behaviour and consequently predict changing movement patterns of avian scavenger species under different scenarios of climate and land use change.

On the other hand, the provision of ecosystem services by vertebrate scavengers has received little scientific attention, and therefore any study identifying, analysing and quantifying scavenger NCP will contribute hugely to helping avian scavengers become socially recognized as key pieces of ecosystems.

The most unknown of the NCP are non-material ones (i.e. cultural services). Thus, standardized and multidisciplinary methodologies will need to be developed to achieve a deep understanding of non-material NCP roots, drivers and operating mechanisms. This kind of research will place value on non-material NCP provided by scavengers and awaken human awareness of scavenger conservation importance. To do this, it should be kept in mind that culture is highly variable in time and space. This implies that future studies of non-material NCP should include all current signs of cultural references and contributions provided by scavengers. This means including not only the traditional supports considered for cultural contributions such as religions, myths, books, films or songs, but also cultural trends, such as tattoos and values placed on the digital world (i.e. through social media data, videogames, etc.).

In addition, future studies analysing all social actors' perceptions of avian scavengers in the Pyrenees (e.g. scientists, farmers, shepherds, conservation managers, local communities, tourists, and conservationists) would be necessary to obtain a more integrate and holistic perspective on the social role of avian scavengers in society. Avian scavenger perceptions of certain social actors have already been widely assessed (e.g. shepherds and farmers), however other stakeholders remain understudied. Future comparative studies encompassing all social actors' perceptions of avian scavengers are required to have a representative current Pyrenean human community perception of this guild.

Finally, a very interesting line of future work in conservation biology would be to spatially combine the two approaches of movement ecology and NCP employed in this thesis. To do so, after identifying and assessing the NCP provided by avian scavengers, we could place them in a spatial explicit context through the study of the movement ecology of the NCP provider species. Thus, we would map the places where the provision of NCP by avian scavengers is occurring, determining the location of these human-scavengers NCP exchange hotspots, but also the places where this NCP provision is lacking or is weaker. This will allow us to focus conservation efforts to offset for NCP shortages until local scavenger populations recover. We will also be able to define and take advantage of the NCP provision hotspots to establish the aforementioned ambiences of socio-ecological value exchange between humans and scavenger birds, always scientifically monitored and driven by conservation principles.

CONCLUSIONS

Photo by Daniel Navarro Samaniego.
A common buzzard perched in a snowy winter's day in Riaño (León).

Conclusions

I

Despite the renewed emerging scientific attention addressed to vertebrate scavengers, the scavenger guild remains still neglected in our present society regardless of its fundamental role in a multitude of ecological processes and their key role in human wellbeing. The collection of information about the basic biological and behavioural traits of endanger scavenger species, as well as the recognition of the socio-ecological role of their guild (including their provision of nature's contributions to people, NCP) is essential to assure their conservation and survival in the current society.

II

Every movement ecology study that uses tracking devices should include an error analysis before reaching any ecological hypotheses or conclusions regarding spatial utilization, since the results can vary substantially depending either on extrinsic factors (both technical and environmental), and/or biological factors. All of these changing elements can influence the data collected and lead to errors in interpreting patterns of movement. Fortunately, technology improvements and research advances in error tracking data are progressively reducing the potential influence of tracking device shortcomings on the recording and interpretation of basic parameters regarding the spatial ecology of a species.

III Both external and internal factors act as main drivers of the daily flight activity pattern of the Pyrenean bearded vulture. Individual flight daily activity was strongly influenced by daylight time, season, and territorial status, while sex and breeding season showed a milder effect on the birds' movement behaviour. Understanding the daily movement ecology of the a poorly known endangered avian scavenger is essential for predicting its future dispersal, foraging and reproductive patterns. This information is crucial to know more about the mortality risks faced by avian scavenger species helping to combat the high adult mortality rates of some of their species. These are also indispensable data for developing future conservation strategies (including reintroduction programs and the use of supplementary feeding sites, SFS, as conservation tools) both in the Pyrenean region and other ecosystems with distinct climatological conditions or food availability.

IV Cultural experiences based on the non-material NCP of avian scavengers can be promoted as means of increasing people's quality of life and generating local revenue. SFS construction should always follow conservation needs, and a scientific monitoring is necessary to constantly evaluate their usefulness as management tools. However, besides conservation purposes, SFS can be employed to enhance a socio-ecological value exchange between humans and avian scavengers through birdwatching, educational, or photographic activities providing an added cultural value to the regional landscape.

V Avian scavengers are recognized as providers of beneficial NCP by certain social actors of the society. As it happens in other types of wildlife-based tourism, people who enjoy avian scavengers by visiting SFS mostly perceived and benefit from non-material contributions, particularly appreciating the supporting identity value of the avian scavenger species. The socio-cultural dimension is a powerful tool that should be considered and integrated in the development of any conservation strategy and management plan to assure a long-term successful implementation.

VI The use of the community-based conservation (CBC) strategy sustained by a sound ecotourism could be a successful conservation policy for avian scavengers in Spain, a predilect country for the scavenger-based tourism given that it hosts the most important breeding populations of the four vulture species within the Western Palearctic region together with a wide array of facultative scavengers. The existence of scientifically monitored recreational and educational activities linked to conservation measures would increase people awareness and popular and ecological knowledge of the scavenger species, therefore promoting a favorable social mindset toward scavengers (both at guild and species level).

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Photo by Juan Carlos García Gómez.
The flight of the red kite.

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SUPPLEMENTARY INFORMATION

Photo by Daniel Navarro Samaniego
The look of the black kite.

SUPPLEMENTARY INFORMATION

This section contains the Supplementary information to the four chapters composing the main body of this thesis:

Chapter 1

García-Jiménez, R., Margalida, A., & Pérez-García, J.M. Influence of individual biological traits on GPS fix-loss errors in wild bird tracking. *Scientific Reports* **10**, 19621 (2020). https://doi.org/10.1038/s41598-020-76455-x.

Chapter 2

García-Jiménez, R., Pérez-García, J.M. & Margalida, A. Drivers of daily movement patterns affecting an endangered vulture flight activity. *BMC Ecology* **18**, 39 (2018). https://doi.org/10.1186/s12898-018-0195-7.

Chapter 3

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

Chapter 4 (under review)

García-Jiménez, Z., Pérez-García, J. M., Margalida, A., & R., Morales-Reyes. Avian scavengers' Contributions to People: the cultural dimension of the wildlife-based tourism.

Supplementary information to Chapter 1

Influence of individual biological traits on GPS fix-loss errors in wild bird tracking

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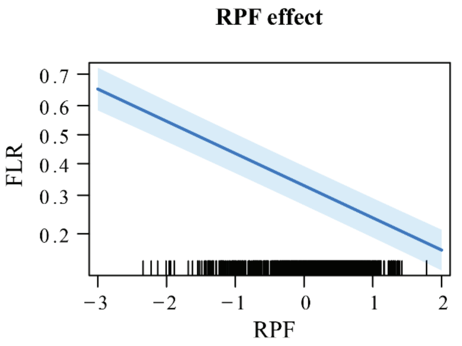
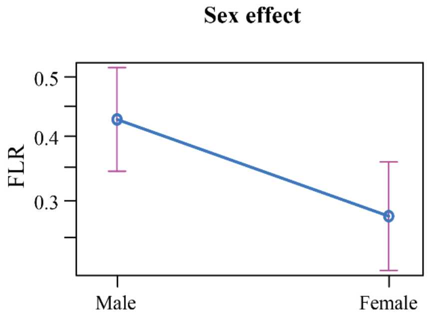
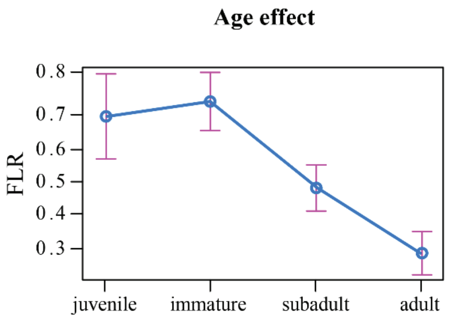
Table S1. Year of capture and PTT activity status of 20 Pyrenean Bearded Vultures tagged by 70 g solar-powered Argos' satellite transmitters (PTT/GPS Microwave Telemetry, Inc. Columbia, MD, USA) between 2006 and 2019. In bold type the three transmitters (platform transmitter terminal, PTT) used for two different birds and * for the PTTs that couldn't be used to compute the mean usage time value.

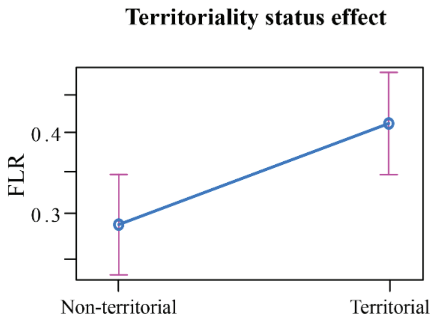
Individuals	PTT	Year captured	PTT activity until 2019 (ending year)
Adrian	PTT1	2009	working
Andreia	**PTT2**	2009	dead (2009)
Pocholo	**PTT2**	2011	working
Batín	PTT3	2008	stopped transmitting (2015)
Cabó	**PTT4**	2007	dead (2008)
Sofia	**PTT4**	2008	stopped transmitting (2012)
Dulantz	PTT5*	2013	dead (2014)
Elisabeth	PTT6	2014	stopped transmitting (2018)
Garrotxa	PTT7	2008	stopped transmitting (2013)
Gervàs	**PTT8**	2007	dead (2009)
Min	**PTT8**	2010	stopped transmitting (2017)
Isaac	PTT9	2010	stopped transmitting (2014)
Jairo	PTT10	2009	stopped transmitting (2016)
Morreres	PTT11	2007	stopped transmitting (2012)
Nicky	PTT12	2009	stopped transmitting (2017)
Noah	PTT13	2008	stopped transmitting (2008)
Revilla	PTT14*	2013	dead (2013)
Sasi	PTT15	2007	stopped transmitting (2008)
Subfli	PTT16	2008	stopped transmitting (2012)
Tossal	PTT17*	2006	unknown (2006)

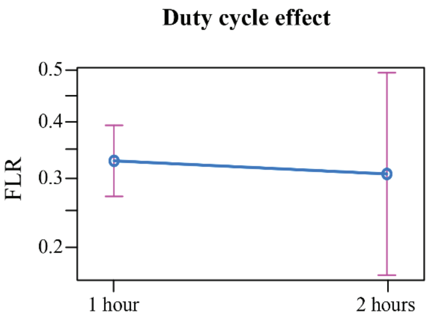
Figure S1: Partial effects of all the explanatory variables included at least in one of the competing GLMMs built to evaluate the influence of different biological traits and extrinsic factors (comprising both technical and environmental variables) on the fix loss rate (FLR). The most parsimonious models were selected using Akaike's Information Criterion (AIC**¡Error! No se encuentra el origen de la referencia.**) and met the delta AIC < 2 criterion. In these models, the biological, technical and environmental variables were included as fixed factors and the individual as a random factor. All continuous variables were centred and standardized before modelling. All the plots were obtained using R statistical software[51] version 3.6.2.

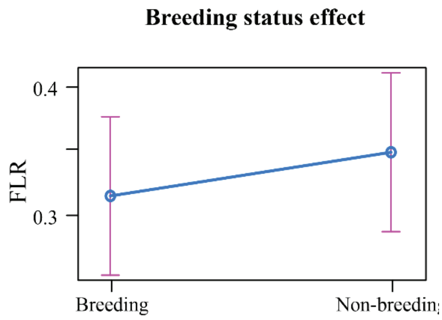

RPF effect
FLR
0.7
0.6
0.5
0.4
0.3
0.2
−3
−2
−1
0
1
2
RPF


Sex effect
FLR
0.5
0.4
0.3
Male
Female


Age effect
FLR
0.8
0.7
0.6
0.5
0.4
0.3
juvenile
immature
subadult
adult


Territoriality status effect
FLR
0.4
0.3
Non-territorial
Territorial


Duty cycle effect
FLR
0.5
0.4
0.3
0.2
1 hour
2 hours


Breeding status effect
FLR
0.4
0.3
Breeding
Non-breedin

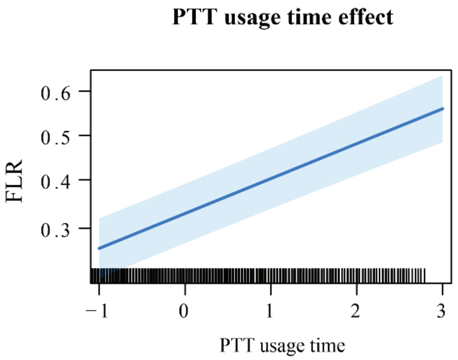
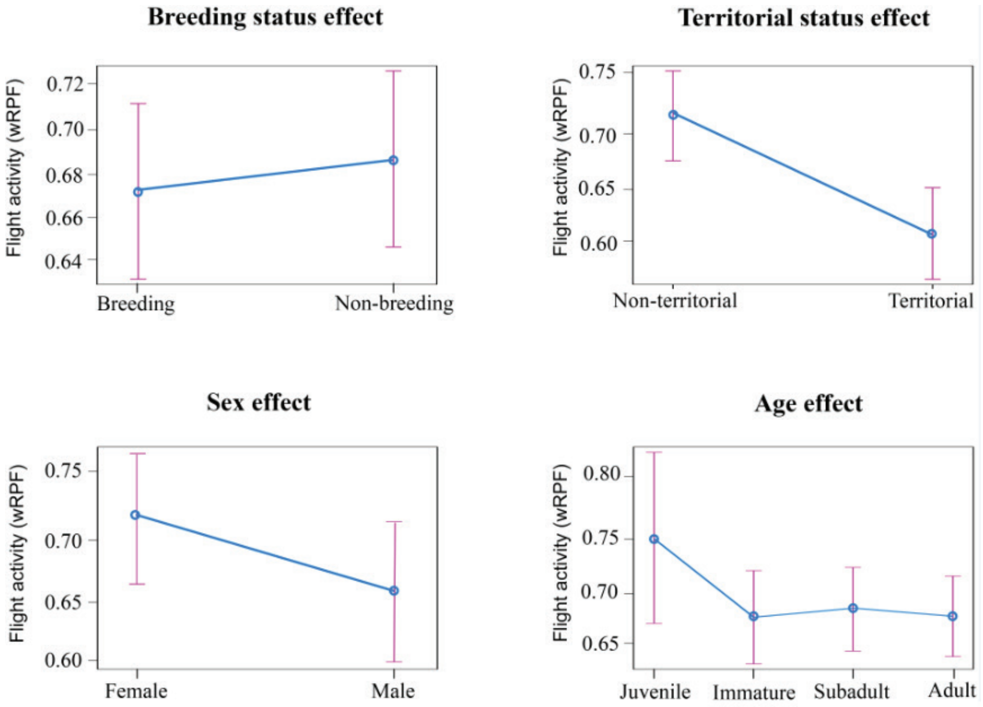

PTT usage time effect
FLR
0.6
0.5
0.4
0.3
−1
0
1
2
3
PTT usage time

Figure S2: Partial effects of all the explanatory variables included at least in one of the competing GLMMs built to evaluate the influence of different biological traits and environmental variables on birds' flight activity. For this analysis, the response variable was measured through a weighted rate of perched fix (wRFP) created by combining the monthly number of perched fix and monthly number of fix in flight. The most parsimonious models were selected using Akaike's Information Criterion (AIC**¡Error! No se encuentra el origen de la referencia.**) and met the delta AIC < 2 criterion. To build the models, the biological and environmental variables were included as fixed factors and the individual as a random factor. All continuous variables were centred and standardized before modelling. All the plots were obtained using R statistical software[51] version 3.6.2.



Supplementary information to Chapter 2

Drivers of daily movement patterns affecting an endangered vulture flight activity

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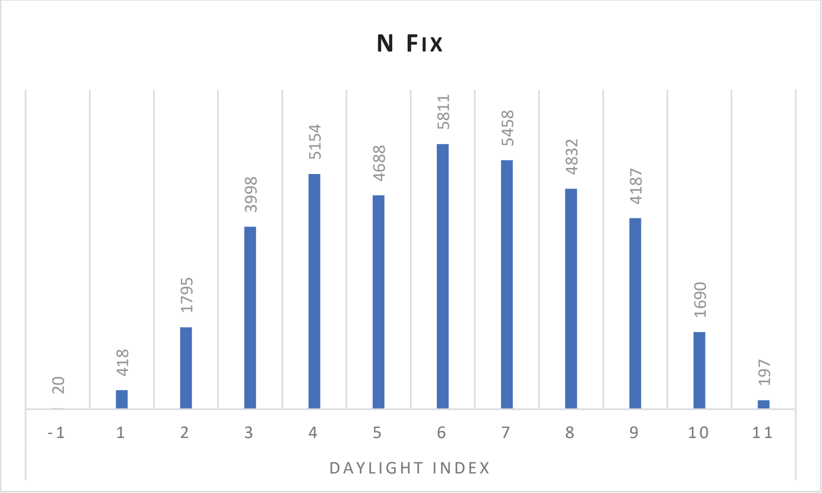
Additional file 1: Mean ± SD values for the three twilight phases, the solar noon and the daylength for each season in UTC Time (hh:mm). Source: www.timeanddate.com .

	Astronomical twilight							
		Nautical twilight						
			Civil twilight					
	Sunrise	Sunrise	Sunrise	Noon	Sunset	Sunset	Sunset	**Daylenght**
Spring	2:56 ± 0:45	3:40 ± 0:38	4:19 ± 0:34	14:05 ± 0:03	19:27 ± 0:29	20:06 ± 0:34	20:50 ± 0:41	13:48
Summer	2:58 ± 0:40	3:42 ± 0:33	4:21 ± 0:29	14:05 ± 0:04	19:29 ± 0:35	20:08 ± 0:39	20:52 ± 0:46	14:08
Fall	4:55 ± 0:27	5:29 ± 0:28	6:02 ± 0:29	10:16 ± 0:04	17:19 ± 0:27	17:52 ± 0:26	18:26 ± 0:25	10:36
Winter	5:18 ± 0:24	5:51 ± 0:25	6:25 ± 0:26	10:14 ± 0:05	17:39 ± 0:32	18:13 ± 0:31	18:46 ± 0:30	10:16

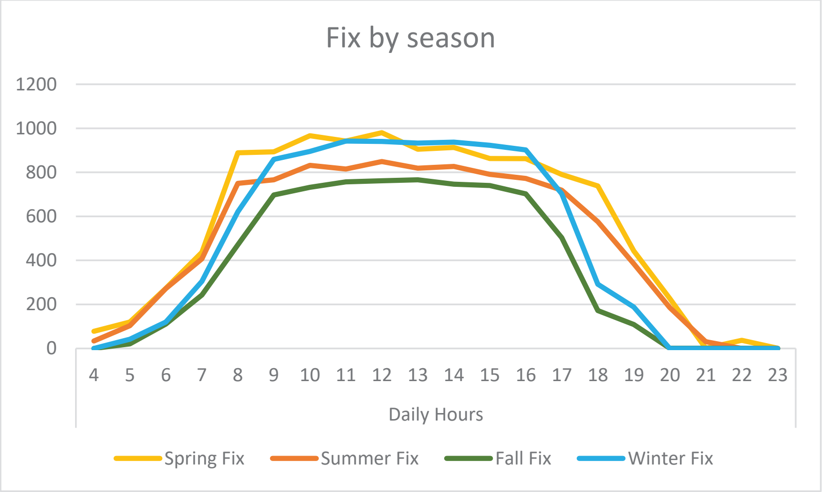
Additional file 2



Additional file 2: Figure S1. Frequencies of fix per daylight percentage range.

Additional file 2: Table S1. Table of frequencies of fix per daylight percentage range.

Integer scale	Daylight units	N fixes
-1	-0.1 - 0	20
0	0 - 0.1	418
1	0.1 - 0.2	1795
2	0.2 - 0.3	3998
3	0.3 - 0.4	5154
4	0.4 - 0.5	4688
5	0.5 - 0.6	5811
6	0.6 - 0.7	5458
7	0.7 - 0.8	4832
8	0.8 - 0.9	4187
9	0.9 – 1	1690
10	1 – 1.1	197
11	1.1 - 1.2	20
Total		**38248**



Additional file 2: Figure S2. Frequencies of fix per season considering UTC Time.

Additional file 3: Standardized weights of all the predictors introduced in the linear mixed models performed (N models) to explore the factors influencing the distance covered estimators (maximum displacement, cumulative distance travelled and hourly distance). Factors included were daylight index (*DI*), climatic season (*Season*), territorial status (*Territ*), breeding season (*Br_S*), and sex (*Sex*) and the simple interactions *Sex:Territ*, *Season:Territ* and *Br_S:Territ*.

	Importance			***N models***
	Max. displacement	**Cum. travelled dist.**	**Hourly dist.**	
DI	1	1	1	10
Season	0,98	1	1	6
Territ	1	0,83	0,99	12
Sex	1	0,61	0,35	7
Br_S	0,02	0,46	0,1	6
Sex:Territ	1	<0.01	<0.01	4
Season:Territ	<0.01	<0.01	<0.01	1
Br_S:Territ	<0.01	<0.01	<0.01	1

Supplementary information to Chapter 3

Economic valuation of non-material contributions to people provided by avian scavengers: harmonizing conservation and wildlife-based tourism

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Table A. The Supplementary Feeding Sites (SFS) currently working and receiving visitors in the Spanish Pyrenees. Those marked with an asterisk are within a national or natural park. Region corresponds to the Spanish autonomous community. We indicate the main activity as: "Photography", "Educational", "Both" (i.e. the SFS was involved both in photography and educational activities), and "Birdwatching" (i.e. the SFS was not used for a specific educational or photography purpose, but rather bird-watching). The mean number of visitors per year was directly reported by the SFS owners or collected from public reports. N questionnaires correspond to the number of surveys obtained at each SFS (*Not considered* were those SFS for which we could not assume that the main reason for the visitors to visit the SFS was mainly to enjoy watching avian scavengers, and *NA* were those SFS for which any fulfilled questionnaire could be obtained).

SFS name	***Region***	***Main activity***	***Visitors/year***	***N questionnaires***
*Alquezar**	Aragon	Birdwatching	At least 9840	*Not considered*
*Escuain**	Aragon	Birdwatching	37000	*Not considered*
*Lacuniacha**	Aragon	Birdwatching	50000	*Not considered*
*Llebreta**	Catalonia	Birdwatching	560723	*Not considered*
*Coll de Pal**	Catalonia	Birdwatching	346000	*Not considered*
Plan	Aragon	Birdwatching	20	NA
Bonansa	Aragon	Photography	57	17
El Cebollar	Aragon	Photography	10	11
*Las Laneras**	Aragon	Educational	2684	17
Las Pichillas	Aragon	Educational	25	NA
*Tiacuto**	Aragon	Both	24	10
Hecho	Aragon	Both	125	9
Santa Cilia de Jaca	Aragon	Both	5	NA
Aínsa	Aragon	Both	6829 to the museum and 450 society members[a]	NA
Boumort	Catalonia	Photography	61	8
Buseu	Catalonia	Photography	180	9
Terrers	Catalonia	Photography	69	3
El Portell/Sant Ponç	Catalonia	Educational	1087	10
Turo de la Colomera	Catalonia	Educational	35	NA
La Terreta	Catalonia	Both	1000 to the museum and 38 to the hide	NA
Total			**12699**	**94**

[a] Both the hide and the museum of Aínsa are managed by the same NGO, but only the society members, who pay an annual rate, have the right to visit the SFS more than once a year.

Table B. Mean standardized price (in €) per night and accommodation-type in the Pyrenees. Adults and children costs were estimated separately. Number of visitors (N) choosing each accommodation-type is shown. *Non-specified* is the mean standardized price for the people who did not indicate their accommodation in the questionnaire.

Accommodation	Adults (€)	Children (€)	N
Apartment	40	15	14
Camping	16	10	12
Hostel	24	15	14
Hotel	45	15	12
Own house, house of relatives or friends	0	0	36
Rural house	49	0	1
Non-specified	29	9	5

Table C. Average estimated prices per meal in Spain. Adults and children costs were estimated separately. The prices were estimated following authors' personal experience while living in the country.

	Breakfast (€)		Lunch (€)		Dinner (€)	
	Adult	**Children**	**Adult**	**Children**	**Adult**	**Children**
Outside the resting place	5	5	13	10	15	10
Inside the resting place	1.5	1.5	3	3	3	3

Table D. Equivalents of average recreational scavenger-based tourism economic income from Euros (€) to United States Dollars (US $). Exchange rate applied of 0.86 €/US $ as of September 24, 2020.

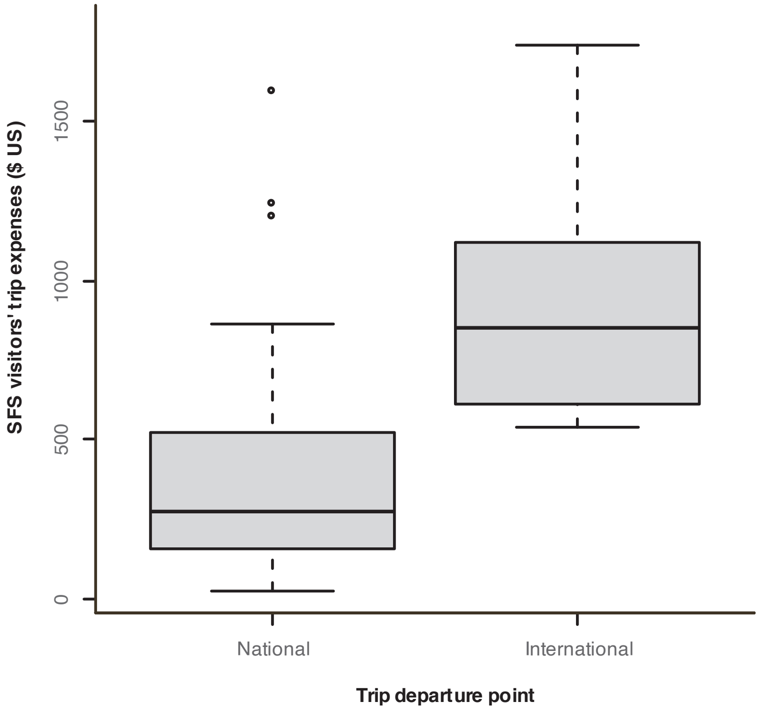
Economic income	€	US $
Mean visitor's trip expenses	379.90 ± 320.52	441.74 ± 372.70
International visitors (trip expense)	822.89 ± 365.78	956.85 ± 425.33
National visitors (trip expense)	312.61 ± 303.92	363.50 ± 353.40
Annual expenditure of SFS visitors	4 214 799.97 ± 2 261 610.03	4 900 930.20 ± 2 629 779.10
Annual economic return to the local community	2 176 101.22€ ± 1 167 669.26	2 530 350.26 ± 1 357 754.95

Table E. Descriptive statistic values for three variables (distance travelled, trip duration and trip expenses) presenting significant differences depending on the SFS visitors' trip departure point (national *vs*. international). Mean ± standard deviation (SD), median and range (minimum and maximum) values are shown. Units of measure are given for each variable in parentheses. Exchange rate applied for SFS visitors' trip expenses values of 0.86 €/US $ as of September 24, 2020.

Variables		**Mean ± SD**	**Median**	**Range**	
				Min.	**Max.**
Distance travelled (km)	National	543.57 ± 564.12	370.00	5.00	2202.00
	International	2805.08 ± 933.07	2803.50	1436.00	4462.00
Trip duration (days)	National	2.33 ± 1.67	2.00	1.00	10.00
	International	4 ± 2.27	3.00	2.00	7.00
Trip expenses (US $)	National	363.50 ± 353.40	276.21	25.29	1608.02
	International	956.85 ± 425.33	855.67	542.09	1747.33

7

Figure A. Boxplot of SFS visitors' trip expenses depending on their trip departure point: national (if the SFS visitors started their trip from anywhere in Spain) *vs*. international (if SFS visitors started their trip outside the country).



Supplementary information to Chapter 4

Avian scavengers' contributions to people: the cultural dimension of the wildlife-based tourism

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Table S1. Information obtained through the questionnaires from the SFS visitors surveyed. The last column shows the possible answers to multiple choice questions. Variables with * were those used as categorical (*) or numerical (**) variables in the two steps cluster analysis. In all cases the scavenger-watching equipment had to be brought by the visitors. The answers to the material brought by the SFS visitors (Q2) were treated as continuous because they were transformed into a numerical additive index ranging between 0 (No material brought) – 4 (specialized photographic or scientific material such as tele-camera lenses, or audio recording equipment) giving the higher values to the more specialized equipment (see Table S3 for the detailed classification).

BLOCKS	**Variables**	**SPECIFIC QUESTIONS**	**CLOSE-ENDED QUESTIONS**	**n**
Ecological interest, perceptions and knowledge of the NCP provided by scavengers	Reason of the visit*	1) Which is the main reason for you to visit this specific SFS?	Birdwatching	93
			Photography	
			Interest in the area	
			It is a family activity (I came here with my partner /children)	
			Species specific interests (in which species?)	
			Educative/instructive	
			By chance (it was on my way to go somewhere)	
			Other reasons	
	Material brought to the SFS**	2) Do you come with specific material?	Bird guide(s)	94
			Binoculars	
			Telescope	
			Cameras	
			Other	
	Previous experience with birds*	3) Have you ever made any activity with birds before?	None	94
			Some (2-5)	
			High (>5)	

	Self-rated interest in the avifauna**	4) Considering all the worldwide fauna, rate your level of interest specifically in the avifauna	0-10 (where 0 means no interest and 10 the maximum interest)	91
	Relationship between work and avifauna*	5) Is your work related with the bird’s world?	Yes / No	93
	Species identification index	6) Identify in the next 14 pictures the main species of necrophagous birds commonly seen in the Pyrenees	–	74[1]
	Times per year going to birdwatching**	7) How often do you go yourself to birdwatching? (times/year)	–	87
	Species recognition index Positive perception index Less positive perception index NCP perception index NCP valuation index	8) Value the next 14 species of avian scavengers and say the reason why you chose that value for each species	1-5 (considering 1 as the lowest value and 5 as the highest)	–
Socio-economic individual characterization	Trip departure origin	9) Where did you start your trip? Specify city and country	–	92
	Gender	10) Gender	–	87
	Age	11) Age	–	86
	Studies	12*) Studies level	None	85

			Until 6-7 years old	
			Until 12-13 years old	
			High school	
			Higher education[2]	
	In couple (Yes/No)	13) About the family	Do you have a life partner? (Yes /No)	62
	Number of children		Do you have children? (Yes / No)	
			If yes, how many?	
	Average monthly income	14) Average monthly income	< 1000€	72
			1000 - 2000€	
			> 2000€	

[1] This question is based over n = 84 surveys (and not 94, as all the rest of the questions are) because the species images could not be joint to the survey in a SFS where 10 surveys were fulfilled.

[2] Education beyond bachelor’s degree.

Table S2. A list of all the species included in the study and about which people were asked in the questionnaire.

Species	English common name	Functional group	Taxonomic group
Gyps fulvus	Griffon vulture	 Obligate scavengers	 Vultures
Aegypius monachus	Cinereous vulture		
Gypaetus barbatus	Bearded vulture		
Neophron percnopterus	Egyptian vulture		
Corvus corax	Raven	 Facultative scavengers 	 Corvids
Corvus corone	Carrion crow		
Pica pica	Common magpie		
Garrulus glandarius	Eurasian jay		
Aquila chrysaetos	Golden eagle		 Birds of prey
Aquila adalberti	Spanish imperial eagle		
Milvus migrans	Black kite		
Milvus milvus	Red kite		
Buteo buteo	Common buzzard		
Circus aeruginosus	Western marsh harrier		

Table S3. Classification based on a numerical additive index for the material brought by the SFS visitors.

Material brought to the SFS		Numerical index
At least and	**Probably**	
None		**0**
Only the **bird guide**	—	**0.5**
A material combination that includes a **photographic camera**	Bird guide	**1**
A material combination that includes **binoculars**	Bird guide Photographic camera	**2**
A material combination that includes a **telescope**	Bird guide Photographic camera Binoculars	**3**
Specialized photographic or scientific **equipment**	Bird guide Photographic camera Binoculars Telescope	**4**

Table S4. Detrimental NCP related to the 14 European avian scavengers studied perceived by SFS visitors. The numerical valuations of avian scavengers (i.e. *NCP valuation index*) and examples of the original reasoned comments of SFS visitors questioned are given. Numerical valuation was classified as *positive* (*NCP valuation index* = 1 or 2), *neutral* (*NCP valuation index* = 3) or *less positive* (*NCP valuation index* = 4 or 5). The classification of detrimental NCP was adapted from Peterson et al. (2010).

NCP category	Numerical valuation	Examples
Animal biodiversity damages	Positive	—
	Neutral	▪ It physically harms other smaller species ▪ It eats other species' eggs ▪ It damages other birds' nests
	Less positive	▪ It is considered as a pest in some zones

Reference: Peterson, M.N., Birckhead, J.L., Leong, K., Peterson, M.J., Peterson, T.R., 2010. Rearticulating the myth of human-wildlife conflict. Conserv. Lett. 3, 74–82. https://doi.org/10.1111/j.1755-263X.2010.00099.x

Table S5. Beneficial NCP related to the 14 European avian scavengers studied perceived by SFS visitors. **Extended version:** the numerical valuations of avian species (i.e. *NCP valuation index*) and examples of the original reasoned comments of SFS visitors questioned are given. Numerical valuation was classified as *positive* (*NCP valuation index* = 1 or 2), *neutral* (*NCP valuation index* = 3) or *less positive* (*NCP valuation index* = 4 or 5). Classification of beneficial NCP based on Díaz et al. (2018).

NCP	Numerical valuation	NCP category	Examples
Material	None	—	—
Non-material	Positive	Learning and inspiration	▪ It gives information ▪ It informs me about Eagles' presence ▪ It warns the other species in the woods
		Physical and psychological experiences	▪ Appearance (e.g. beauty, colour of the plumage, silhouette) ▪ Size appreciation (e.g. It is big/small) ▪ Carriage, elegance, impressive bird ▪ Habitat ▪ It's nice to watch while flying (agility) ▪ Pleasant squawk ▪ A species rarely photographed ▪ It's peasant to watch it closely ▪ It's entertaining the way it feeds
		Supporting identities	▪ All the spp are important ▪ Power, majesty, amazing species ▪ Singularity, peculiarity ▪ Nature icon, an ecology symbol ▪ They play their role, they are necessary ▪ Cultural importance ▪ Intelligence ▪ Threat level ▪ I see it in my village, close to my home
	Neutral	Physical and psychological experiences	▪ Appearance (e.g. beauty, colour of the plumage, sexual dimorphism) ▪ Size appreciation (e.g. It is not so big/small, with a long tail) ▪ Habitat ▪ Not very eye-catching
		Supporting identities	▪ Cultural importance ▪ They play their role ▪ Threat level
	Less positive	Physical and psychological experiences	▪ Appearance (e.g. beauty, colour of the plumage) ▪ Size appreciation (e.g. It is small, with a long tail) ▪ It is boring ▪ Unpleasant squawk
		Supporting identities	▪ They play their role
Regulating	Positive	Regulation of detrimental organisms and biological processes	▪ It is a hunting/scavenger/super-predator species ▪ They have a cleaning role in the nature ▪ It has an important ecological role[1] ▪ Facultative scavengers cover those tasks that larger scavengers cannot

			▪ It balances rodent populations ▪ It has an essential role in the food chain ▪ Sanitary role
	Neutral	Regulation of detrimental organisms and biological processes	▪ They have a cleaning role in the nature ▪ It maintains the balance
	Less positive	—	—
Maintenance of options	Positive	—	▪ It is a conservation thermometer

[1] This comment was only classified as “regulating NCP” when the same person only used this argument for some of the four European vulture species. When it was not the case, the comment was classified as “Supporting identities (non-material NCP)”.

Reference: Díaz, S. et al. 2018. Assessing nature’s contributions to people. Science, 359, 270–272. https://doi.org/10.1126/science.aap8826.

Table S6. Socio-demographic characteristics of the SFS visitors. For the categorical variables (all except *Age*), percentages (n) were shown. For the numerical variables (*Age*), mean ± SD were given.

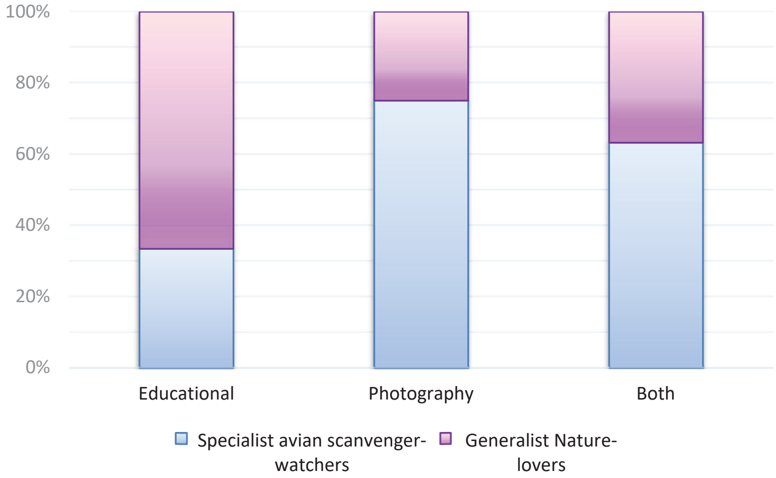
Trip departure origin[1]	International (European countries)	National (Spain)			
	13.04 (12)	86.96% (80)			
Gender	Female	Male			
	29.89 (26)	70.11 (61)			
Age[2]	47 ± 12 years old				
In couple	No	Yes			
	81.71 (67)	18.29 (15)			
With children	No	Yes			
	27.42 (17)	72.58 (45)			
Studies	None	Until 6-7 years old	Until 12-13 years old	High school	Higher education
	0 (0)	8.24 (7)	5.88 (5)	17.65 (15)	68.24 (58)
Average monthly income	<1000€	1000-2000€	>2000€		
	13.89 (10)	54.17 (39)	31.94 (23)		

[1] See García-Jiménez et al., (2021) for more detail about the SFS trip duration and visitors' expenses estimation.

[2] Most of the responders were between 21 and 72 years old (there were only two 9-year-old children and 1 teenager of 15 years old that answered the survey).

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

Figure S1. Avian scavenger-watchers and nature enjoyers distribution among SFS offering three different types of recreational activities: educational, photography and both (i.e., educational and photography simultaneously). Birdwatching was not considered because no questionnaires were fulfilled in any of the SFS offering exclusively this recreational experience.



Indices construction

To determine the visitors' knowledge of avian scavengers we built two different indices:

Species identification index. Number of species visually identified by visitors relative to the total number of species asked about in printed colour images (see Table S2 in Supplementary Information1 for species list). Ranged from 0 to 1. See Table S1 in Supplementary Information1 for the specific question (Q6).

Species recognition index. Number of species culturally recognized by visitors (i.e. correctly identified (Q6) and numerically valuated (Q8), or correctly reasoned valuated (Q8) and numerically valuated (Q8)) relative to the total number of species asked about (see Table S2 in Supplementary Information1). Ranged from 0 to 1. See Tables S1 for the specific questions (Q6 and Q8)

We distinguished between species visual identification (*Species identification index*) and cultural recognition (*Species recognition index*) because visitors could be culturally familiarized with certain species (e.g. by tales, flag symbolisms, documentary films, etc.), but not necessarily be able to identify species in the field. Since in *Question 8* (Table S1) people could read the common name of the species, they could have recognized the species even if they were not certain about its appearance. Visitors who did not numerically valuate any of the 14 species were excluded for the *Species recognition index* calculations.

In addition, to determine the visitor perceptions and interest about the avian scavenger guild, we built two more indices:

Positive perception index. Number of species perceived as very beneficial by visitors (i.e. number of species correctly identified and/or recognized whose numeric valuation —*NCP valuation index*— ranged from 4 to 5) relative to the total number of species asked about (see Table S2 in Supplementary Information1). Ranged from 0 to 1. See Table S1 in Supplementary Information1 for the specific question (Q8).

Less positive perception index. Number of species perceived as not so beneficial by visitors (i.e. number of species correctly identified and/or recognized whose numeric valuation i.e., *NCP valuation index,* ranged from 1 to 2) relative to the total number of species asked about (see Table S2). Ranged from 0 to 1. See Table S1 in Supplementary Information1 for the specific question (Q8).

To describe SFS visitors (see Table 2) we used the following indices:

Species visually identified. Mean ± (SD) number of species visually identified by visitors. Values obtained from the transformation of the *Species identification index* (see above).

Species culturally recognized. Mean ± (SD) number of species culturally recognized by visitors. Values obtained from the transformation of the *Species recognition index* (see above).

Species positively perceived. Mean ± (SD) number of species perceived as very beneficial by visitors (i.e. *NCP valuation index*— ranged from 4 to 5). Values obtained from the transformation of the *Positive perception index* (see above).

APPENDICES

Photo by Juan Carlos García Gómez.
A raven feeding.

Photo by Juan Carlos García Gómez.
A raven feeding.

APPENDIX I: ORIGINAL PUBLICATIONS

This PhD thesis is based on three published original articles and a fourth one under review in Ambio. Additionally, a published article complementary to the thesis topic was also added in the *Appendix II* as it did not compose the body of this thesis.

Chapter 1

García-Jiménez, R., Margalida, A., & Pérez-García, J.M. Influence of individual biological traits on GPS fix-loss errors in wild bird tracking. *Scientific Reports* **10**, 19621 (2020). https://doi.org/10.1038/s41598-020-76455-x.

Chapter 2

García-Jiménez, R., Pérez-García, J.M. & Margalida, A. Drivers of daily movement patterns affecting an endangered vulture flight activity. *BMC Ecology* **18**, 39 (2018). https://doi.org/10.1186/s12898-018-0195-7.

Chapter 3

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

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Influence of individual biological traits on GPS fix-loss errors in wild bird tracking

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In recent decades, global positioning system (GPS) location data and satellite telemetry systems for data transmission have become fundamental in the study of basic ecological traits in wildlife biology. Evaluating GPS location errors is essential in assessing detailed information about the behaviour of an animal species such as migration, habitat selection, species distribution or foraging strategy. While many studies of the influence of environmental and technical factors on the fix errors of solar-powered GPS transmitters have been published, few studies have focussed on the performance of GPS systems in relation to a species' biological traits. Here, we evaluate the possible effects of the biological traits of a large raptor on the frequency of lost fixes—the fix-loss rate (FLR). We analysed 95,686 records obtained from 20 Bearded Vultures *Gypaetus barbatus* tracked with 17 solar-powered satellite transmitters in the Pyrenees (Spain, France and Andorra), between 2006 and 2019 to evaluate the influence of biological, technical, and environmental factors on the fix-loss rate of transmitters. We show that combined effects of technical factors and the biological traits of birds explained 23% of the deviance observed. As expected, the transmitter usage time significantly increased errors in the fix-loss rate, although the flight activity of birds revealed an unexpected trade-off: the greater the proportion of fixes recorded from perched birds, the lower the FLR. This finding seems related with the fact that territorial and breeding birds spend significantly more time flying than non-territorial individuals. The fix success rate is apparently due to the interactions between a complex of factors. Non-territorial adults and subadults, males, and breeding individuals showed a significantly lower FLR than juveniles-immatures females, territorial birds or non-breeding individuals. Animal telemetry tracking studies should include error analyses before reaching any ecological conclusions or hypotheses about spatial distribution.

Obtaining a global positioning system (GPS) fix and the reliability of location data are primarily subject to satellite acquisition, a process mainly shaped by technical, environmental, and behavioural factors[1]. External factors such as GPS satellite geometry (satellite constellation), topography and land surface roughness, vegetation, fix interval (time lapse between successive fixes), or even GPS-tag position and orientation, all limit a transmitters' ability to make contact with at least three satellites during a period of GPS activation[2–4], causing GPS misconnections. Some authors have even observed: (1) an association between resource use, habitat selection, and fix-loss rate; and (2) interactions between animal behaviour and local habitat conditions which have to be considered particularly when assessing a species' habitat use[4–8]. However, one of the biggest gaps in our understanding of GPS performance is related to species-specific behavioural effects. For example, the position of an individual animal changes the orientation of a receiver, and its performance. Some studies of large mammals have demonstrated that inactive animals have higher fix-loss rates and lower fix accuracy than active ones[1,4,9]. But very little is known about how, or to what extent, individual biological traits such as sex, age, size, territorial or breeding status, and their associated behaviour and ecology may affect satellite connection, fix-loss and location accuracy[10–13]. This kind of information is essential to properly interpret geolocation data and to draw useful conclusions regarding animal movement patterns or species behaviour.

During the last 40 years, Argos Platforms Transmitter Terminals (PTTs) have provided the world's most commonly used tracking coverage technology for the remote study of free-ranging animal movements, mainly because of their integration of GPS fixes (i.e. satellite locations) with data transmission technologies (i.e. the

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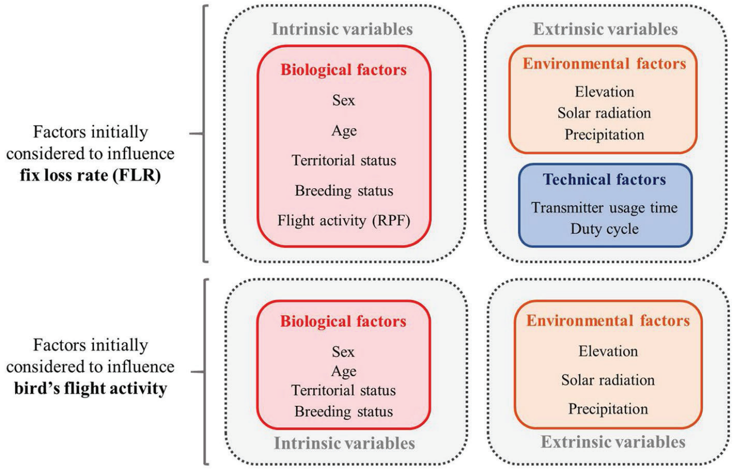

Figure 1. Factors considered to influence Fix Loss Rate (FLR) and bird's flight activity (composed considering both monthly numbers of fix perched and fix in flight).

Argos data transfer system), particularly from the mid-1990s when GPS receivers became able to record high-spatial-resolution tracking data[14–17]. However, the raw data registered through GPS-Argos telemetry still suffer from errors and biases (e.g. fix rate bias, fix-loss errors and spatial location errors) that must be considered to avoid drawing incorrect conclusions and making the wrong management recommendations[13,15,18]. These tracking problems are especially relevant for threatened species where reliable information is particularly important for reintroduction projects and conservation plans.

The endangered Bearded Vulture *Gypaetus barbatus* represents a good case study for assessing GPS fix-loss errors—measured in this study though the monthly fix-loss rate, FLR (for more details see "Methods" section). In the first instance, this species inhabits rugged mountain landscapes (in the Pyrenees, average home range kernel 90% varying between 63 km^2 for territorial individuals to 11,600 km^2 for non-territorial ones[19]) that allows the evaluation of the influence of abrupt topography on GPS fix-loss. Second, the long daylight hours and sunny climatic conditions favour at the same time flying behaviour and the charging of transmitter solar batteries. Third, the territorial behaviour of breeding individuals is very different to the behavioural pattern of non-territorial individuals, which fly over greater distances due to the lack of a nest site acting as a central foraging point[19,20]. Four, the changing seasonal and weather conditions in the Pyrenees allow the comparison of transmitter performance during different solar radiation conditions. Finally, Bearded Vultures are an endangered species (more specifically, classed by the BirdLife International 2017[21] as vulnerable in Europe, and globally near threatened) for which accurate GPS data is important to improve management and conservation actions. The species is being reintroduced in several European countries, and GPS transmitter monitoring is one of the main tools used by managers and conservationists to assess its habitat use and reintroduction success[22].

Technological improvements enabling the use of Argos GPS-lightweight PTTs (< 80 g) in marine mammals, birds, or even small animals up to 300 g[23,24], have prompted new research into sources of GPS errors associated to wildlife telemetric tracking, especially when fix-loss rate is related to animal behaviour or habitat use. This study focuses on the biological, environmental, and technical factors affecting the fix-loss rate—either caused by GPS misconnections or battery undercharging—in Argos GPS PTTs. We considered specific biological traits of Bearded Vultures including sex, age, territorial and breeding status, and flight activity (derived from the monthly rates of fixes of perched and flying birds) as biological factors. Concurrently, we considered environmental variables including topographic altitude, surface solar radiation, and total precipitation, as well as technical factors considering the transmitter usage time and the duty cycle (i.e. fix recording scheduled regimes), as extrinsic factors. Afterwards, given the flying nature of our case study species and the effect that this kind of movement behaviour has showed over some technological characteristics of the GPS transmitters in previous studies[25], we explore the influence of these biological and environmental variables over the flight activity trying to better understand this behavioural parameter and consequently its effect on the FLR (see Fig. 1). Based on previous solar-powered GPS tracking studies[13,25–27], our hypothesis was that both FLR and flight activity of birds are strongly influenced either by specific biological traits and/or extrinsic factors, especially those related to technical factors. We hypothesized that individuals with greater flight activity (higher rates of fix in flight, RFF—reasonably assumed to be non-territorial individuals, who usually travel larger distances[19,20]), would be more exposed to direct solar radiation, thus present increased battery charging, and a lower FLR compared to territorial individuals. Considering extrinsic factors, weather conditions will affect fix reception success because periods with more daylight hours (i.e. summer, presenting the highest surface solar radiation and lowest total precipitation) also favour thermal conditions for flight, in contrast to winter, promoting thus birds' flight activity.

Topographic altitude will also probably affect FLR due to the challenging GPS connection in steep terrains. At the same time, it is expected that the transmitter usage time will negatively affect transmitter performance as a consequence of the decreasing battery and electronic system performance of the device.

Results

A total of 95,686 location results from 20 Bearded Vultures tracked with 17 transmitters in the Pyrenees were recorded from 2006 until January 2019. Of these records: 32.6% were from females and 67.4% from males; 83.8% were from adults and 11.0% from subadults; 4.6% were from immatures and 0.6% from juveniles; 35.6% were from territorial birds and 64.4% from non-territorial ones.

Fix-loss rate (FLR). We found a substantial FLR variability showing significant differences between individual birds (Kruskal–Wallis, $\chi^2 = 278.13$, df = 18, $p < 0.001$) and also between individual PTTs ($\chi^2 = 251.39$, df = 15, $p < 0.001$). Five PTTs showed an FLR less than a 30%, seven showed FLRs of between 30 and 40%, one had an FLR of 48.2%, and the remaining five registered an FLR equal to or higher than 50% (Table 1). The FLR was highly variable at the individual level: seven birds had an FLR less than 30%; another seven showed FLRs between 30 and 40%; two ranged from 40 to 50%; and four showed an FLR higher than 50% (Table 1). However, FLR barely fluctuated between months, showing no significant differences over the year (Kruskal–Wallis, $\chi^2 = 10.92$, df = 11, $p = 0.45$), ranging between mean values of 0.31 ± 0.24 in May to 0.37 ± 0.23 in October.

The total conditional R^2 obtained from the GLMM built to evaluate the joint contribution of the biological, technical and environmental factors to the FLR was 0.148 (0.093 of the marginal R^2 corresponding to the fixed effects + 0.055 of deviance corresponding to the random effects). The highest was provided by the sum of both technical factors (single effect of 1.5%) and biological traits (with the highest single retained effect of 5.8%) and its interactions with the other groups (− 0.6% shared between both groups, − 0.5% shared between technical factors and environmental factors, 3.3% shared between biological traits and environmental factors, and 13.1% resulting from the interaction of the three groups). Environmental factors retained a single effect of − 7.8% (Fig. 2).

Regarding the GLMMs results (Table 2), we found two models from the total selection that met the delta AIC < 2 criterion. The parameters influencing the efficient performance of the transmitters included all of the biological and technical variables tested. Non-territorial birds, males, and breeding individuals showed a significantly lower FLR than females, territorial birds or non-breeding vultures. The rate of perched fixes (RPF) showed a negative relationship with the FLR, while the PTT usage time exerted the opposite effect, so that the higher the RPF and—in parallel—the smaller the PTT usage time, the lower the FLR becomes. Indeed, longer duty cycles provoked also lower FLR, although this variable was only selected for one of the two final models selected. Regarding age, adults and subadults showed significantly lower FLRs. None of the environmental variables were included in the significant GLMMs eventually built. The partial effects of all the explanatory variables included at least in one of the two final models selected are shown in Supplementary Figure S1.

Flight activity. Considering all the data, we observed an average of 64.3 ± 20.0% rate of perched fixes (RPF) and 31.8 ± 16.5% rate of fixes in flight (RFF). Of the 20 Bearded Vultures tagged, 65.0% (n=13) showed a quite homogeneous flight activity pattern, their mean RPF ranging between 87.4 and 68.8%. Three individuals showed rates of 61.3–63.5% and the other four showed perched fix rates lower than 52.8%. Even so, three of the birds exhibited a higher monthly RFF than RPF (Table 1).

The RPFs ranged significantly between 70.4% in summer and 66.4% in winter (Kruskal–Wallis, $\chi^2 = 21.12$, df = 3, $p < 0.001$). The variables selected for the competing GLMMs influencing flight activity (Table 3) were territoriality, breeding status, age, and sex (although, the last two were not always included in the final models). Territorial and breeding individuals showed significantly lower RPFs than non-breeding and non-territorial ones. The mean RPF and RFF were 50.2 ± 25% and 39.3 ± 22.6% for territorial individuals and 72 ± 10.5% and 27.6 ± 10% for non-territorial birds, respectively. The environmental variables were not included in the final models. The partial effects of all the explanatory variables included at least in one of the four final models selected are shown in Supplementary Figure S2.

Discussion

Studies of movement ecology often suffer from lost geolocation information due to: (1) technical glitches such as insufficient battery power; (2) environmental factors such as the roughness of the terrain (i.e. the conjunction of vegetation and topography[28]) or changing climatological parameters; and (3) intrinsic factors (i.e. biological traits) such as the behaviour of individuals[25,29]. Our findings point out that a combination of technical variables and biological traits gave the best explanation of maximum deviance (22.6%), suggesting that these two groups of factors have a much greater influence on the monthly FLR than environmental factors. This was also one of the main conclusions achieved by Hofman et al.[27], in a study where they gathered information of 167 projects deployed on 62 species in 142 study areas worldwide through some questionnaires with the aim of assessing the performance of satellite telemetry units (predominantly collars) tracking terrestrial wildlife. Concretely, they found out that the transmitter performance was strongly influenced by unit and species characteristics while environmental conditions increased the variability, influencing the transmitters' technique effectiveness. Concurrently, we propose that it could be that technical and biological variables already gather part of the deviance explained by the environmental factors. Such is the case for the breeding status, a parameter directly related to time of year, seasonality, solar radiation, and daylight duration in addition to its biological significance for the species. Another technical variable that affects the FLR, the transmitter battery level, is also related to solar energy availability, and hence to the time of year (through the seasonal variations in solar irradiance received by the device)[25,26]. Battery power limits the time for the transmitter to search satellites to obtain a location and

Individuals	PTT	Sex	Age (years)	Territorial status	FLR	Time period	Usage time (years)	RPF	RFF
Adrian	PTT1	M	4	T (2012–2016)	0.30 ± 0.15	05/2009–01/2019	9.8	0.72 ± 0.26	0.28 ± 0.26
Andreia	**PTT2**	H	≥ 7	T (2009)	0.29 ± 0.15	03/2009–09/2009	0.6	0.47 ± 0.32	0.52 ± 0.32
Pocholo	**PTT2**	M	≥ 7	NT	0.16 ± 0.14	07/2011–01/2019	7.6	0.75 ± 0.23	0.25 ± 0.23
Batín	PTT3	M	≥ 7	T (2008)	0.29 ± 0.15	05/2008–04/2015	7.0	0.50 ± 0.33	0.50 ± 0.33
Cabó	**PTT4**	H	≥ 7	T (2007)	0.47 ± 0.15	11/2007–08/2008	0.7	0.53 ± 0.37	0.47 ± 0.37
Sofia	**PTT4**	H	≥ 7	NT	0.34 ± 0.20	11/2008–05/2012	3.6	0.71 ± 0.29	0.29 ± 0.29
Dulantz	PTT5	M	6	NT	0.22 ± 0.19	04/2013–10/2014	1.5	0.64 ± 0.30	0.37 ± 0.30
Elisabeth	PTT6	H	18	NT	0.30 ± 0.21	03/2015–01/2018	2.9	0.77 ± 0.23	0.23 ± 0.23
Garrotxa	PTT7	H	5	T (2012)	0.40 ± 0.29	05/2008–06/2013	5.2	0.61 ± 0.31	0.38 ± 0.31
Gervàs	**PTT8**	H	≥ 7	T (2007)	0.28 ± 0.19	05/2007–04/2009	1.9	0.69 ± 0.28	0.31 ± 0.28
Min	**PTT8**	M	5	NT	0.56 ± 0.30*	05/2009–08/2017	8.4	0.73 ± 0.27	0.27 ± 0.28
Isaac	PTT9	M	5	NT	0.19 ± 0.16	11/2010–01/2014	3.2	0.70 ± 0.26	0.29 ± 0.26
Jairo	PTT10	H	4	T (2014)	0.32 ± 0.17	11/2010–06/2016	5.6	0.76 ± 0.27	0.24 ± 0.27
Morreres	PTT11	M	1	NT	0.28 ± 0.15	11/2007–09/2012	4.9	0.62 ± 0.31	0.37 ± 0.31
Nicky	PTT12	M	5	T (2011)	0.64 ± 0.30*	06/2009–05/2017	8.0	0.53 ± 0.34	0.47 ± 0.34
Noah	PTT13	H	≥ 7	NT	0.48 ± 0.13	04/2008–09/2008	0.5	0.84 ± 0.23	0.16 ± 0.23
Revilla	PTT14	H	5	NT	0.33 ± 0.17	04/2013–11/2013	0.6	0.87 ± 0.17	0.13 ± 0.17
Sasi	PTT15	M	1	NT	0.61 ± 0.24*	08/2007–06/2008	0.9	0.78 ± 0.24	0.22 ± 0.24
Subfli	PTT16	H	4	T (2012)	0.33 ± 0.17	05/2008–04/2012	4.0	0.72 ± 0.28	0.28 ± 0.28
Tossal	PTT17	H	≥ 7	T (2006)	0.74 ± 0.27*	11/2006–12/2006	0.1	0.82 ± 0.22	0.18 ± 0.22

Table 1. Basic biological traits and individual measures of fix loss rate (FLR) during a set period of time; rate of fix in flight (RFF) and rate of perched fixes (RPF) (mean ± SD for the monthly FLR, RPF and RFF individual values) for 20 birds tagged with 1770 g solar-powered Argos' satellite transmitters (PTT/GPS Microwave Telemetry, Inc. Columbia, MD, USA) all bought in 2005–2008. In bold indicate transmitters (platform transmitter terminal, PTT) that were used on two different birds and * indicates when FLRs were equal or higher than 50%. For the territorial status (*T* territorial, *NT* non-territorial) the years of the beginning and ending (if any before 2019) are shown. The PTT FLRs were the same as the individual values of FLRs showed in this table, excepting for the case of the three PTTs that were reused: PTT2 presented a mean monthly FLR = 0.17 ± 0.14; PTT4 presented a mean monthly FLR = 0.36 ± 0.21 and PTT8 presented a mean monthly FLR = 0.50 ± 0.30*.

so influence in the number of satellites acquired for the process[1], however it is a parameter only available in the newer GPS models. In this respect, the logger generation, transmitters' manufacturers, and data receiving system—all of the three uniform parameters for our study case given that all the 17 devices were Microwave solar-powered Argos-GPS bought between 2005 and 2008—are also important technical variables that need to be considered when studying GPS accuracy and location errors[25,29,30]. On the other hand, our results show that individual flight activity could be one of the most influential factors determining the fix performance of a device. Contrary to previous studies[19,36] and our initial hypothesis, the greater the proportion of perched fixes, the lower is the resulting FLR. One possible explanation for this observation could be related to the difficulty of satellite acquisition while a bird is flying, as has been noted for moving animals in various mammal studies[29,31,32], perhaps because of changes in the position and orientation of the GPS transmitter. Our findings also confirmed that longer duty cycles (of 2 h compared with those of 1 h) produced lower FLR, probably associated with the fact that more intense duty cycles increase the transmitter energy consumption and consequently reduce the device usage time[33]. In fact, Silva et al.[25] suggested that FLR due to poor GDOP (when Geometric Dilution of Precision limits the transmitter to contact with enough satellites to produce a fix) increased when the birds moved.

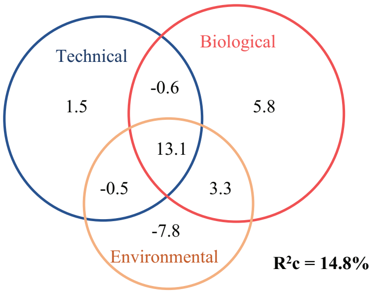

Figure 2. Conditional R^2 partitions resulting from a partial regression analysis of 17 Microwave PTTs monthly fix-loss rates. Percentages of conditional R^2 (deviance explained by the entire model, including both fixed and random effects) explained by each group of variables: *Technical* (PTT's lifetime and duty cycle), *Biological* (rate of perched fixes, sex, age, territorial and breeding status), and *Environmental* (surface solar radiation, total precipitation, and topographic altitude) and by their interactions. The total conditional R^2 of the model is also shown.

Model	Factors	K	AIC	ΔAIC	W
M1	T_PTT − RPF + Age + Sex + Territ + Br_S + (1|Indiv)	10	6929.6	0	0.725
M2	T_PTT − Dcycle − RPF + Age + Sex + Territ + Br_S + (1|Indiv)	11	6931.6	1.94	0.275

Table 2. Competing GLMMs to evaluate the influence of different biological traits and extrinsic factors (comprising both technical and environmental variables) on the fix loss rate (FLR). The individual (Indiv) was included as a random factor. We present the most parsimonious selected model with ΔAIC < 2. *K* total number of parameters (explanatory terms + random term + residual deviance), *AIC* corrected Akaike information criterion, *ΔAIC* difference between the AIC value for that model and the best model, *W* Akaike weight. Biological traits included: flight activity measured through the rate of fix perched (RPF), age (Age), territorial status (Territ), breeding season (Br_S) and sex (Sex). Technical variables were transmitter usage time (T_PTT) and duty cycle (Dcycle), and environmental variables were topographic altitude, surface solar radiation, and total precipitation.

Model	Factors	K	AIC	ΔAIC	W
M1	Territ + Br_S + (1|Indiv)	4	7154.2	0.00	0.3
M2	Sex + Territ + Br_S + (1|Indiv)	5	7154.4	0.19	0.3
M3	Age + Sex + Territ + Br_S + (1|Indiv)	8	7155.1	0.90	0.2
M4	Age + Territ + Br_S + (1|Indiv)	7	7155.4	1.17	0.2

Table 3. Competing GLMMs for evaluating the influence of different biological traits and environmental variables on birds' flight activity (computed as a weighted rate of perched fix). The individual (Indiv) was included as a random factor. We present the most parsimonious selected models with ΔAIC < 2. *K* total number of parameters (explanatory terms + random term + residual deviance), *AIC* corrected Akaike Information Criterion, *ΔAIC* difference between the AIC value for that model and the best model, *W* Akaike weights. Biological traits included: age (Age), territorial status (Territ), breeding season (Br_S), and sex (Sex). Environmental variables were topographic altitude, surface solar radiation, and total precipitation, but none was selected for the final models.

Nevertheless—considering that the time to obtain a fix increase in dynamic versus static conditions—longer duty cycles (of 2 h compared to 30 s and 15 min interval times) would produce higher fix loss rates while flying, but the opposite situation could happen while the birds are perched, when the length of the fix interval is not so relevant. In addition, as it was predicted, the FLR increases with transmitter usage (as happened in[27,34]), a relevant information considering that the mean usage time for our PTTs was 5.34 ± 3.03 years (n = 14).

Given the number of studies which point to landscape structure as an important driver of the FLR[2,35], we expected the topographic altitude as a variable influencing FLR. However, our monthly-scale analysis could have diluted the effect of this environmental variable and a complementary shorter time-scale FLR study (e.g. daily or hourly) may show a higher influence of this specific variable on the fix loss errors. Notwithstanding these uncertainties, our analyses of the possible effects of Bearded Vulture biological traits on the FLR constitutes a novel approach to the better understanding of the treatment of PTT locations. All the biological variables tested in this study influenced the RPF and also significantly affected the fix reception success. Interestingly, non-territorial Bearded Vultures travel further and later in the daylight than territorial birds[20], but exhibit significantly higher RPFs (72 ± 10.5% for non-territorial individuals versus 50.2 ± 25% for territorial birds). At the same time, breeding and territorial adults showed lower FLRs even if they spent less time perched than non-breeding, non-territorial and younger individuals. Probably their daily activity related to parental duties (nest-building, territorial defence, and foraging) results in increased flight activity and a higher proportion of their time spent flying, even if the distances covered are shorter than those of non-territorial birds[19,20,36].

Our results showed an overall monthly mean FLR of 34.5 ± 24.72% ranging between a minimum of 3% and maximum of 100% (n = 17). This is lower than the values found for analogous transmitters by Silva et al.[25], used on the same Pyrenean and Cantabrian population of Bearded Vultures (FLR = 0.40 ± 0.12), and those recorded by Soutullo et al.[24], for lightweight Argos GPS transmitters used on Golden Eagles *Aquila chrysaetos* in a rocky cliff area in Eastern Spain (FLR = 0.45). In this latter study, breeding season also influenced the FLR (probably through seasonal effects), as was the case in our study. Nevertheless, our findings show the importance of understanding that significant variations in FLR may be due either to variations in individual bird behaviour or to variations in technical glitches affecting each PTT performance. Therefore, it should be expected that both biological and technical factors play a fundamental role in the correct performance of the GPS fix programming.

The significant differences in FLR between male and female birds are not easily explained from a behavioural and ecological perspective (mean values of 0.32 for males cf. 0.39 for females), even if non-territorial males do indeed exploit larger areas and fly over longer distances, as it is the case of territorial females[19,20]. The specific relationships between the biological traits of this species and RPF or RFF are clear, but even if their influence on the FLR is also obvious, it is more difficult to explain the effect of certain biological variables such as territoriality or sex on FLR. The fix success rate results are most likely due to a synergy between complex interactions; for instance, between flight height and terrain roughness, or between the availability of environmentally optimal flight conditions (which are also favorable for solar battery charging) linked to the likelihood of flight activity and the resulting associated increase in transmitter movement. In any case, it is clear from this study that biological factors such as sex, age, breeding and territorial status have particular effects on FLR and must be considered when studying fix error rates in other flying species (e.g. bird and bat species). Even considering the apparent limitations of working with a single species in a GPS fix loss error study, as it has been shown, our findings can be extrapolated to different medium and large-size animal populations and species. Moreover, technological improvements of materials and both hardware and software enhancements are leading to increasingly better transmitters' performance with improved location accuracy and reduced FLRs. However, there are still many transmitters in use (in addition to the quite a few already developed) that present scheduled location duty cycles, data receiving Argos-GPS system and device manufacturers similar to the ones evaluated in this study, so these findings obtained remain relevant for long-term conservation studies.

Every animal telemetry tracking study should include an error analysis before reaching any ecological conclusions or hypotheses regarding spatial utilization, since the results can vary substantially depending on extrinsic factors such as GPS transmitter model, retrieval data system, PTT usage time, season, etc., or biological factors such as those analysed in this study. All of these changing elements can influence the data collected and lead to errors in interpreting patterns of movement. Fortunately, these kinds of tracking error, together with accuracy biases in the horizontal plane (x and y coordinates) are being addressed and overcome as transmitter technology improves, thus reducing the potential influence of tracking device shortcomings on the recording and interpretation of basic parameters regarding the spatial ecology of a species[26,29,30,37,38].

Methods

Study area. We assessed the GPS fix loss errors resulting from Bearded Vultures studied in the Pyrenees, a steep mountainous region with maximum altitudes of 3400 m, located in the north of the Iberian Peninsula on the border between France and Spain. It includes three different bioclimatic areas (Montane, Sub-Alpine and Alpine) with average annual temperatures between 0 and 20 °C, and a four-season Mediterranean climate with seasonal weather conditions[39].

Study species. The Bearded Vulture is a territorial, cliff-nesting vulture specialized in feeding on the bones of medium size ungulates[40]. In common with other avian scavengers it exploits thermal and orographic updrafts to use the least energy as possible when foraging. It is an endangered species now only found in certain mountainous areas of Europe, Asia, and Africa[21,41]. In the Pyrenees, the spatial ecology of this species has been studied since the 1980s', originally using conventional VHF radio tracking[42–44] and more recently with the solar-powered Argos or GSM data recovery system with GPS-PTTs[19,20,45].

Tracking and data origin. Between 2006 and 2019, twenty Bearded Vultures were tagged with 17 different 70 g solar-powered Argos' satellite transmitters (PTT/GPS Microwave Telemetry, Inc. Columbia, MD, USA, all of the 2005–2008 logger generation)—three of which were reused on new individuals—attached to the bird's back with a breakaway thoracic junction stitched with cotton thread harness made of 0.64 cm Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA) (for further details see[15]). The usage time of the transmitters was 5.34 ± 3.03 years (n = 14) on average. To compute this mean value for the three reused PTT, we summed the time usage of each peer of individuals using the same PTT, and for the rest of the PTTs, we excluded the records corresponding to the birds dead on the field (n = 3) since their transmitters could not be recovered and the reason for stopping fix recording was unlikely related with technical causes. We only considered the records of individuals whose PTTs stopped working properly, accounting times from the moment the PTTs were turned on until the moment we stopped receiving location data (see Supplementary Table S1). All of the transmitters were programmed to report hourly GPS fixes between 04:00 and 22:00 UTC hours each day (manufacturer estimated error ± 18 m), except for two individuals whose PTTs transmitted every 2 h. Regarding the biological factors: (1) age of individuals were assigned to four different age classes according to plumage characteristics: juvenile (1 year old); immature (2–3 years old); subadult (4–5 years old); and adult (> 6 years old) (for details see[19,20]); (2) sex was determined by molecular analysis of blood samples (PCR amplification of the CHD-W gene as described in[46]); (3) territoriality was described as territorial or non-territorial individuals, depending on their breeding behaviour[20]; (4) breeding season was defined either as *breeding period* (1st January to 31st July) or *non-breeding period* (1st August–31st December)[15]; and (5) flight activity was defined according to Silva et al.[25] by the complementary rates of perched fixes (RPF, calculated from monthly fixes with speeds slower than 1.39 m/s) and fix in flight (RFF, calculated from monthly fixes with speeds equal or faster than 1.39 m/s) (Tables 1 and 2). Regarding the extrinsic factors: for technical variables, (1) we accounted for the device usage time and (2) duty cycle (as mentioned, of 1 or 2 h depending on the individual) and for environmental variables, (3) topographic altitudes were obtained using a Digital Elevation Model (ASTER Global DEM, 1 arc-second spatial resolution); and (4) surface solar radiation and (5) total precipitation were obtained from an interim full-daily at surface forecast (European Centre for Medium-Range Weather Forecasts, 0.75° each 3 h). Monthly means of all three parameters were calculated using the Movebank Env-DATA track data annotation service[47,48] (Fig. 1).

Data processing and statistical analysis. The fix-loss rate (FLR) used in this study was calculated as a monthly value for each individual consisting of the proportion of days per month on which no fixes were recorded. We evaluated the effects of both biological and extrinsic factors (including both technical and environmental variables) on the performance of the 17 transmitters represented by monthly FLRs computed as the number of days per month on which no data were collected, divided by the total number of days on which data were scheduled to be collected. We generated a data set of monthly observations (n = 889), each with its own FLR. Since we reused three of the 17 transmitters to track the movement pattern of 20 birds, we needed to distinguish between two different levels when computing mean FLRs: the PTT/transmitter level and the individual level. For instance, the PTT usage time depends directly on the transmitter but variables related with the biological traits depend uniquely on the individual.

At first, we examined the FLR with some non-parametric explorative analyses to evaluate possible differences among these two levels and to evaluate the influence of the month on the FLR yearly distribution. Secondly, we grouped all the predictor variables: (1) age, sex, breeding and territorial status, and RPF (this latter describing flight activity) as biological factors; (2) PTT usage time per month and duty cycle as the technical factors; and (3) monthly means of topographic altitude, surface solar radiation, and total precipitation as environmental factors (see Fig. 1).

Thirdly, we performed a deviance partitioning analysis[49] to evaluate the effect on FLR of the single and joint contributions of each of the three groups of variables comparing by basic algebra the percentage of the explained conditional R^2 of each of the best generalized linear mixed models (GLMMs)[50] built including the aforementioned biological, technical and environmental factors as fixed factors (where applicable) and the individual as a random factor. Thus, we built seven separate GLMMs to evaluate: (1) the single contribution of the biological factors, (2) the single contribution of the technical factor; (3) the single contribution of the environmental factor; (4) the joint contribution of the biological and technical factors; (5) the joint contribution of the biological and environmental factors; (6) the joint contribution of the technical and environmental factors; and (7) the joint contribution of the biological, technical and environmental factors (see more details about how to perform a deviance partitioning analysis in[51]). These analyses were computed using R statistical software[52] version 3.6.2. For the GLMMs, we applied the "glmer" function of the "lme4" R package[53] with a binomial error distribution and logit-link function. All the deviance explained by the different groups of variables was expressed in percentages when we referred to the deviance partitioning results.

Fourthly, to determinate the significant variables influencing the FLR, we constructed the full model with all of the biological, technical and environmental variables as fixed factors and the individual as a random factor considering again a binomial error distribution and logit-link function, made a model selection using Akaike's Information Criterion (AIC[54]), and chose the best models with a delta AIC < 2 (Fig. 1).

And fifthly, to better understand the individual flying behaviour and how it could affect FLR, we analysed the influence of all of the same biological and environmental factors on the flight activity of the birds. For this analysis, a weighted RPF (wRFP) was created combining the monthly number of perched fix and monthly number of fix in flight (see Zuur et al.[55] for applying binomial generalized models for proportions). Thus, we modelled wRPF using a GLMM (binomial error distribution and logit-link function) with all the biological and environmental variables as fixed factors and the individual as a random factor, and then selected models giving delta AIC < 2 (Fig. 1). Technical factors were not included as predictors in this model because of their obvious absence of influence over the flight activity of the birds.

For all the mixed models built in this study, the relative contributions of the fixed and random factors to R^2 were estimated with the "r.squaredGLMM" function from the package "MuMIn"[56]. We also reviewed for the variance inflation factors (VIF) for all the predictor variables at the first stages of the GLMMs building using the "car" package[57] to assess collinearity (accepted VIF values < 3). In fact, we firstly considered season (defined as yearly quarterly periods i.e.: winter, from January to March; spring, from April to June; summer, from July to September; and fall, from October to December) and month for all the GLMMs' analyses, but they were finally excluded because of their high correlation with breeding season and surface solar radiation. All continuous variables were standardized and centred before modelling using the "scale" R function and all of the non-parametric analyses were performed after checking for the absence of a normal distribution.

Tracking data are inherently auto-correlated, although if fixes are taken infrequently enough so as to be longer than the autocorrelation timescale of the data, data can be considered independent, especially for animals that move long distances in short periods of time[5,58]. This is the case for our study species in this study, which present minimum duty cycles of 1 h (see also[19]).

Ethics statement. All the work was conducted in accordance with relevant national and international guidelines, and conforms to all legal requirements. Captures and blood sample collection were carried out in compliance with the Ethical Principles in Animal Research. Thus, protocols, amendments and other resources were conducted in accordance to the guidelines approved by the Catalan Autonomous Government (Generalitat de Catalunya) following the R.D.1201/2005 (10 October 2005, BOE 21 October 2005) of the Ministry of Presidency of Spain. All experimental protocols were approved by the Catalan Autonomous Government and MAGRAMA (References 15.546 and 25.306).

Data availability

The datasets used and analyzed during the current study are available from AM on reasonable request.

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Author contributions

All authors designed the study. A.M. conducted the fieldwork. R.G.J. wrote the manuscript with contributions from J.M.P.G. and A.M.; R.G.J. performed exploratory and statistical analysis under the supervision of J.M.P.G. All authors read and approved the final manuscript.

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Competing interests

The authors declare that no competing interests.

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Drivers of daily movement patterns affecting an endangered vulture flight activity

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Abstract

Background: The development of satellite tracking technology enables the gathering of huge amounts of accurate data on animal movements over measured time intervals, to reveal essential information about species' patterns of spatial use. This information is especially important in optimizing the design of conservation and management strategies for endangered species. In this study, we analysed the main drivers of daily patterns in the flight activity of the threatened Bearded Vulture *Gypaetus barbatus*. We studied 19 Bearded Vultures tagged with solar-powered GPS transmitters from 2006 to 2016 in the Pyrenees (Spain). We assessed the relative influence of external factors (season and daylight time) and internal factors (sex, breeding season and territorial status) on their daily activity behaviour by computing mean hourly distance travelled, maximum displacement and cumulative distance travelled per hour.

Results: Our findings showed a clear difference in all the estimators between territorial and non-territorial (floating) members of the population, showing that non-territorial individuals spent much longer in flight and travelled larger distances per day. We detected an important influence of daylight time and season on the daily rhythms of Bearded Vultures; flight activity increased during the last three quarters of daylight and was greatest in the spring. Breeding period and sex had also an effect on the maximum displacement and cumulative distance travelled. Individuals flew more during the breeding period and females tended to exhibit greater cumulative and maximum distances per hour than males regardless of breeding season.

Conclusions: Pyrenean Bearded Vultures flight daily activity was strongly influenced by daylight time, season, and territorial status, while individual sex and breeding season showed a milder effect on the birds' movement behaviour. This study gives a novel insight into how external factors act as main drivers of the daily flight activity pattern of a long-lived avian scavenger.

Keywords: Daily movements, Daylight time, GPS, *Gypaetus barbatus*, Season, Spain, Territorial status

Background

Interest in movement ecology has increased in recent years due to its key role in the design of more specific and efficient management and conservation strategies. The development of satellite tracking technology enables the gathering of huge amounts of accurate data on animal movement over measured time intervals, to provide essential information on species' patterns of spatial use [1, 2]. Modern satellite transmitters can also record individual physiological parameters during flight [3, 4]. The activity decisions made by individuals influence overall population behaviour and so affect population viability as each individual decides its own specific demographic process, such as migration, feeding, and reproductive behaviour [5]. The assessment of space use and territory occupancy patterns is particularly useful in bird community studies (e.g. [6–8]). Beyond the direct information gathered on dispersal [9, 10], roost site selection [11], and foraging activity [12, 13], study of movement ecology provides information indirectly related to an animal's behaviour in reaction to prevailing climatic conditions [4, 14, 15], on the effects of food availability on the use of space and on population trends [16, 17].

Avian scavengers provide human society with indispensable ecological services, recycling carrion biomass

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through their removal of waste and preventing the accumulation of dead animal biomass, so reducing the spread of diseases and contributing to nutrient cycling [18, 19]. Due to the ephemeral occurrence and random distribution of carcasses, vultures have evolved adaptive traits to exploit carrion as effectively as possible [20–22]. The balance between their maximization of food intake and minimization of energy expenditure has therefore developed to determine the daily foraging movements of scavenging species [23, 24]. To date, several internal and external factors have been suggested as drivers of the daily activity movement patterns of scavengers, acting either independently or in synergy. Intrinsic factors include biological and physiological parameters such as territorial status, sex, breeding season and level of hunger [23, 25–27]. External factors are mainly characterized by weather conditions and—both of which generally change seasonally—[4, 28], food availability [20], and intra- or interspecific interactions [20].

The Bearded Vulture *Gypaetus barbatus* is a long-lived territorial vulture inhabiting Old World mountain biomes with a diet consisting 70–90% of bones from wild and domestic ungulates, and therefore occupies a very specialized trophic niche [22, 29, 30]. Despite the increment of the Pyrenean population in the last 30 years, this positive tendency could be menaced by mortality factors such as the illegal use of poison baits, lead intoxication, food shortages, and anthropogenic habitat changes [31–35]. This situation highlights the need for an in-depth understanding of the potential threats, including mortality hotspots, the causes of breeding failure, and limitations on the species' use of space. For instance, information regarding their daily activity patterns is especially useful in planning reintroduction conservation programs and to enhance any future conservation or management action considering its habitat use and spatial behaviour.

This study set out to assess the influence of internal and external factors on the daily activity patterns of Pyrenean Bearded Vulture flight activity. To this end, we analysed 38,248 data obtained from a population of 19 GPS-tracked Bearded Vultures in the Pyrenees (Spain) between 2006 and 2016, to examine the effect of internal factors such as sex, territorial status and breeding season, and of external factors such as daylight time and season.

Methods

Study species

The habitat distribution of Bearded Vultures has been shrinking since the 1970s (with only 243 pairs remaining in the European Union in 2016). During the last 30 years a variety of management and conservation programs have been developed for this threatened species, achieving a substantial rise in the Pyrenean population, although, the overall distribution of Bearded Vulture has scarcely expanded [36]. This species is enlisted as near threatened by the IUCN Red List [37].

Study area

This study was conducted in Pyrenees, located in the border area between France and Spain, in the Eurosiberian region. In this area the Bearded Vulture population comprises more than 70% of the European breeding population. The most important breeding areas lies on the southern slopes of the Pyrenees, with the highest nesting densities in steeply sloping areas over 1000 m height level, where human access is limited and orographic updraughts are more frequent [30].

Capture, tracking and data collection

Twenty Bearded Vultures were captured in the period 2006–2016 using radio-controlled bow-nets at supplementary feeding stations (n = 17), at nests (n = 1), or as injured individuals recovered at official wildlife recovery centres (n = 2), where birds are released following rehabilitation (for more details about these individuals' capture see [17, 38]). We monitored their movement patterns using 70 g solar-powered Argos satellite transmitters (PTT/GPS Microwave Telemetry, Inc. Columbia, MD, USA) attached by means of a breakaway harness with a 0.64 cm Teflon ribbon (Bally Ribbon Mills, Bally, PA, USA). The transmitters were programmed to send a fix (manufacturer's estimated error ± 18 metres) each hour from 4:00 to 22:00 UTC, with the exception of two individuals, whose transmitters sent a GPS location every 2 h. Birds were aged into four different classes using plumage characteristics: juveniles (birds until the 1st year), immatures (2–3 years), sub-adults (4–5 years) and adults (6 years or over). Identification of gender was performed using blood samples by PCR amplification of the CHD-W gene [39]. We defined territorial Bearded Vultures when exhibited spatially aggressive defense, nest-building behaviour and sexual activity on a fixed area [38–41].

Data processing and statistical analysis

We analysed the daytime routine of Bearded Vultures by calculating three different estimators: maximum displacement, defined as the average Euclidean distance between the initial daily location and any position reached on the consecutive hours; hourly distance, approximated as the average straight-line distances covered in an hour and cumulative distance travelled, estimated as the sum of straight-line distances covered during each hour on a given day. To build a uniform and robust data base, we selected only data from days where at least seven consecutive GPS-locations were recorded during day with a maximum time lapse of 4 h between fixes. One of the tracked birds did not meet this minimum set of criteria for locations, so we exclude all its data from the analysis.

We studied differences in the daily movement parameters according to three internal factors: sex, breeding season, and territorial status; and two external factors: daylight time and season.

To evaluate the influence of sex on the daily movement of Pyrenean Bearded Vultures we considered only territorial individuals. For breeding season comparisons of daily activity patterns, we divided the data in the two breeding periods (*breeding period*, from 1st January to 31st July, and the *non-breeding period*, from 1st August to 31st December) based on Margalida et al. [38]. To study the possible influence of season on the daily pattern of flight activity we defined four seasons conforming to the Mediterranean climate: spring (from 21st March to 20th June); summer (from 21st June to 22nd September); fall (from 23rd September to 20th December); and winter (from 21st December to 20th March). We did not include age in the analysis because our previous studies showed it to be subordinate compared to territorial status [38]. Differences in maximum displacement, cumulative distance travelled and hourly distance travelled for different territorial status and breeding season were compared using the Wilcoxon Mann–Whitney tests. Sex related differences between territorial individuals were also tested for these three variables. We analysed each relationship independently.

To standardize the seasonal variation in daylight, we generated an index of daylight duration (hereinafter called daylight index) which denotes the daylight time considering the astronomical twilight as the start and the end of a daylight length setting sunrise -the astronomical dawn, the time when the geometric centre of the Sun is 18 degrees below the horizon in the morning—(value 0) and sunset—the astronomical dusk, when the geometric centre of the Sun is 18 degrees below the horizon preceding the night—(value 1) for each day. We included the three twilight periods before sunrise (astronomical, nautical and civil twilights; data obtained from www.timeanddate.com and summarised in Additional file 1) because several authors have suggested that they mark the beginning of the first daily peak of activity in bird's circadian pattern [42–44], as well as a short time after sunset during which birds were observed making the journey back to their roosting sites. We computed this daylight index as the division of daylight elapsed fix time by daylight length, where the numerator is the period of daylight spent until the fix transmission, and denominator is length of daylight hours within a given 24 h day.

To analyse and represent the data we grouped the daylight index ranges into an integer scale from 0 to 10 following the scale described above, but to a higher decimal order. We incorporated also some locations before and after the astronomical twilight (with index values -1 and 11, consecutively) to evaluate the behaviour of the birds some dark hours previous to sunlight incidence (Additional file 1, Additional file 2: Figure S1 and Table S1).

To examine the relationship between movement parameters and biological (sex, breeding season, and territorial status) and external (daylight time and season) factors we used linear mixed models (LMM) with individual as a random factor [45]. We compared each model with the null case, including both the variables and the interactions. Model comparisons were carried out using Akaike information criteria (AICc; [46]). We computed delta AICc to determine the strength of evidence, and AICc weights to represent the relative likelihood of each model [46]. Models with delta $\text{AICc} > 4$ were discarded. All analyses were conducted using R statistical software (v 2.3-2. R Development Core Team 2007, http://www.R-project.org) with the lme4 package for LMM analyses. All tests were two-tailed and statistical significance was set at $\alpha \leq 0.05$. All results were shown as mean ± 1 SD.

Results

We recorded 78,814 GPS locations from 20 Pyrenean Bearded Vultures, during November 2006 to December 2016. After filtering, we analysed 38,248 fixes from 19 individuals. The highest frequencies of locations were recorded from 9:00 to 16:00 UTC usually concurring with the hours with major sunlight availability (Additional file 2: Figure S1, S2 and Table S2). The records were—according to sex—34.1% females and 65.9% males and—in terms of the age class and territorial status—86.6% adults (of which 28.6% were locations from territorial birds), 11.3% were from subadults, 2.0% were from immatures, and 0.1% were from juveniles.

Territorial status and breeding season

The floating population (non-territorial birds) exhibited a significantly greater daily activity pattern compared to territorial birds. Significant differences were found in cumulative distance travelled (Wilcoxon test, $Z = 13.0$, $p < 0.001$), maximum displacement during the daylight ($Z = 40.2$, $p < 0.001$) and hourly distance travelled ($Z = -3.4$, $p < 0.001$) according to their territorial status. Non-territorial individuals exhibited the highest values for the three daily distance covered estimators during the breeding period (Figs. 1, 2 and 3). In non-territorial individuals, the maximum mean cumulative distance travelled was c. 42 km, showing a marked rise during the two middle daylight quarters (from daylight

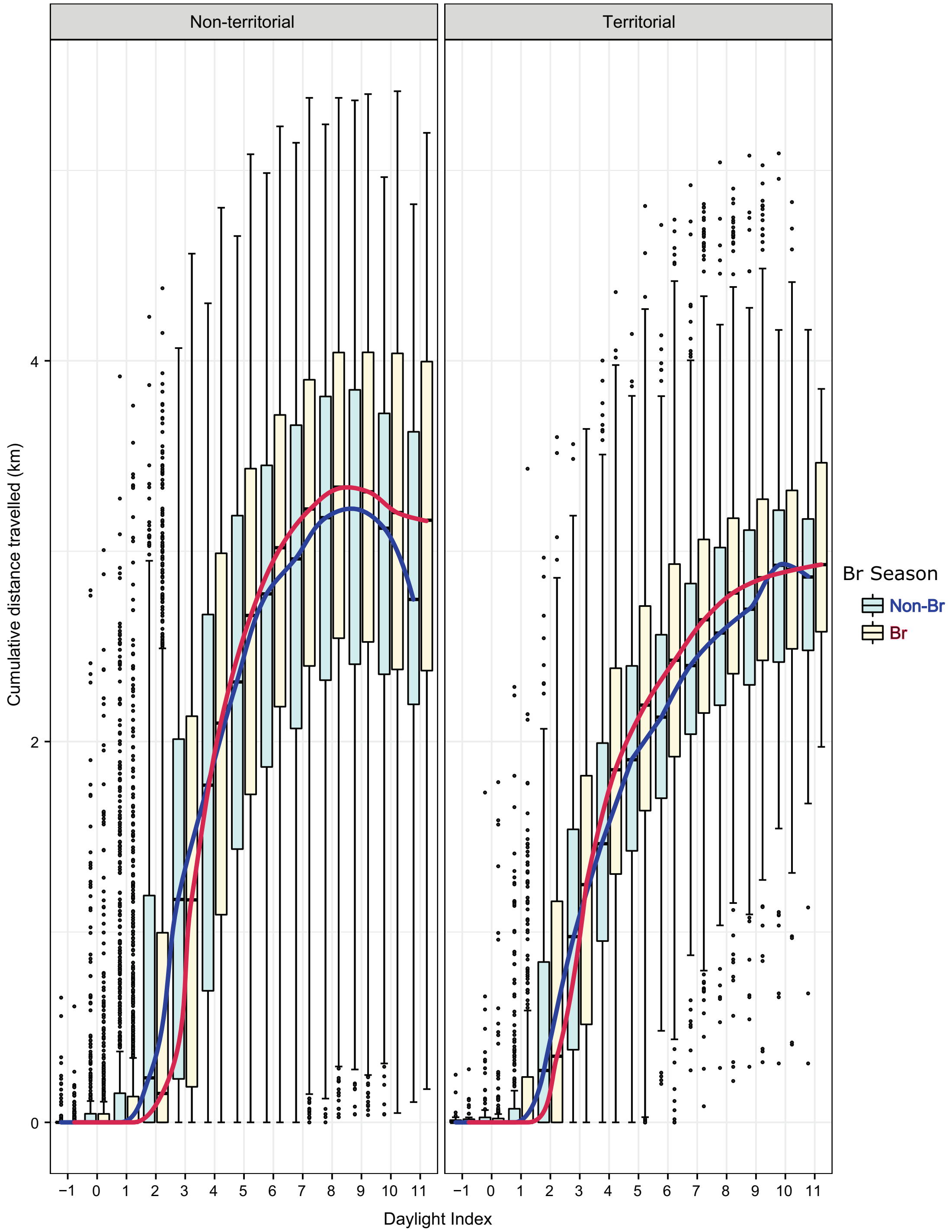

Fig. 1 Influence of territorial status (left: non-territorial, right: territorial) and breeding season (blue: non-breeding, red: breeding) on the cumulative distance travelled. The response variable, log (y + 1), has been transformed to represent the variation graphically

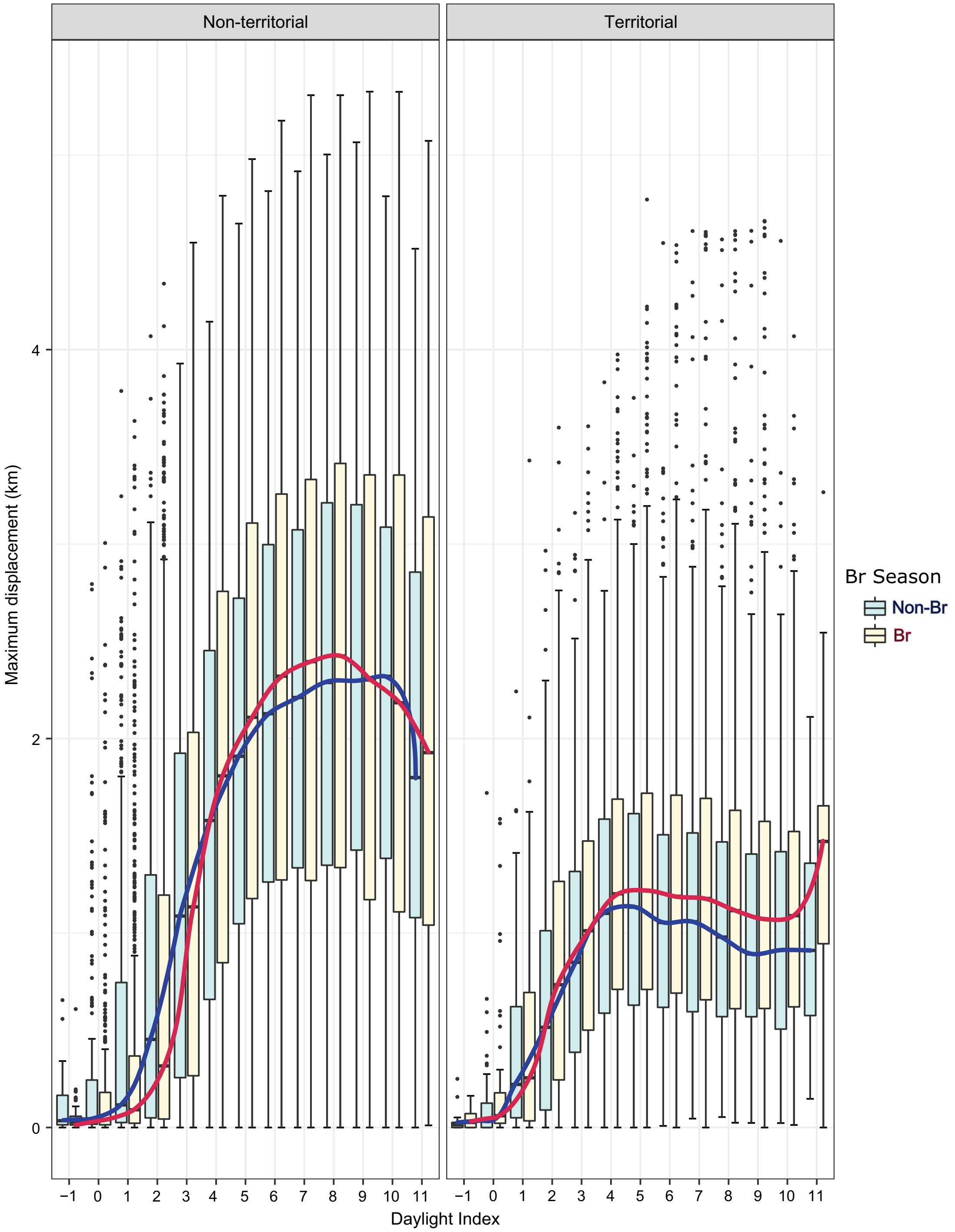

Fig. 2 Influence of territorial status (left: non-territorial, right: territorial) and breeding period (blue: non-breeding, red: breeding) on the maximum displacement travelled by adult territorial individuals

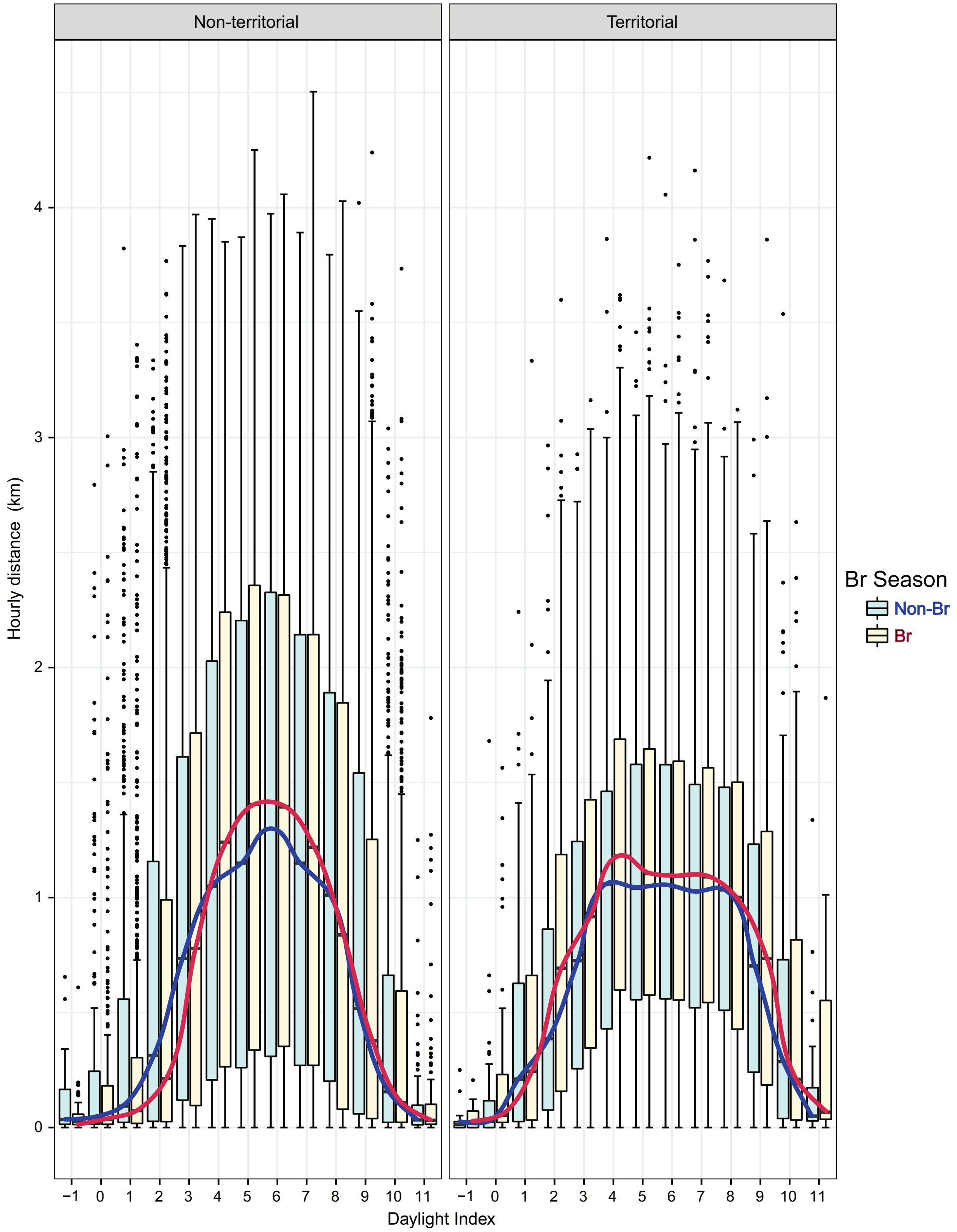

Fig. 3 Influence of territorial status (left: non-territorial, right: territorial) and breeding period (blue: non-breeding, red: breeding) on the hourly maximum displacement. The response variable, log $(y+1)$, had been transformed to represent the variation graphically

index values of 2–8), while territorial individuals showed a gradual increase in this distance estimator throughout the daylight hours (Fig. 1), reaching maximum medium values of 20–22 km cumulative distance travelled. The same pattern was observed for the maximum daytime displacement in the non-territorial birds, although territorial vultures showed increasing mean values until the middle of the daylight period, followed by stabilization of these values (Fig. 2). Independently of territorial status, the longest average hourly distances were travelled during the middle of the daylight period, although the greatest distances were achieved by non-territorial individuals (6.75 ± 9.05 km), regardless of breeding season (Fig. 3). Furthermore, non-territorial individuals during the breeding period showed a range of maximum average displacements between 0.06 ± 0.11 and 20.77 ± 26.51 km, while non-breeding birds had a significantly lower mean maximum displacement range of between 0.14 ± 0.21 and 16.83 ± 21.01 km ($Z = -7.4$, $p = 0.01$). Breeding season also significantly affected territorial individuals: during the breeding period they exhibited a notably higher maximum distance from the nest 5.25 ± 13.56 km, and longer mean cumulative distance travelled of 22.07 ± 21.48 km, compared to the maximum daily displacement of 3.72 ± 8.41 km ($Z = -7.5$, $p < 0.001$) and daily covered distance of 20.02 ± 18.06 km ($Z = -5.7$, $p < 0.001$) observed during the non-breeding period. The territorial birds also showed significantly higher values of hourly displacement during the breeding period ($Z = -4.6$, $p < 0.001$; see Fig. 3).

The effect of sex in territorial Bearded Vultures

During the breeding period, females showed higher flight activity than males, performing maximum distances travelled per day of 14.31 ± 28.93 km, cumulative distances travelled of 37.38 ± 37.45 km, and hourly distances travelled of 5.22 ± 7.45 km, in contrast with males which travelled mean maximum day distances of 5.07 ± 6.76 km ($Z = 5.2$, $p < 0.001$), cumulative daily distances of 21.67 ± 17.53 km ($Z = 2.4$, $p = 0.02$) and hourly distances of 3.24 ± 4.27 km ($Z = 3.3$, $p = 0.001$). A similar trend was also observed within the non-breeding birds, where males achieved a maximum displacement of 3.20 ± 4.12 km and hourly distances of 3.04 ± 3.94 km at least 1 km significantly less than females, which achieved maximum distances covered per day of 6.96 ± 17.94 km ($Z = -2.6$, $p = 0.009$) and hourly movements of 4.42 ± 5.48 km ($Z = -3.0$, $p = 0.002$; see Figs. 4, 5 and 6).

Seasonal patterns

Based on the linear mixed models results, season is a highly significant factor leading to remarkable differences between the mean seasonal values of all three flight distance estimators (Table 1).

Flight activity of non-territorial birds stands out in spring, when they reached the greatest maximum daytime displacement, cumulative distance travelled, and hourly distance. Nevertheless, a similar flight pattern was observed for non-territorial Bearded Vultures in every season, showing a growing trend for the daily maximum displacement and cumulative distance travelled from 8 h since 18 h (UTC), excepting fall, when the peak of activity was achieved a little before (around 16–17 h, UTC). In spring and summer (the two seasons with the highest daylight availability) the Bearded Vulture flight activity extended longer (until 22 h UTC). The second greatest maximum displacement and cumulative distance travelled was recorded in winter (Fig. 7).

Territorial Bearded Vultures presented an increased flight activity during spring and summer achieving the peak approximately at 18 h UTC. In fall and winter even though the flying activity decreased, the rise was interestingly detected at 19 h, coinciding with the hours around astronomical sunset. No data were registered after 20 h for territorial birds (Fig. 7).

Concerning hourly distance, all the individuals showed a uniform movement pattern during all the year, attaining the maximum values around 13 h UTC. During fall, individuals travelled the shortest distances (Fig. 7).

Multifactorial model

The daylight index and seasonal factors were the most influential of all the parameters tested in every linear model since they were selected in each of the models built for the three distance covered estimators. Consecutively, territorial status had the next most noticeable effect on cumulative distance travelled and hourly displacement, followed by the effect of sex which only appeared in the cumulative distance travelled model. Breeding season was the factor with the weakest relationship with all of the three distance covered estimators.

The best explanatory model for maximum displacement involved the interaction between sex and territorial status, daylight index, and seasonal variables. In the hourly distance case, the model comprising territorial status, season and daylight index overcame the null model, while for the cumulative distance travelled estimator, the best model involved all of the variables tested (Table 1, Additional file 3).

Discussion

Our results on daily flight behaviour show an important spatial decoupling between the territorial and non-territorial individuals in the Pyrenees. Because non-territorial individuals are not central place foragers, they exhibited

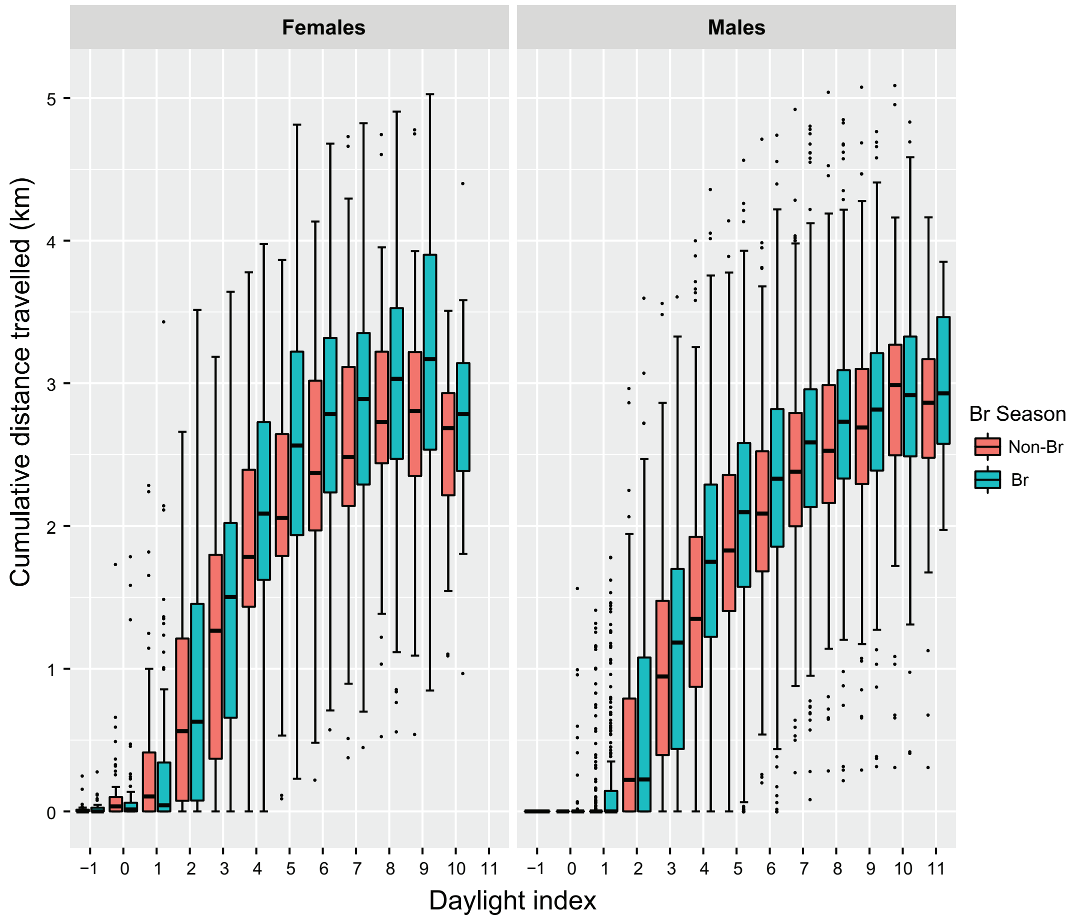

Fig. 4 Influence of sex and breeding period (red: non-breeding, blue: breeding) on the cumulative distance travelled by adult territorial individuals

greater daily flight activity travelling longer distances, showing greater cumulative distances covered in an hour, higher maximum displacements, and greater hourly distance rate. These findings agree with the results regarding foraging movements obtained by Krüger et al. [26] in South Africa and by Margalida et al. [38] in the Pyrenees, in which territorial status influenced spatial distribution patterns of Bearded Vultures. In these studies, non-territorial individuals exhibited Kernel 90% home ranges of between 10,500–26,000 km^2 in South Africa and 1800–11,600 km^2 in the Pyrenees, areas that are significantly larger than those covered by territorial individuals of 286 ± 361 km^2 in South Africa and 63 ± 59.5 km^2 in the Pyrenees. In addition, our results show a daily temporal dissociation according to the status of an individual (territorial vs non-territorial); non-territorial birds showed greater increments in maximum distance covered and the cumulative distance covered. The non-territorial status of these individuals allows them to travel farther and until later into the daylight period (i.e. during the last third of the daylight hours) compared with territorial individuals, who increased their maximum daily distance travelled until the period close to noon after which their daily maximum distance values stabilised (Figs. 1, 2, 3, 4, 5, 6).

Our findings suggest that breeding period also has an influence over the daily flight activity, but lower than other internal factors. As with other obligate avian scavenger species, breeding Bearded Vultures experience an increased energy requirement due to parental effort. These reproductive tasks could explain the noticeable rise in the three different distance parameters measured during the last three quarters of the daylight period in the territorial birds. This accords with

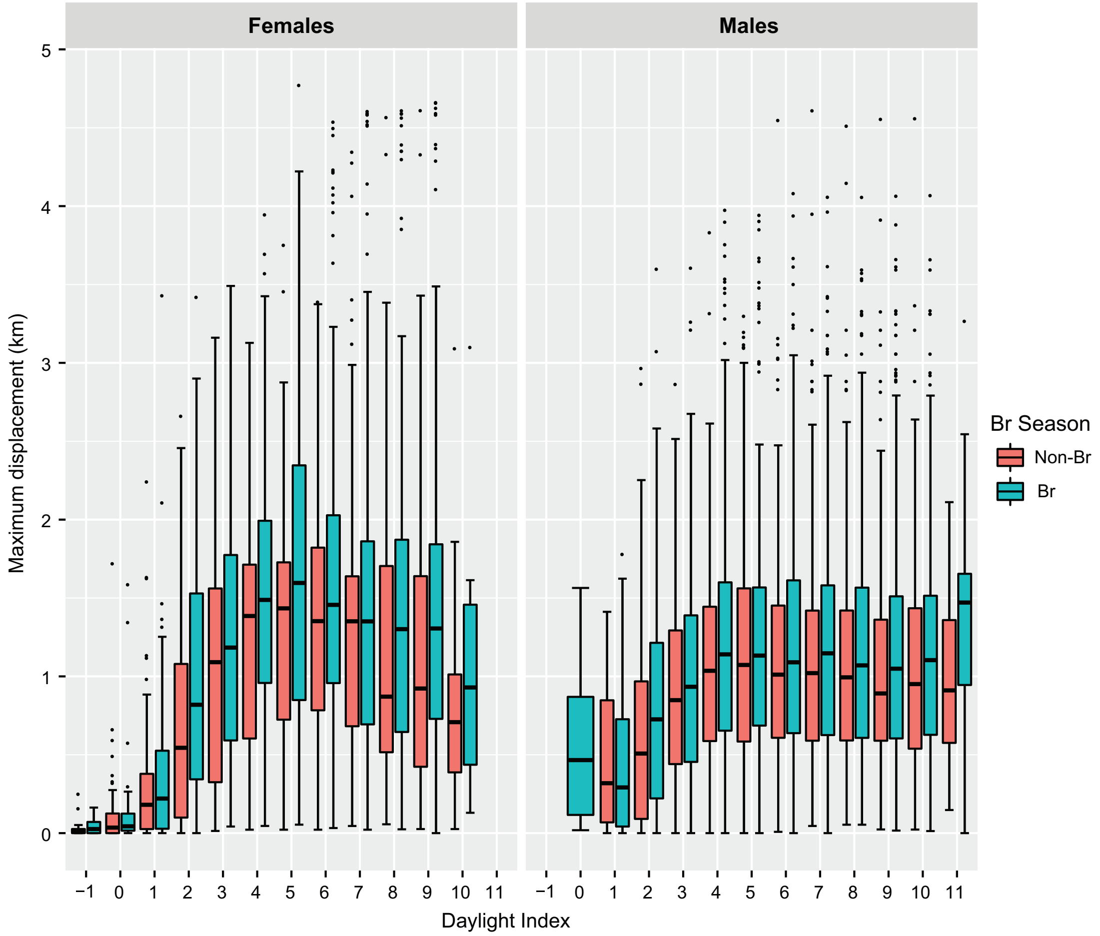

Fig. 5 Influence of sex and breeding period (red: non-breeding, blue: breeding) on the maximum displacement travelled by adult territorial individuals

the significant seasonal effect detected in their daily activity patterns because the greatest distance of maximum displacement, cumulative distance and hourly distance travelled were observed in spring -especially for non-territorial birds -, coinciding with the peak of the breeding period, whilst the shortest were realized in fall during the non-breeding period (Fig. 7). However, our results only showed a significant effect of the breeding period on the cumulative distance travelled. Reproductive failure is a factor which should also be considered because it would allow the vultures to travel further afield, especially during March and April, when reproductive failure rates (hatching period and first days of the chick) are at their highest.

The influence of season has been generally evident in other studies of the circadian rhythm of birds [24, 47, 48], because variations in the quantity and intensity of solar radiation throughout the year determinate the timing of a bird's circadian behaviour [49], and conditioning intrinsic factors such as the speed of migration [50]. Seasonal effects can also influence external factors such as variation in carrion food availability due to seasonal transhumance of livestock [17], thus shaping vultures' daily activity patterns, and biasing the performance of solar powered GPS transmitters [51]. We detected a seasonal influence on the values of the distance covered estimators, the longest distances being recorded in spring. Flight activity pattern seems to increase similarly

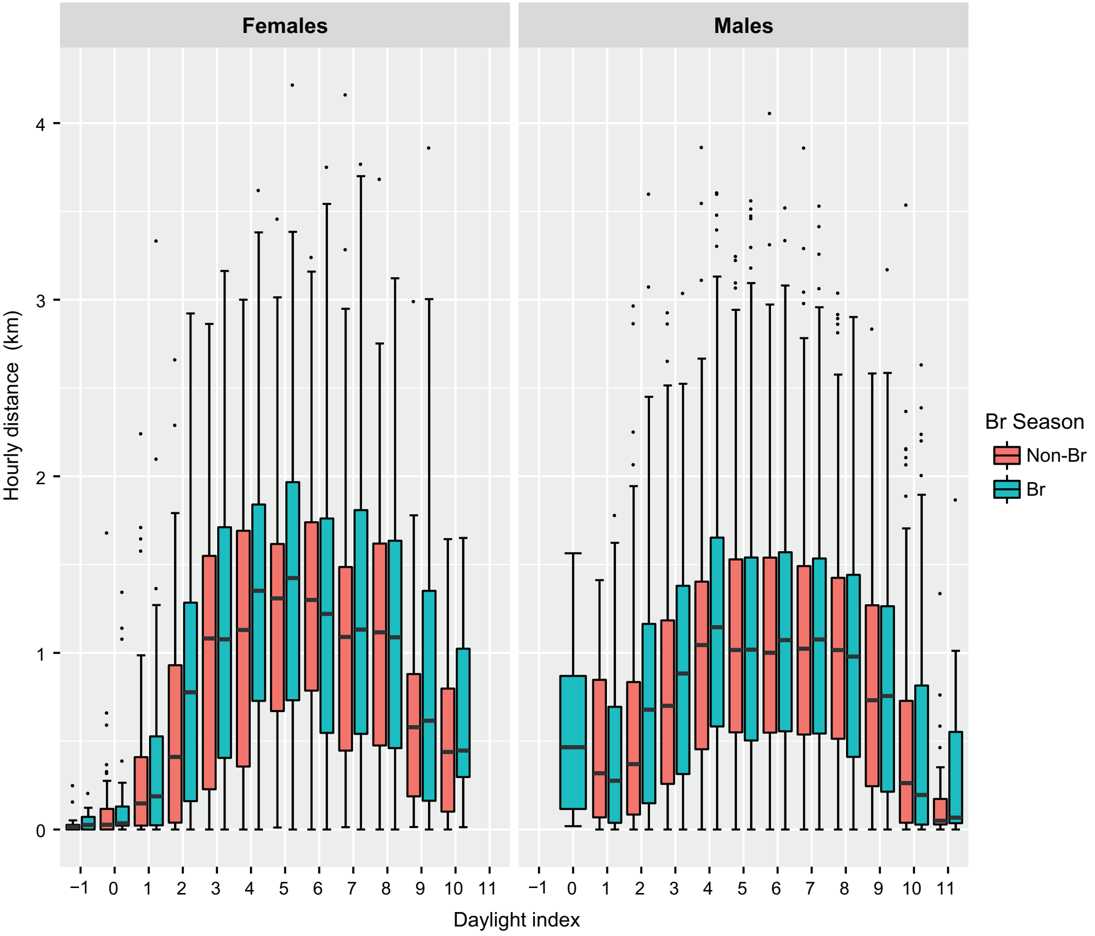

Fig. 6 Influence of sex and breeding period (red: non-breeding, blue: breeding) on the hourly mean distance travelled by adult territorial individuals

Table 1 Linear mixed models to explore the factors influencing the distance covered estimators (maximum displacement, cumulative distance travelled and hourly distance)

Model	Factors	K	AICc	ΔAICc	W
Maximum displacement	*Territ* Sex+Season+DI*	10	101,320.8	0.00	0.99
Cumulative travelled distance	*Territ+Season+DI+Sex+Br_S*	10	107,447.1	0.00	0.65
	Territ + Season + DI	8	107,449.3	2.28	0.21
Hourly distance	*Territ+Season+DI*	8	89,516.3	0.00	0.64
	Territ + Season + DI + Sex	9	89,518.2	1.93	0.24
	Territ + Season + DI + Sex + Br_S	10	89,519.6	3.29	0.12

Factors included were territorial status (*Territ*), daylight index (*DI*), climatic season (*Season*), breeding season (*Br_S*), and sex (*Sex*) and the simple interactions *Sex*Territ*, *Season*Territ* and *Br_S*Territ*. The model with the lowest AIC value (in italics) is the most parsimonious. K: total number of parameters (explanatory terms + random term + residual deviance); AICc: corrected Akaike information criterion; ΔAICc: difference between the AICc value for that model and the best model; and, W: Akaike weights on every season during the same daylight time (at the last third of the daylight) differentiating between the two territorial status. An elevated flight activity is maintained by non-territorial individuals some hours after astronomical sunset for every season, whilst territorial birds seem to sustain or even augment their activity pattern after dusk particularly in winter (but not in spring or summer), probably related with the reproductive period (Fig. 7). In addition, the flying fixes ratio registered in winter (37%) was higher than all of the other seasons (the lowest was logged in summer (32.5%), considering flying fixes > 1.39 m/s following Silva et al. [51]). This supports our aforementioned hypothesis that the energetic requirements of Bearded Vultures rise during the breeding period (winter and spring) combined with the decrease in of food availability in this time of year [17] which forces them to fly for longer periods and over longer distances. However, despite this, we did not observe a clear seasonal variation in the daily activity patterns of the territorial Bearded Vulture flight behaviour.

While timing of sunrise and sunset determines the daily start and end of aerial activity in most obligate scavengers [52], Bearded Vulture is able to continue flying after the sunset. In fact, maximum air temperature and wind speed in temperate climate ecosystems, and thus the best wind uplift conditions for large avian scavenger flight, occur in summer during the hours around noon [49, 53]. So, even while the greatest chances of finding profitable carcasses are in the early morning hours because ungulate mortality peaks during the night [20, 24], the highest displacements of Pyrenean Bearded Vultures are recorded during the second half of the daylight, regardless of season, by virtue of their energy-efficient foraging flight and reduced wing loading in comparison with other vulture species [15, 49, 54]. This allows Bearded Vultures to profit the later daylight hours of convective updraughts to return to the nest or to search for a roosting site [15]. Moreover, the specific diet of this vulture—based mainly on the exploitation of bone remains, a resource which is preserved long time after a carcass has died—[29, 55] releases it from interspecific competitive pressures, reasonably diminishing the impact of the optimal time to exploit carrion in the species daily feeding habits [22]. All these physiognomical and ecological attributes enable Bearded Vultures to solve the trade-off between the ideal feeding time and the availability of wind resource performing the furthest travelling distances during the afternoon, even though the greatest hourly distances travelled are achieved at mid-day.

The sex of an individual influenced the longest distances covered in a day and our results showed intra-sexual, but not inter-sexual, differences for this estimator. Concretely, both adult non-territorial females and males travelled significantly farther in a day than territorial individuals. However, an unexpected asymmetry was detected between the sexes for the cumulative distance travelled. Females covered significantly more kilometres than males during a day, consistent with the trend in spatial use already described for the same Pyrenean Bearded Vulture population [38]. Several studies of avian species underpin this inter-sexual spatial pattern discordance relating to the behavioural differences in reproductive roles between the sexes [56, 57] as well as individual or even sex-size variations [24, 58, 59]. However, the Bearded Vulture is a monomorphic species and parental care is divided equally between the male and female [60], and therefore we would predict similar energy requirements for both sexes. A possible explanation of this sexual difference in daily distance covered during the breeding period could be due to the raised female energy demand resulting from the egg biosynthesis and the reproductive jeopardy if this is not met. In spite of the differences in daily spatial behaviour between the sexes, there are no differences in the temporal daily flight patterns between them.

According to our findings, the daytime flight behaviour of the Bearded Vulture does not follow a random pattern. The external factors studied (daylight index and season) strongly regulate the daily flight activity, while internal factors such territorial status, sex, and breeding period mould its flight dynamic. The synergy between both categories of factors enables the Bearded Vulture to confront the trade-off between travel costs—mostly constrained by weather conditions—and energy requirements. In addition, territorial status was, predictably, the most influential of all the internal factors studied. Other interesting drivers of flight behaviour have come to light, such as the relationship between territoriality and breeding season and the influence of sex in this monomorphic species, suggesting that these synergistic and intrinsic factors may play a currently unexplored role in this species' flight patterns.

Understanding the daily movement ecology of the Bearded Vulture is essential for predicting its future dispersal, foraging and reproductive patterns. These data are interesting for developing future conservation strategies (such as those related to the management of Supplementary Feeding Sites) both in the Pyrenean region and other ecosystems with distinct climatological conditions or food availability. Indeed, given the variety of mortality risks faced by this species and its high adult mortality rate [32, 36, 61], information on the daily distances travelled by juveniles during their early dispersal stages might help to improve the design of future conservation measures.

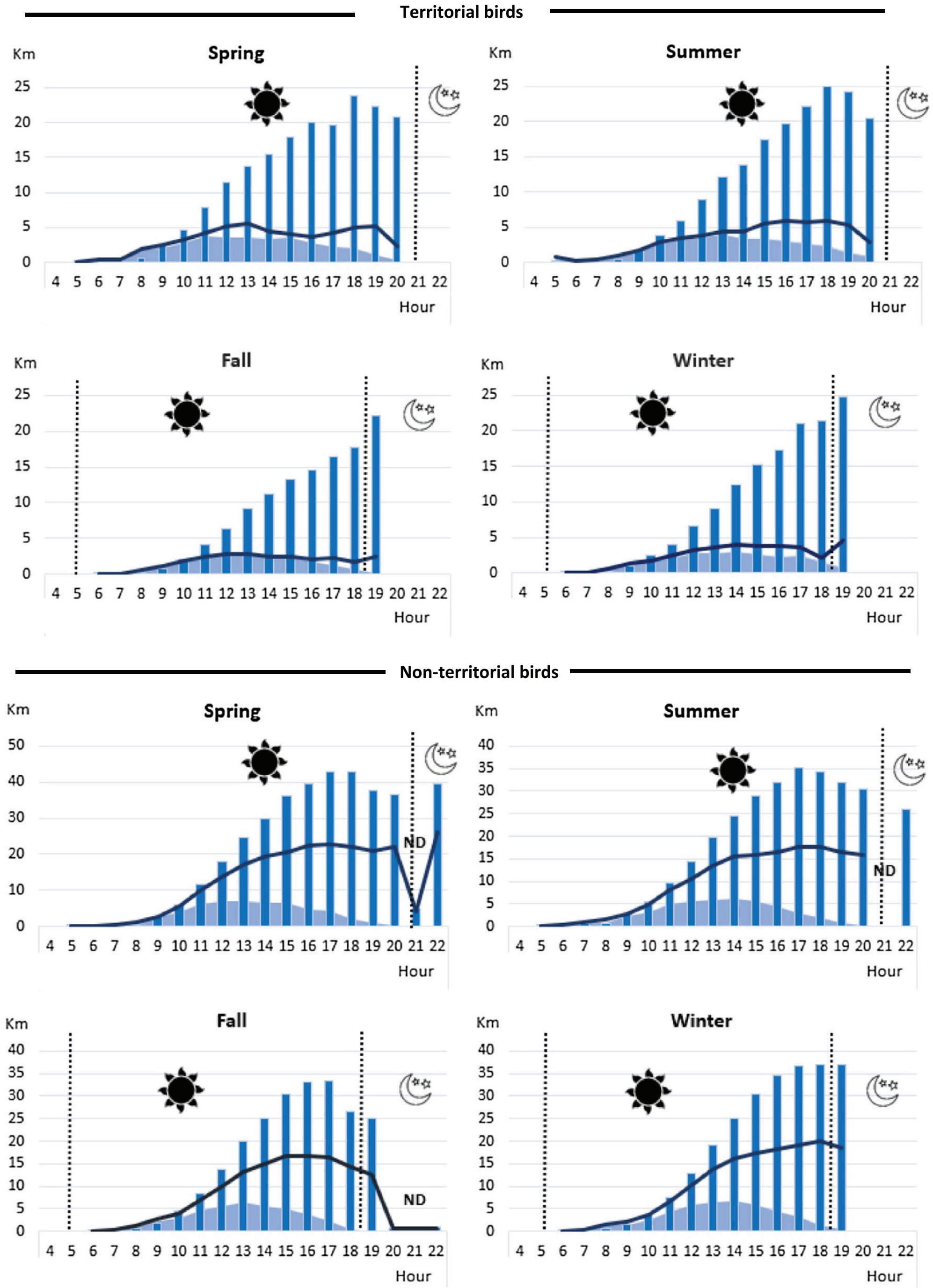

Fig. 7 Influence of season and territorial status on Bearded Vultures flight activity represented by three estimators: maximum displacement (line chart), cumulative distance travelled (bar chart) and hourly distance travelled (area chart). *ND* not enough data available at that level. Astronomical twilight is marked—if it is present—with a dashed line. The sun is placed at noon time

Conclusions

This study is the first detailed daily activity analysis developed on the Bearded Vulture improving our knowledge on the movement ecology of this threatened species trough a finer spatio-temporal information about the daytime flight routine of the species. Our findings show that the main drivers of the Bearded Vulture daily flight activity are daylight time, season, and territorial status of the individual. This agrees with several authors' hypothesis supporting the daylight time as the most influential factor of all of the external factors determining circadian behaviours [62]. Pyrenean Bearded Vultures covered the furthest travelling distances during the afternoon. Moreover, internal factors as territorial status had a remarkable effect on the daily activity patterns of the vulture. Non-territorial Bearded Vultures presented the greatest daily flight patterns. Both individual's sex and breeding period mildly shaped the flight activity resulting in the females and breeding individuals travelling further afield than males and non-breeding individuals.

Additional files

Additional file 1: Mean ± SD values for the three twilight phases, the solar noon and the daylength for each season in UTC Time (hh:mm). Source: www.timeanddate.com.

Additional file 2: Figure S1. Frequencies of fix per daylight percentage range. **Table S1.** Table of frequencies of fix per daylight percentage range. **Figure S2.** Frequencies of fix per season considering UTC Time.

Additional file 3: Standardized weights of all the predictors introduced in the linear mixed models performed (N models).

Authors' contributions

All authors designed the study. AM conducted the fieldwork. RGJ wrote the manuscript with contributions from JMPG and AM, RGJ performed exploratory analysis and JMPG executed statistical analysis. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The datasets used and analyzed during the current study are available from the corresponding author on reasonable request.

Consent for publication

Not applicable.

Ethics approval and consent to participate

The study was conducted in full compliance with Spanish laws and regulations. Captures and blood sample collection were carried out in compliance with the Ethical Principles in Animal Research. All experimental protocols were approved by the Catalan Autonomous Government and the Spanish Ministry of Agriculture and Fisheries, Food and Environment (References 15546 and 25.306).

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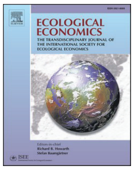

ANALYSIS

Economic valuation of non-material contributions to people provided by avian scavengers: Harmonizing conservation and wildlife-based tourism

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ABSTRACT

Nature's contributions to people (NCP) are fundamental to human well-being. In particular, non-material NCP, defined as effects on personal perspectives which enhance people's quality of life, are currently the most abstract and least well-defined NCP. Avian scavengers are a globally threatened guild that plays a key role in our society but currently only valued for their NCP of disease control and carcass removal. We describe the first economic valuation of the recreational and educational experiences brought by avian scavenger-based tourism in Spain, concretely, at vulture supplementary feeding sites (SFS) in the Pyrenees and their important contribution to the incomes of the local human population. Between February 2018 and January 2020, we collected information on the management and characteristics of 53 (c. 80%) of the Pyrenean SFS using telephone interviews and questionnaires. We estimated that photography and avian scavenger-watching at SFS produce an average of US $4.90 ± 2.67 million annually, including US $2.53 ± 1.36 million in direct economic benefits to the local population. Using a conservative economic approach, this study is one of only a few to value some of the important non-material contribution provided by avian scavengers to our society. Our study also suggests that further research on non-material NCP provided by avian scavengers at SFS is needed. Finally, we discuss the delicate balance between recreational experiences arising from wildlife-based tourism and biodiversity conservation, contrasting the contribution of SFS to the income of local human populations against the problems they raise for vulture conservation.

1. Introduction

Ecosystem services are the direct and indirect benefits that humans obtain from ecosystems and therefore play an essential role in human well-being. They have received increasing attention over the last 20 years, especially since the term was popularized by the Millennium Ecosystem Assessment in 2005 (MA, 2005; Costanza et al., 2017). However, in 2017, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) introduced a new and closely related concept, Nature's Contributions to People (NCP) (Christie et al., 2019). NCP have been defined as all the contributions of living nature to people's quality of life, including both the positive (i.e. beneficial) and negative (i.e. detrimental) inputs that people obtain from the ecosystems (Díaz et al., 2018). Each specific cultural setting would condition their classification through three partially overlapping groups: material (actual goods provided by nature, such as food, energy, or medicinal products; e.g. Bondé et al., 2020), non-material (the effect of nature on the subjective or psychological aspects supporting people's quality of life such as recreational, aesthetic, learning, and inspirational experiences; Chan et al., 2011), and regulating NCP (functional and structural aspects of organisms, ecosystems and biodiversity that contribute to society's well-being by changing the environmental conditions which affect humans and regulate the other two kinds of NCP; e.g. Martín-López et al., 2019) (Díaz et al., 2018).

Only during the last two decades have non-material NCP (i.e. cultural services) been socially recognized. They are very difficult to assess, especially because they appear intangible and usually manifest as indirect benefits (Hernández-Morcillo et al., 2013; Milcu et al., 2013).

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Consequently, they have been given little or no scientific, social, or economic value, leading to some conservation decisions (e.g. ignoring local knowledge, and/or people perceptions) with serious negative consequences for our environment and society (Butler and Oluoch-Kosura, 2006; Zografos and Howarth, 2010; Barua et al., 2013). Since the end of the 20th century, one of the most common methods for trying to place a true value on these non-material NCP have been economic evaluations of recreational activities (Martín-López et al., 2009; Everard and Kataria, 2011; Milcu et al., 2013). Although the published information on NCP valuation is increasing, some important species or specialized guilds are frequently ignored by the general public and undervalued by scientific educationalists and the specific stakeholders directly related to them. Such is the case of the vertebrate scavengers (Moleón and Sánchez-Zapata, 2015; Cailly Arnulphi et al., 2017), a guild with a fundamental role in many ecological processes, functions, and ecosystem services (Moleón et al., 2014; De Vault et al., 2016).

Humans and vertebrate scavengers, including obligate scavengers (such as vultures, whose food comes exclusively from scavenging) and facultative scavengers (such as raptors, corvids, or mammalian carnivores), have been directly interdependent since the Late Pliocene, when our ancestors started to eat meat. Indeed, the NCP provided by this guild have benefited our species from the very first biped hominids (Moleón et al., 2014; Morelli et al., 2015). For example, humans have obtained different ornamental resources, such as feathers, from scavengers (a material NCP) (Finlayson et al., 2012). Regarding regulating NCP, scavengers' ability to dispose of waste and organic matter preventing disease transmission to humans (e.g. brucellosis, tuberculosis, or anthrax) and their role in the nutrient cycle in processing carcasses have been widely recognized as providing substantial benefits to human health (Swan et al., 2006; Markandya et al., 2008; Ogada et al., 2012a; O'Bryan et al., 2018), contribute to the long-term maintenance of soil structure (Wilson and Wolkovich, 2011; Beasley et al., 2015) and reduce environmental pollution (Markandya et al., 2008; Morales-Reyes et al., 2015). However, very few studies have highlighted the importance of scavengers in the provision of non-material NCP, for example where scavengers form the basis for spiritual experiences (rituals and celebrations), wildlife-based tourism (recreational experiences) or supporting personal identity (the satisfaction derived from knowing that a particular species exists) (see e.g. Becker et al., 2005; Morelli et al., 2015; Aguilera-Alcalá et al., 2020). Indeed, these cultural values are widespread in human societies and intertwined, connecting all NCP with each other.

Terrestrial vertebrate scavengers (especially obligate scavengers and large mammalian scavengers) have been declared one of the world's most endangered guilds in recent decades (Hoffmann et al., 2010; Ogada et al., 2012b; Ripple et al., 2014). Old World vultures and condors are the most globally threatened avian functional guild due to the recently suffered severe declines in many of their populations across the globe (Buechley and Şekercioğlu, 2016; Safford et al., 2019). To mitigate these sharp population declines, many conservation and population rescue plans have emerged (Astore et al., 2017; Botha et al., 2017). Among other remedial initiatives, supplementary feeding sites (SFS, also known as "feeding stations" or "vulture restaurants") have been established. Feeding stations provided a conservation tool to: fight illegal poisoning and reduce lead or pharmacological toxic risks (the main threats to vulture mortality); encourage species dispersion into new areas; improve breeding success and survival; remedy population declines; and to compensate for decreases in carcass availability resulting from sanitary policies developed to reduce bovine spongiform encephalopathy (Houston, 2006; Donázar et al., 2009). The balance of pros and cons of the specific management and uses of this conservation tool has been broadly discussed (Piper, 2005; Donázar et al., 2009; Cortés-Avizanda et al., 2016). For instance, the initial conservation reason for constructing an SFS has recently been corrupted by the increasingly popular tendency to build SFS strictly to serve tourist interests (e.g. birdwatching, wildlife photography) with the consequent economic benefits. In fact, the wildlife-based touristic value of vulture breeding areas and SFS has become a notorious source of income for many local economies (Anderson and Anthony, 2005; Piper, 2005; Ferrari et al., 2009). Perhaps surprisingly, the scale of the economic benefits of these non-material contributions that vultures provide at SFS has not been quantified before.

Spain is one of the most popular European countries for ornithological tourism specifically to see scavengers, particularly vultures, since it hosts most of the European vulture population (Margalida et al., 2010). Concretely, there are more than 90% of the European breeding populations of cinereous (*Aegypius monachus*), 90% of the griffon (*Gyps fulvus*), 47% of the Egyptian (*Neophron percnopterus*), and 63% of the European bearded vultures (*Gypaetus barbatus*) (Margalida et al., 2010; Del Moral, 2017; Del Moral and Molina, 2018a; Del Moral and Molina, 2018b; Margalida and Martínez, 2020). Spain has also established a large network of SFS since the 1980s, most being built initially as management-conservation tools recurrently applied by administrations (Moreno-Opo et al., 2015). We based our study in the Spanish Pyrenees, taking advantage of the fact that it is inhabited by all four European vulture species and also has a wide network of SFS, and where efforts have been made to try to harmonize the conservation purposes of SFS with recreational experiences and environmental educative activities through wildlife-based tourism.

The main goal of this study was to evaluate the economic benefit of non-material NCP provided by the European avian scavengers through recreational and educational activities (i.e. wildlife-based tourism) at the SFS in the Pyrenees. In addition, we discuss the sensitive trade-off between recreational experiences associated with wildlife-based tourism and conservation in a situation in which, on the one hand, SFS provide important contributions to local human population's incomes and, on the other, must ensure the conservation of European avian scavengers.

2. Material and methods

2.1. Study area

The Pyrenees is a $>$ 400 km long mountain range located on the border between southern France and northeastern Spain. There are currently at least 67 working SFS in the Pyrenean and Pre-Pyrenean area (seven in France and 60 in Spain) each with very different spatial and temporal feeding routines. Of these, 29.85% ($n = 20$) located in the eastern Spanish Pyrenees (Aragon and Catalonia autonomous communities) receive visitors (people who visit a hide or viewpoint specifically linked to an SFS normally under the guidance of the organization in charge of the SFS). Only the entrance of the field technicians directly to the SFS is allowed. Hides built, managed, and exclusively intended for photography were not included either in this study or in the descriptive statistics. All SFS considered here had been created for the principal purpose of scavenger conservation.

2.2. Data collection

Data were gathered between February 2018 and January 2020. Data collection was systematically divided into two main stages. First, basic information on the management and structural characteristics of each SFS was collected through telephone interviews with the managers of 53 (79.1%) of the Pyrenean SFS, 18 of which were part of the 20 SFS that formally receive visitors. The information obtained included the mean number of people visiting each SFS each year and the price, if any, of entrance and/or the main recreational activity offered (birdwatching, photography and/or educational activities). Of those SFS accessible to the public, 35% ($n = 7$) were inside a protected area (national or natural parks). Of these, we could only find data on the actual number of visits for two of them, so we did not include the other five (marked as "not considered" in Table A in the Appendix A) in the economic analysis. This was because, unlike the other 15 SFS receiving visitors, we could not assume that the main reason for all public visits to the parks (some of which receive up to 561,000 visitors per year; GenCat, 2019) was mainly to enjoy watching avian scavengers (Tables 1 and A).

Second, 94 survey questionnaires (either in English or Spanish) were randomly distributed among 9 of the 15 SFS to gather information on the travel, subsistence (food, lodging), and opportunity costs (see Section 2.3(5)) incurred by each visitor (i.e. the trip characterization). Given the diverse management dynamic of the SFS (only two of the SFS surveyed offered scheduled visits), the questionnaires could not be made face-to-face. At each SFS, a hard copy of the questionnaires randomly distributed to each visitor at the end of the recreational and/or educational activities and they were fulfilled by each visitor. Questions covered information about where people came from, the duration of the entire trip (travel time / time spent at the SFS / time in the general area), the place (s) where they were lodging, the meals they were eating away from their accommodation, whether they came alone or with their children (how many), and their socio-economic status (monthly income) (see Table 1). We met the ethical standards governing social surveys by informing respondents in writing at the beginning of the questionnaire that their participation was voluntary and that their anonymity would be ensured.

2.3. *Economic valuation*

First, we used the descriptive nonparametric Wilcoxon and Mann-Whitney *U* tests (α = 0.05) to explore if there were significant differences in the mean trip expenses and specific trip parameters such as distance travelled (distance by road in km) between the trip departure point and the SFS visited and trip duration (see Table 1) between visitors who started their trip from anywhere in Spain (national visitors) and those with departure points outside the country (international visitors). We used the Kruskal-Wallis test (α = 0.05) to determine whether there were substantial differences in trip expenses depending on the SFS visited.

Table 1
Information obtained from telephone interviews with SFS managers and from the SFS visitors surveyed (questions included in the questionnaires are shown). The last column shows the possible answers to the multiple-choice questions.

Source of information	Type of information	Specific questions	Close-ended questions
SFS managers	Management characteristics of the SFS	Main activity offered	Birdwatching Educational Photography
		Mean number of annual visitors	–
		Entrance cost (in €)	–
SFS visitors	Trip characterization	Where did you start your trip? (city and country)	–
		Trip duration, including travelling time (in days)	–
		Accommodation	Hotel Hostel Apartment Camping Rural house Relatives' or friends' house Own house
		Meals usually eaten outside accommodation	Breakfast Lunch Dinner
		How many people are travelling with you?	–
		Are there any children travelling with you?	Yes / No
		If yes, how many?	–
	Socio-economic status	Average monthly income	< 1000€ 1000–2000€ > 2000€

Second, we calculated the specific costs of each trip parameter:

1. *Travel costs*. For national visitors and those coming from southern France, we calculated the travelling costs considering the distance by road (km) between the departure point and the specific destination (the SFS visited). For international visitors and those from the Spanish Islands (considered national visitors in the non-parametric tests), we first calculated the distance by road (km) from their home to the closest city with an airport and then estimated the mean cost of a plane ticket from that airport to Barcelona. Then we calculated the distance by road (km) from Barcelona to the destination SFS and added the cost of renting a car (estimated mean US $17.4 per day after consulting the prices on several car renting websites in the Barcelona airport area). We calculated the cost of a round trip in all cases and used US $0.22 /km (0.19 €/km) as the cost of car travel expenses according to Spanish income tax claim guidelines (Orden EHA/3771/2005, 2021) and assumed the shortest route by road taking into account any necessary road tolls.
2. *SFS entrance cost*. We collected data on the specific entrance price, if any, of the different SFS.
3. *Accommodation costs*. We calculated a mean price for each type of accommodation for all the SFS surveyed by averaging the prices of three in the same category, for the high and low seasons separately, to arrive at a mean price per night for each type of accommodation. The overall mean price of US $33.7/adult and US $10.5/child per night was applied to those people who did not indicate their accommodation in the questionnaire ($n = 5$) (Table B in Appendix A).
4. *Food costs.* We asked which of the three main daily meals the visitors were eating away from their accommodation, and then used that information combined with some approximate prices per meal in Spain (Table C in Appendix A). Children's costs were always estimated separately from adults' costs both for the accommodation and cost of meals.
5. *Opportunity costs.* We included the opportunity cost of the time spent on the entire trip, taking four hours for the arrival and departure days and eight hours for each other day spent away. The opportunity cost is usually measured as the monetary value of what an individual could have been doing with their time instead of the activity they are on, generally calculated as 25% of the income of a working hour, at the given individual's salary (McKean et al., 1995; Becker et al., 2005). Working hours were assumed to be 40 h/week, as they would be in a normal full-time job in Spain. Children were omitted from the opportunity cost estimates.

We did not include the estimated cost of birdwatching and photographic equipment per visitor in the economic expenditure because we could not assume that the equipment had been acquired solely for scavenger-watching activities (especially for the cases where cameras were used).

Finally, we summed all these specific costs of each trip parameter for the entire trip to calculate the visitors' trip expenses and then computed a mean trip expenses/visitor value, as follows:

$$\text{Visitors'trip expenses} = \text{T} + (\mathbf{SFSe} + \mathbf{A} + \mathbf{F} + \text{O}) \times \text{trip duration.}$$

(Children's rates, shown **in bold**, were added if the visitor declared having made the SFS visit with accompanying children)

$$\text{Mean visitors'trip expenses} = \sum \text{Visitors'trip expenses} \Big/ \text{n.}$$

where: travel costs (*T*); SFS entrance (*SFSe*, which depended on the trip duration only for SFS offering a photographic activity, but not for the SFS offering birdwatching and educational activities, where we considered it as a fixed cost independent from the trip duration); accommodation costs (*A*); food costs (*F*); and opportunity costs (*O*). Costs were calculated in € and then translated into US $ (Table D in Appendix A), trip duration in days, and *n* represents the total number of visitors for which a visitor trip expense could be estimated ($n = 91$). Of these 91 visitors, four people did not respond to the trip duration question, so we assumed a minimum trip duration of two days based on the rest of the answers given in the questionnaire.

Based on the mean trip expenses per visitor and the mean annual number of visitors per SFS, we were able to estimate the annual expenses associated with the non-material NCP (recreational and educational experiences) provided by vultures at the Pyrenean SFS for which visits were allowed. We summed the total economic benefits estimated for the nine SFS surveyed and the estimated economic benefits for the other six, differentiating between the expenses resulting from visits made by nationals and international visitors to arrive at an average expense per person.

3. Results

3.1. SFS, visitors and trip characterization

We obtained a mean of 10 ± 4 completed questionnaires per SFS surveyed (range 3–17, Table A), whereas usable responses varied depending on the question, ranging from 76.6% ($n = 72$) answers giving monthly incomes to 98.9% ($n = 93$) answers giving the number of people who they were visiting the SFS with.

Of the respondents, 86.96% ($n = 80$ out of 92) were national visitors, coming mostly from the closest regions (Aragon and Catalonia, $n = 27$ and $n = 25$, respectively) within approximately 200 km of the SFS. However, national visitors came from all over Spain, 2500 km being the maximum distance travelled from the trip departure point (Canary Islands) to the SFS. The other 13.04% of respondents were international visitors starting their trip in a European country including Belgium, Denmark, France, Germany, Netherland, Hungary, Portugal, and the United Kingdom. The mean distance travelled by national visitors (mean ± SD: 543.57 ± 564.12 km) was significantly lower compared with that travelled by international visitors (2805.08 ± 933.07 km; Mann-Whitney *U* test, U = 17, $p < 0.001$; see Table E in Appendix A for median and range values).

The SFS entrance price ranged between US $0 and US $209 per day per person, depending on the specific SFS and the duration of the visit. Normally, the entrance price of an SFS offering a photographic recreational activity varies depending on the number of days spent visiting. The longer the stay is, the more economical the price per day becomes. The SFS offering birdwatching only frequently charge no entrance fee. Those promoting an educational activity have the most variable fees because are either linked to a museum with a nominal entrance price, managed by a nature conservation NGO which only accepts donations, or offer a paying guided environmental education activity.

Most visitors, 40.45% ($n = 36$) incurred no accommodation expenses because they stayed in their own homes or with friends. These options were almost entirely chosen by national visitors ($n = 35$; 97.22%). The other 59.55% of the respondents were nearly equally distributed between all the different types of accommodation, except rural houses (only one person chose this option) (Table B).

Visitors ate an average of 1.20 ± 0.79 meals away from their accommodation, lunch being the most frequent meal eaten outside; 74.39% ($n = 61$) of the visitors had lunch away from their accommodation, compared with 28.05% ($n = 23$) for breakfast or dinner.

We found significant differences in trip duration depending on the point of trip departure (national: 2.33 ± 1.67 days, $n = 76$ vs international visitors: 4 ± 2.27 days, $n = 11$) (Mann-Whitney U test, U = 218, $p = 0.008$; see Table E). Overall, 65.52% of the visitors ($n = 57$) spent only one or two days on their visit, most of them staying in their own home or with friends or relatives (57.89%; $n = 33$).

3.2. Economic valuation

We calculated the trip expenses of 91 visitors. The overall average expense per person per trip (i.e. mean visitor's trip expenses) was US $441.74 ± 372.70. However, there were significant differences depending on which SFS was being visited (Kruskal-Wallis test, $\chi^2 = 51.38$, df = 8, $p < 0.001$) ranging from US $46.09 ± 14.23 to US $791.13 ± 524.86 and depending on the departure point of the trip (Wilcoxon test, W = 88.5, $p < 0.001$). The trip expense was quite variable among visitors (Fig. A in the Appendix A), but on average it was higher for international (US $956.85 ± 425.33) than for national visitors (US $363.50 ± 353.40) (Tables D and E). Accordingly, the higher mean visitor trip expenses were spent in the SFS receiving higher proportions of international visitors.

The mean number of visitors was 812 ± 1,816 people per year per SFS (range 4–6,829 people depending on the SFS). The SFS receiving most visitors per year were those dedicated to educational activities, such as group guided visits around the SFS whose main focus was the vultures, or those linked to a nature conservation museum specializing in scavengers. In fact, when we excluded those SFS mainly promoting educational activities and look at those focusing on birdwatching and avian scavenger photography, we obtained a mean of 113 ± 137 visitors per year per SFS. The total number of people visiting the studied SFS in the Pyrenees in 2019 were 12,668 ($n = 20$, Table A).

We found an annual expense estimated at US $4,900,930.20 ± 2,629,779.10 accruing from the non-material NCP provided by European avian scavengers through recreational and educational wildlife-based activities at the SFS in the Pyrenees, comprising 32.13% in travel expenses, 22.93% in SFS entrance fees, 10.78% in accommodation expenses, 17.92% in food expenses, and 16.24% in opportunity costs (Fig. 1). This means that, in the region overall, at least US $2,530,350.26 ± 1,357,754.95 (51.63% of total annual economic profits; i.e. SFS entrance cost + accommodation expenses + food expenses) are injected annually into local Pyrenean communities thanks to recreational and educational experiences based on avian scavenger-focused tourism at SFS alone (Table D).

4. Discussion

4.1. The relevance of the economic valuation of NCP provided by avian scavengers

Our findings showed that the non-material NCP provided by European avian scavengers through recreational and educational activities (i.e. scavenger-based tourism) at SFS produces a relevant economic income to the Pyrenean community. On average, we estimated an annual economic value of US $4.90 ± 2.67 million; including US $2.53 million ±1.36 million of direct economic benefits to the local community (see Table D for results in Euros). It is important to note that this economic assessment is probably an underestimate because of our conservative approach to estimation of the individual trip expense parameters (e.g. car rental and food costs). In addition, accounting for the median trip durations of the national (two days) and international visitors (three-four days) estimated in our study (Table E) and the difficult access to the SFS (only available by road and not always waymarked), we assumed that the main reason of the visitors for doing the trip was to watch avian scavengers. Indeed, interestingly national visitors were willing to cross over half of the country (i.e. mean of 544 km) to arrive to the SFS just for a weekend visit, and, on the other hand, international visitors were willing to travel almost across the whole European continent (i.e. mean of 2800 km) to watch and enjoy avian scavengers at SFS (Table E). This is an interesting result in the case of Europe, where the distances between different countries is tiny compared with other continents (e.g. Africa or America), and also specifically in the case of the Pyrenees, a

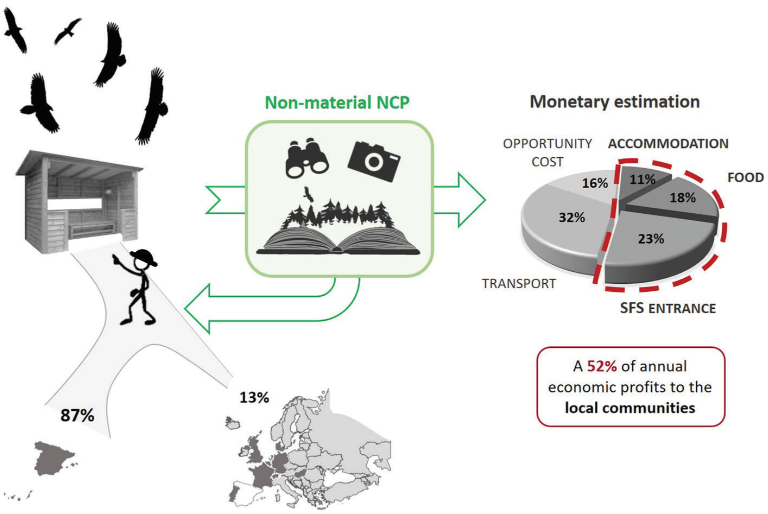

Fig. 1. Schematic representation of the economic valuation of the non-material contributions to people (non-material NCP) provided by avian scavengers through recreational and educational activities (i.e. wildlife-based tourism) at Supplementary Feeding Sites (SFS) receiving visitors in the Spanish Pyrenees. The main activities were birdwatching, photography and/or environmental education focused on scavengers. All these non-material NCP not only bring significant economic benefits to local communities, but also have an important effect on people's well-being in today's societies.

border area where visitors could be registered as "international", but come mainly from the South of France, having travelled only a few hundreds of kilometers. Moreover, this economic assessment is strongly dependent on the number of SFS visitors and, as it is a factor highly variable over time (on a yearly scale), even if we worked with yearly means of visitors, extrapolations to the future economic benefits obtained though scavenger-based tourism at SFS must account for this variability.

Because of an innate bird enthusiasm and the consequent investment that birdwatchers are willing to pay to practice this activity, birding is becoming "the fastest-growing and most environmentally conscious segment of ecotourism and the best economic hope for many beleaguered natural areas" (Salzman, 1995). Nevertheless, currently, there are very few studies that empirically assess the recreational (Becker et al., 2005, 2009, 2010), sanitary (Markandya et al., 2008) or environmental economic value (Margalida and Colomer, 2012; Morales-Reyes et al., 2015) provided by vultures. Thus, to our knowledge, this is the first economic valuation of recreational and educational experiences through avian scavenger-based tourism in a European country. Becker et al. (2005) estimated that 85% of the visitors to a nature reserve in Israel (i.e. Gamla) came specifically to view threatened griffon vultures, and that this activity produced a potential annual value of US $1.1–1.2 million. Then, also Becker et al. (2009) estimated through the travel cost method (TCM) an economic benefit of US $2.4 million and of US $2.94 million per year at two different nature reserves in Israel (i.e. Hai-Bar and Gamla, respectively) for the enjoyment of visiting the areas fitted with griffon vultures and a willingness to pay (WTP) for protecting this species of US $0.98 million at Hai-Bar and US $2.70 million at Gamla. Some of these sums resemble the benefits that we found were injected annually into local communities in the Pyrenees (US $2.35 million), which were generated uniquely through specific recreational/educational wildlife-based activities associated with the non-material NCP provided by the European avian scavengers. And that is only considering the SFS scavenger-based tourism of the region, leaving out of account specific avian scavenger festivals or guided photographic tours around the Pyrenean area, or even visitors looking for nature enjoyment beyond avian scavengers watching (further on detailed in Section 4.2). This is a significant amount, especially if we consider that, according to a Spanish Environmental Ministry report of 2017, the estimated national economic revenue of direct expenses derived from nature-based tourism (i.e. a tourism mainly motivated by the development of recreational, leisure, interpretive, educational and sport activities in nature) was on average 9 million € (i.e. US $10.47 million) (SGAPC and MAPAMA, 2017).

Markandya et al. (2008) calculated the human health cost of medicines, doctor remuneration, and work compensation associated with human rabies transmitted by feral dog bites in India at an estimated annual mean of US $2.43 billion. Such rabies transmission increased alarmingly almost three decades ago following the dramatic decline of vultures in India. This drastic and sudden vulture decline resulted in an increase of facultative scavenger populations (e.g. feral dogs), which led to an increase in dog bites, and consequently rabies cases in humans. On the other hand, the monetary value of regulating NCP is undeniably relevant considering that, in Spain, vulture populations have been estimated to dispose of an average of >8000 metric tons of animal biomass annually, saving the country an estimated US $1.6 million each year (Margalida and Colomer, 2012). Likewise, Morales-Reyes et al. (2015) estimated that natural removal of extensive livestock carcasses by scavengers would yearly save Spain 77,344 metric tons of CO_2 eq. emissions produced by the artificial collection and transport of this rotting matter to authorized plants and US $50 million yearly in payouts to insurance companies. Studies like these (including this present one) clearly demonstrate the important social and economic benefits that avian scavengers provide to humans.

Our results showed the need to do more analyses of this type —and not only from an economic perspective— to improve appreciation of the societal value of both the avian scavenger guild, and the individual scavenger species. Economic valuations, such as the presented here, provide interesting perspectives on the important roles played by the scavenger guild and ornithological tourism in Spanish society today. They can help to reveal the as yet often hidden benefits for human well-being arising from the non-material NCP provided by scavengers.

Given the relevant potential to improve the financial and environmental well-being of local communities that birdwatching tourism has demonstrated (Şekercioğlu, 2003), highlighting the revenue and financial savings provided by vultures' NCP could help to promote the conservation of these globally threatened species. However, the economic outcome should not be taken as the sole reference to valuate NCP, since it is largely determined by the prevailing temporal and socio-institutional contexts, which means that this value is neither universal nor invariable across time or cultures (Kallis et al., 2013). Economic valuation needs to be complemented by other innovative NCP evaluation and analysis methodologies, such as social multi-criteria analysis (Munda et al., 1994; De Marchi et al., 2000), or deliberative valuation

(Howarth and Wilson, 2006; Kelemen et al., 2013; Kenter et al., 2016).

Some recent complementary studies have emphasized the conservation values of the non-material NCP provided by vultures, highlighting their importance in addition to the purely economic benefits (Cortés-Avizanda et al., 2016; De Vault et al., 2016; Echeverri et al., 2020; Aguilera-Alcalá et al., 2020). In this context, further research is needed to evaluate also other non-material NCP provided by avian scavengers at SFS such as their contributions to aesthetic and learning values, sense of place, or spiritual awareness.

4.2. Characterizing avian scavenger-based tourism

We have evaluated a form of wildlife-based tourism aimed at a specific stakeholder group interested in enjoying a birdwatching, photographic, or educational activity focused specifically on the avian scavenger guild. However, we should not forget the interests not covered by our study. Non-specialist visitors to the region surrounding the study area and other national and natural parks also make an economic contribution: hunters and sportspeople, or those with a more generalist interest in nature and landscape-based leisure activities. They do not travel to protected regions specifically to see avian scavengers, but enjoy the general psychological, physical, and social benefits of being in contact with nature (Velarde et al., 2007; Abraham et al., 2010; Hausmann et al., 2020). That said, such visitors would likely profit from some of the direct and indirect non-material contributions provided by avian scavengers and appreciate their positive added value.

The recreational and educational experiences linked to SFS mainly promote domestic tourism, since 87% of the people visiting the SFS described here were national visitors (departing from somewhere inside Spain), while only 13% were international visitors coming from multiple European countries. National visitors came from all over Spain (travelling an average 544 km), although most were from areas surrounding the SFS; 87% of the national visitors came from a 200 km radius. The proximity of these visitors to SFS (mostly staying at their home or with friends) enabled an average stay in the study area of only two days. In contrast, international visitors, whose average journey was five-fold longer, spent twice as much time in the area. Interestingly, a study by Puhakka et al. (2016) in Finnish protected areas demonstrated that increasing length of stay, and especially the number of nights spent in the protected region, was positively correlated with an increase in the perceived well-being benefit felt by visitors, and the same is probably true for people visiting Pyrenean SFS. This relationship is probably linked to the feeling of escape from everyday routine that is one of the most common motivations in tourism (Iso-Ahola, 1982), and is probably an important subjacent reason for spending more than one day visiting an SFS, where the recreational and/or educational activities proposed (i.e. birdwatching, educational, or photography) could be easily done in a single day.

A longer stay also meant that international visitors spent significantly more on their trip expenses than national visitors. The most common plan for up to 65.52% of visitors was to sleep at a friend's or relative's house (an option generally preferred by national visitors) and to eat only one meal away from their accommodation each day. As many as 74.39% of the visitors ate lunch away from their accommodation during their visit, while fewer than half took breakfast or dinner out. This meant that restaurants and food markets earned almost double the money taken by landlords and hotels as a result of visiting tourists.

Our findings also indicate that the SFS promoting educational activities (more likely to be visited by families) received higher incomes each year than those only offering photographic activities (usually specifically aimed at keen photographers, foreign visitors, or those with greater purchasing power). This is because SFS with an educational agenda generally get more visitors and therefore obtain greater annual incomes despite their lower entrance fees. Beyond solely recreational experiences, some SFS also play an important role in providing non-material learning and inspiration NCP, values that start to be assessed in vertebrate scavengers by some scientists (Aguilera-Alcalá et al., 2020). Regardless of the recreational and educational offer, SFS can offer professional training opportunities for field technicians and provide valuable resources for population censuses, demographic studies, and tagging of avian scavengers for scientific population monitoring (e.g. Margalida et al., 2020). Some studies analyzing these specific non-material NCP have already been published (e.g. Brink et al., 2020), but more studies should be designed to quantify and evaluate the impacts of these cultural contributions. In any case, we should never lose sight of the fact that scavengers are the NCP providers and the SFS only some platforms (although not the unique ones) that allow us to enjoy and benefit from these non-material NCP.

4.3. Conservation value and economic balance of SFS

Previous research in two nature reserves in Israel performed a cost-benefit analysis of the conservation efforts to preserve the endangered griffon vultures (Becker et al., 2009), showing that to be economically efficient, SFS should help increase the vulture population by an average of 0.24–2.20 individuals per year. In addition, Donázar et al. (2009) estimated the cost of building a new SFS, either in France or Spain, at between US $21,900 and US $54,700, plus US $21,900 each year for its maintenance costs. If we project this data to the 67 SFS currently operating in the Pyrenees, it results in approximately US $1.47 million to US $3.66 million in building expenses and US $1.47 million in annual maintenance costs. Therefore, even taking into consideration the highest SFS estimated expenditures, a simple monetary balance shows that the mean annual economic benefit indirectly accruing to the Pyrenean human community from SFS avian scavengers-based tourism represents almost half of this initial building investment. Considering our conservative approach, at least US $2.53 million are recovered annually from visitor expenditure on accommodation, food, and SFS entrance costs. This is an interesting reflection especially if we take on board that most of the investment to build and maintain SFS originated with a conservation purpose are publicly funded in Spain.

Leaving aside the simple economics of SFS, their sensitive contribution to conservation strategies must also be considered (Brink et al., 2020; Cortés-Avizanda et al., 2016). While their potential benefits for wild fauna conservation and reintroduction are clear, a number of recent studies have shown that SFS are only useful conservation tools in specific contexts (i.e. when food availability is low, or there are risks from illegal poisoning) and during limited periods of time (i.e. critical breeding periods such as when chick are hatching and during their first days of life). Indeed, some studies have shown that the aggregating effect of SFS on the Pyrenean population of bearded vultures may cause reduced geographical expansion, declining breeding output, and the loss of habitat quality due to a conspecific attraction/aggregation and consequent shrinkage of territories and increase in intra-specific competition (Carrete et al., 2006; Margalida et al., 2016). SFS have been shown to cause monopolization of resources by certain species or individual age classes (Cortés-Avizanda et al., 2012; Duriez et al., 2012; Moreno-Opo et al., 2020), and can also act as sources of pharmaceutical rich residues in carcass debris from domestic livestock or promote the spread of pathogens from livestock to wildlife and the existence of multi-drug resistant pathogens (e.g. Plaza et al., 2020).

Therefore, even if SFS do act as a significant economic engine through nature-related sustainable tourism, we must not forget their original purpose of avian scavenger conservation. SFS are conservation feeding structures that may offer some exceptional times (i.e. only 30% of Pyrenean SFS) recreational and educational activities. Thus, SFS are not designed for tourism, but because of a conservation necessity. Consequently, they are ruled by conservation principles and when they are no longer needed, they stop working. In this sense, the scavenger-based tourism promoted by SFS could be considered such as the one linked to some no massed wildlife watching trips used to the population census, or environmental conservation projects that are partially funded and supported by volunteering work (Ellis, 2003; Wearing, 2004; Hughes et al., 2014), where the conservation practices would be equally developed even in the absence of tourists/volunteers and the main priority is the ecosystem preservation.

On balance, we need to ensure that potential cultural added value and economic and social benefits of SFS in fostering recreational activities (birdwatching, educational, or photographic opportunities) add to, rather than detract from, their conservation aims. To do so, a scientific lead is required to determine conservation priorities such as specific species needs, increasing carrying capacity in relation to food availability and expansion of scavenger species' geographic range (e.g. Margalida et al., 2020). Future management of SFS should therefore determine the priorities of the existing SFS and how best to harmonize conservation with recreational activities. Scientist should apply their professional expertise to supervising periodic monitoring of the continuing conservation value of SFS. This would be the only strategy to prevent at all times the possibility that this kind of wildlife-based tourism provoke short- or long-term behavioural disorders in the local wildlife (as it has already happened, for example, with sharks, marine mammals, polar bears, turtles, and birds in wildlife tourism experiences, e.g. Corkeron, 2004; Dyck and Baydack, 2004; Arcangeli et al., 2009; Landry and Taggart, 2010; McFadden et al., 2017; Cisneros-Montemayor et al., 2020).

5. Conclusions

In a society where the scavenger guild is frequently neglected regardless of its fundamental role in a multitude of ecological processes and key role in human well-being (Moleón et al., 2014; De Vault et al., 2016), there is an urgent need to make the NCP provided by these species known and put them in value. Our findings contribute to highlighting the important role of avian scavengers in providing non-material NCP through recreational/educational activities at SFS. To this end, this study supports last years' call to better integrate scavenger conservation into the IPBES (Martín-López et al., 2018 and improve our understanding of the link between the today's human society and the scavenger guild. Nowadays, wildlife-based tourism is an important source of income for many local communities. Touristic activities associated with SFS have been discussed by Anderson and Anthony, 2005; Piper, 2005; and Ferrari et al., 2009, which frequently point out that the necessary harmonization between nature conservation and economic development is all too often forgotten. While recognizing that SFS construction should always follow conservation needs, and that scientific monitoring is necessary to constantly evaluate their usefulness as management tools, multiple cultural experiences based on the non-material NCP of avian scavengers can be promoted as means of increasing people's quality of life and generating local revenue. Birdwatching, educational, or photographic activities enrich the recreational experience of visitors to SFS, provide added cultural value to the regional landscape, and make a real contribution to the income of local communities. Future research in this area should seek to discover more about the potential value of SFS and the social value of iconic species as providers of non-material NCP, including the role they play in shaping visitors' perceptions of the scavenging fauna.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

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APPENDIX II: COMPLEMENTARY PUBLICATION

This is a published article complementary to the thesis topic by García-Jiménez *et al.*: García-Jiménez, R., Martínez-González, J. M., Oliva-Vidal, P., Piqué, J., Sesé, J. A., & Margalida, A. (2020). Nocturnal flights by Bearded Vultures *Gypaetus barbatus* detected for the first-time using GPS and accelerometer data. *Bird Study* **67**(1), 135-141. https://doi.org/10.1080/00063657.2020.1781054.

BIRD STUDY
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Nocturnal flights by Bearded Vultures *Gypaetus barbatus* detected for the first-time using GPS and accelerometer data

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ABSTRACT

Capsule: We document previously undescribed nocturnal flight behaviour by Bearded Vultures *Gypaetus barbatus* using a combination of accelerometer and global positioning system (GPS) information.

Aims: To study the nocturnal flight activity of the Bearded Vulture and determine whether nocturnal flights could be linked to foraging behaviour.

Methods: We used both accelerometer and GPS location data of 11 Bearded Vultures in the Spanish Pyrenees along with 88 carcasses monitored with camera traps.

Results: Over half (55%, $n = 11$) of the individuals tracked were recorded flying between 0.7 and 6.1 km on at least 19 different nights, including 37% that occurred when less than 20% of the moon was illuminated. Bearded Vultures displayed feeding activity in only 8.2% of the 146 feeding events existing during the hour after dawn and the hour before dusk.

Conclusions: Our findings suggest that foraging benefits do not explain the nocturnal flights. Disturbances or adverse weather conditions may result in the abandonment of an overnight roosting site. This could also explain why individuals recovered in the field showed impact injuries.

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The nocturnal activity of diurnal raptors is a topic that has attracted increasing attention of ornithologists over the last century (Kendeigh 1934, Moore 1945). A recent comparative evolutionary analysis of 120 vision genes based on retina transcriptome sequencing suggested that a substantial visual modification was found in owls compared with diurnal raptors. The strong selection for nocturnal vision in owls may compensate for their loss of the genes involved in daylight or colour vision, suggesting a sensory trade-off (Wu *et al.* 2016).

With respect to diurnal raptors, nocturnal behaviour has recently been documented: during migration in the Osprey *Pandion haliaetus* (DeCandido *et al.* 2006); in Swainson's Hawks *Buteo swainsoni* and Turkey Vultures *Cathartes aura* (Riba-Hernández *et al.* 2012); during arrival at roosting sites in migrant Levant Sparrowhawks *Accipiter brevipes* (Yosef 2003); in Peregrine Falcons *Falco peregrinus* while hunting and feeding (Wendt *et al.* 1991, Rejt 2004a, 2004b); and in Lesser Kestrels *Falco naumanni* in both natural (Gustin *et al.* 2017) and artificial light conditions (Negro *et al.* 2000). However, most of these observations only provide anecdotal evidence of this unusual behaviour of a diurnal raptor, describing a particular event observed at night. Until recent years, technical limitations on monitoring diurnal avian species at night were probably the main factor preventing more extensive and regular tracking of nocturnal activity. Nevertheless, with the abundance of modern transmitters currently deployed on different species, we can easily determine the frequency of nocturnal activity displayed by diurnal species.

Vultures are diurnal scavengers which feed mainly on the carcasses of wild and domestic ungulates and forage over large areas (Houston 2001). The temporal and spatial unpredictability of carcass availability requires scavengers to forage over extensive areas during daylight (Ruxton & Houston 2004). However, observations of nocturnal activity suggest that vultures could occasionally visit carcasses at night. Several researchers have documented both New and Old-World vultures which have developed nocturnal scavenging behaviour (Naoroji 2006, Charette *et al.*

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2011, Mateo-Tomás & Olea 2018). Nocturnal feeding may benefit individuals by reducing interspecific and intraspecific competition and providing them with advantages over other diurnal competitors (Charette *et al.* 2011), but this behaviour also has potential costs. For example, the risk of being predated or injured at night could overtake the benefits of competition avoidance since avian scavengers appear to be less efficient at night than nocturnal mammalian scavengers whose nocturnal rate of net energy intake is normally higher (Ruxton & Houston 2004, Spiegel *et al.* 2013). In some species (including mammals), nocturnal activity appears to be strongly influenced by the amount of available moonlight (Russell 1991, Fernández-Duque 2003). In the case of diurnal raptors, occasional nocturnal flights by migrating raptors may represent an adaptive behavioural response to varied or changing weather or feeding conditions encountered *en route* (Russell 1991).

In general, large raptors use the energy of the landscape's updrafts to minimize travelling energy costs (Ruxton & Houston 2004). They exploit rising thermal uplifts, convection cells caused by the day-time heating of the land surface by solar radiation, and orographic uplifts, caused by deflection of air masses resulting from their collision against steep terrain (Bohrer *et al.* 2012). However, there are no thermal uplifts at night due to the absence of sun, so nocturnal flights will be more prevalent in lighter-weight raptors species (i.e. presenting a low mass to wing surface area ratio) whose flight strategies are not based on soaring but which profit mainly from orographic uplifts for flying.

Here we document the previously undescribed nocturnal flight behaviour by Bearded Vultures *Gypaetus barbatus*, using a combination of accelerometer and global positioning system (GPS) tracking data. In addition, we analysed diurnal and nocturnal feeding events on experimental carcasses with the help of camera traps, to establish whether nocturnal flights could be linked to the foraging behaviour of this species.

Methods

We marked 11 Bearded Vultures in the Spanish Pyrenees with GPS-GSM 50 g Ornitela and E-obs Bird Solar 57 g transmitters, between 2018 and 2019 (Table 1). The transmitters on each bird were programmed differently, but all recorded accelerometery and positional data 24 h a day from 1st October 2018 to 15th April 2019. We considered nocturnal flight activity as any spatial displacement during the night initially detected through GPS location data which were then confirmed, when possible, by acceleration data, to avoid the transmitters' horizontal inaccuracy. Based on our stationary tests the transmitters were accurate to within 4.5-25 m, as they were influenced by a rough orography and device orientation due to animal movement. Accelerometery can only provide information on a bird's behaviour during the precise seconds registered, while the GPS data can describe the general movement and spatial position of the animal through time. Distances travelled by vultures were calculated using basic trigonometry and flight speed was consequently the distance covered during the time between consecutive locations. We recorded a total of 38,601 nocturnal locations and 81,490 twilight locations, defining the beginning and end of the nocturnal period (also called 'night') based on the timing of astronomical twilight (data in www.timeanddate.com). We also monitored 88 carcasses of wild and domestic ungulates (Sheep *Ovis aries*, Goat *Capra hircus*, Wild Boar *Sus scrofa* and Roe Deer *Capreolus capreolus*) using camera traps in the same study area during December 2017 to January 2019, to determine whether nocturnal behaviour could be related to foraging movements.

The carcasses were monitored with Moultrie camera traps (M-990i GEN2 10MP and M-999i 20MP) programmed to take a set of three photographs when movement was detected and wait 15 s before taking the next series of photographs.

Results

Nocturnal flights

The nocturnal activity data recorded 55% (*n* = 6) of the tracked individuals flying between 0.7 and 6.1 km on at least 19 different nights (Table 1). We summarize the most striking cases below.

First, on 24th November 2018, a non-territorial adult (Coto) had been perched at a roosting site since 15:00 (Coordinated Universal Time – UTC). The night of 24th–25th November was defined from 18:04 to 5:18. From GPS and accelerometer records, it abandoned this roost between 03:00 and 3:30 on 25th November 2018 and flew over a small town before perching again at a new nocturnal roosting site between 3:30 and 4:01, where it remained until 10:00 (Figure 1(a, b)). It flew 4.9 km between the two roost sites, while 97% of the moon was illuminated.

Second, on 3rd March 2019 (when the night of 3rd–4th March was defined as 19:19–4:51), Coto travelled

Table 1. Detailed characteristics of the 11 Bearded Vultures *Gypaetus barbatus* tracked for nocturnal activity between 1st October 2018 and 16th April 2019 in the Pyrenees. The *periods* described are always delimited by the time of the two GPS locations covering the nocturnal flight, but do not necessarily strictly define the time during which the bird is actually flying (the bird's flight normally takes only a few minutes within these *periods of nocturnal activity*). For this parameter, italic letters correspond to strictly nocturnal times (defined through the end and onset of astronomical twilight), bold letters denote twilight times, and normal font letters correspond to periods including times of several of the aforementioned phases of the day. Universal Time Coordinated (UTC) time was used in all cases.

Name	Age class (years)	Transmitter type	Days tracked	Night Flight Activity	Night data provision (%)	Twilight (Dusk)	Night	Twilight (Dawn)	Periods of nocturnal activity
Bolisna	Ad (>7)	E-obs	197	**Yes** (2 nights)	0.29	17:26–19:01	19:01–5:14	5:14–6:48	**18:00–18:30** & 18:30–6:50
						17:51–19:25	19:25–4:43	4:43–6:16	*23:22–00:02 & 00:30–2:11 & 3:10–3:51*
Cano	Juv (0–1)	E-obs	197	No	2.03	–	–	–	–
Coto	Ad (8)	E-obs	187	**Yes** (8 nights)	11.76	16:48–18:23	18:23–4:51	4:51–6:27	20:31–5:00
						16:25–18:04	18:04–5:16	5:16–6:55	*19:30–20:30 & 2:30–4:00*
						16:25–18:04	18:04–5:18	5:18–6:56	*3:00–4:00*
						16:22–18:04	18:04–5:37	5:37–7:19	17:00–21:31
						16:34–18:16	18:16–5:42	5:42–7:23	18:00–23:01
						16:56–18:34	18:34–5:36	5:36–7:14	*19:00–20:00*
						17:31–19:05	19:05–5:08	5:08–6:42	18:01–23:00 & *23:31–00:30 & 3:00–4:00*
						17:45–19:19	19:19–4:51	4:51–6:25	*19:25–19:40*
Espluga	Juv (0–1)	Ornitela	197	No	11.90	–	–	–	–
Galbana	Ad (>7)	E-obs	69	**Yes** (3 nights)	4.52	16:20–18:02	18:02–5:32	5:32–7:14	17:30–19:00 & *19:00–20:00 & 1:00–3:00*
						16:20–18:02	18:02–5:33	5:33–7:14	17:00–19:00 & *19:00–20:31 & 23:31–1:31 & 2:30–3:30*
						16:21–18:02	18:02–5:33	5:33–7:15	*18:00–19:30*
Genova	Ad (>7)	E-obs	131	**Yes** (2 nights)	18.68	16:21–18:02	18:02–5:25	5:25–7:04	*19:00–19:30 & 23:30–00:00*
						16:34–18:16	18:16–5:42	5:42–7:23	*18:30–21:00*
Lluna	Juv (0–1)	Ornitela	197	No	10.37	–	–	–	–
Lluvia	Ad (>7)	E-obs	188	**Yes** (1 night)	18.72	17:47–19:21	19:21–4:48	4:48–6:21	*1:15–1:40*
Moleta	Ad (>7)	E-obs	155	**Yes** (3 nights)	9.75	16:59–18:37	18:37–5:35	5:35–7:13	*2:00–2:30*
						17:13–18:49	18:49–5:25	5:25–7:01	*2:30–3:30*
						17:11–19:46	19:46–3:12	3:12–4:47	2:20–4:21
Segarra	Juv (0–1)	Ornitela	197	No	1.87	–	–	–	–
Viu	Juv (0–1)	Ornitela	197	No	10.11	–	–	–	–

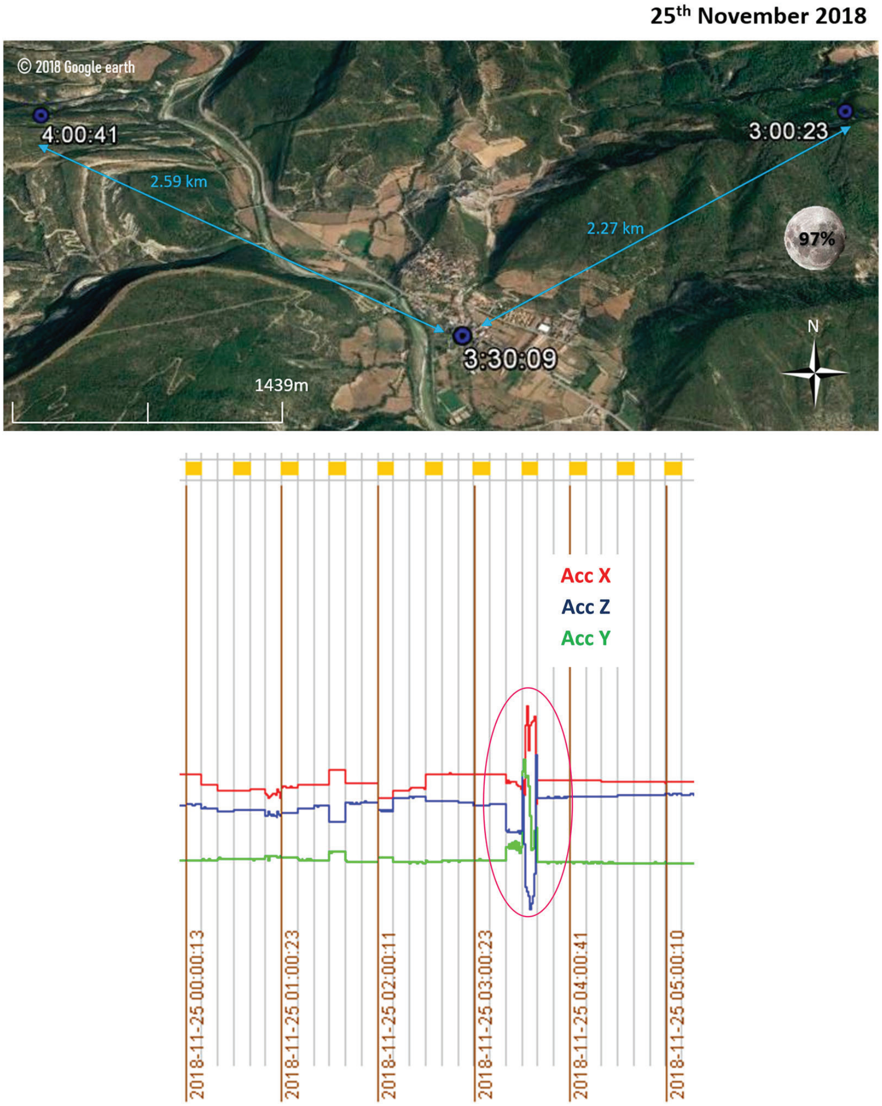

Figure 1. (a) Route of a nocturnal movement by a non-territorial adult Bearded Vulture *Gypaetus barbatus* derived from three GPS locations recorded in the Pyrenees (Spain) from 3:00 to 4:01 during the night of 24th–25th November 2018, when 97% of the moon was illuminated. Notice that at 3:30 the bird is clearly flying over a small town. It flew 4.9 km considering a straight-line distance. (b) Accelerometery data from an E-obs transmitter on 25th November 2018 between 00:00 and 5:00 visualized using the Acceleration Viewer program. At the top, the yellow marks show the GPS locations registered in parallel to the accelerometery activity. Red, green and blue lines correspond to the acceleration in the *X*, *Y* and *Z* axes respectively, reflecting a flapping flight moment at 3:30, while the GPS locations registered at the same time indicated a 'ground-speed' of 10.66 m/s.

6.1 km between 19:25 and 19:40 between two nocturnal roosting sites, again flying close to a small town and over farmland, while only 8% of the moon was illuminated. Coto achieved a minimum flight speed of 24.4 km/h, the highest minimum speed registered for all the nocturnal displacements analysed (Table 1, online supplementary Figure S9).

Third, a non-territorial adult (Galbana) occupied the same nocturnal roosting site located close to a village over three consecutive days from 15:30 on 11th December 2018 to 10:00 on 14th December 2018 (night defined from 18:02 to 5:33), despite the accelerometery and nocturnal GPS data indicating that it suffered unsettled nights, and made multiple short

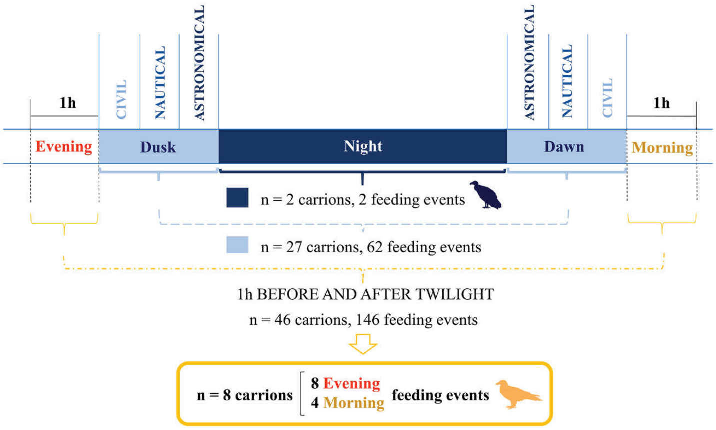

Figure 2. Feeding activity around nocturnal hours by avian scavengers of the study area. We detected 64 feeding events in 28 carrions at night and twilight periods, having place only 2 feeding events at night, both carried out by Griffon Vultures. Bearded Vultures presented feeding activity at the two periods of one hour after dawn (4 feeding events) and one hour before dusk (8 feeding events), considering a total of 146 feeding events recorded in 46 carrions for these two 1 h periods.

nocturnal flights over a maximum distance of 0.5 km. During those three nights Galbana travelled frequently between two slopes of the same valley, each time flying over both a road and a river, while the fraction of the moon illuminated was between 18% and 38% (Table 1, online Figures S10-S12).

In a fourth case, a territorial adult (Moleta) flew 3.9 km between 2:30 and 3:30 on the morning of 7th February 2019 (when the night of 6th–7th February was defined from 18:49 to 5:25), with only 3% of the moon illuminated, changing its night roosting site and coming to rest on a hill next to a small city inside its own territory (Table 1, online Figure S17).

Feeding behaviour

We recorded 847 feeding events at the 88 monitored carcasses. We detected feeding activity during the night and at dawn and dusk (both defined by the civil twilight) at 32% of the carcasses ($n = 28$), recording a total of 64 (7.6%) feeding events. Of these 64, only 3.12% ($n = 2$) occurred during the night at two different carcasses visited by Griffon Vultures *Gyps fulvus*, which were recorded feeding until 18:54 and 22:15 on 1st November 2018 and 15th December 2018, respectively. Analysing the two periods of one hour after the end of the dawn civil twilight and one hour before the beginning of the dusk civil twilight, we observed feeding activity at 52.3% ($n = 46$) of the carcasses monitored, documenting 146 feeding events; with only 8.2% ($n = 12$) carried out by Bearded Vultures. Consequently, we only detected Bearded Vulture feeding activity during the two periods of one hour after dawn and one hour before dusk (Figure 2).

Discussion

The cases of nocturnal flights by Bearded Vultures suggest that nocturnal flight could be more common than previously realized. In fact, Turkey Vultures have been documented flying at night when the moon was full and other environmental factors were favourable (Tabor & McAllister 1988). Our findings show that most of the tracked flights were in the area surrounding the nocturnal roosting site. However, in Pyrenean Bearded Vultures, during the non-breeding period maximum distance reached from the initial point per day ranged between 0.14 ± 0.21 km and 16.83 ± 21.01 km in the case of non-territorial adults, 3.72 ± 8.4 km for territorial adults, and 5.7 km in the case of juveniles (Margalida *et al.* 2016, García-Jiménez *et al.* 2018). Interestingly, all six adults equipped with transmitters in this study showed nocturnal flight activity, but this pattern was not observed among juveniles. Older birds could possibly have better knowledge of their territory and be more confident in flying at night. On the other hand, this age stratified behaviour may also be associated with differences in the transmitters' programming, since adult data records represented 64% of all the night fixes recorded, therefore it is possible that a more intensive nocturnal accelerometery and GPS tracking on juveniles would also detect some nocturnal activity within this age class.

Bearded Vultures probably benefit from their lighter wing loading (0.56 g/cm^2 for the Bearded Vulture, 0.60 g/cm^2 for the Egyptian vulture *Neophron percnopterus* and 0.77 g/cm^2 for the Griffon Vulture, Donázar 1993) which allows them to utilize weaker orographic uplifts than many other vulture species. Although the reasons behind nocturnal flights are still unknown, it seems that foraging benefits could be excluded as a general explanation. Our results suggest that Bearded Vultures almost exclusively fed by day, and that there was no link between their nocturnal flights and foraging behaviour. In addition, the specialized osteophagous diet of the Bearded Vulture seems to have certain advantages because bones remain edible for much longer periods than the soft tissues required by meat-eating vultures (Houston & Copsey 1994, Margalida & Villalba 2017). In fact, dry bones retain 90% of the protein found in fresh bones (Margalida & Villalba 2017) enabling Bearded Vultures to effectively store bones to be consumed at a later stage (Margalida & Bertran 2001, Margalida 2008).

Based on our results, it seems that although nocturnal feeding activity could be more common than expected in this diurnal species, the nocturnal flights of Bearded Vultures are not related to foraging behaviour. This contrasts with nocturnal feeding activities we observed on Griffon Vultures (3% of both nocturnal and twilight feeding events, $n = 2$, Figure 2), as it has been previously documented in this and other *Gyps* vulture species (Naoroji 2006, Mateo-Tomás & Olea 2018). It may be that some individuals are able to benefit from artificial light and are not concerned about flying close to villages or paved roads, even at night (on 58% of nights on which nocturnal flights were made by four adults, flights were close to, or over man-made structures). Presumably, disturbances (e.g. provoked by the presence of wild and domestic ungulates) or adverse weather conditions may result in the sudden abandonment of an overnight roosting site even when the moon is not at its brightest. In this sense, predatory animals (e.g. Red Fox *Vulpes vulpes*, Stone Marten *Martes foina*), might visit regularly nesting or roosting sites of Bearded Vulture because of the food they store (Margalida & Bertran 2003, authors pers. obs.) and cause disturbance at night. Indeed, 37% of the nocturnal flights analysed occurred when less than 20% of the moon was illuminated (online Table S1). This behaviour could explain the cases of individuals recovered in the field showing impact injuries (authors unpubl. data). Even though interspecific and intraspecific interactions frequently produce serious injuries (Blanco *et al.* 1997), nocturnal flights must carry an increased risk of collision accidents, especially at low moonlight intensities. Since we currently only have a small number of nocturnal flight records, we cannot yet distinguish between the different hypotheses discussed here, or be sure how common nocturnal flight behaviour is either in Bearded Vultures or other diurnal raptor species. Future research on diurnal raptors should take nocturnal movements and foraging ecology into account, in order to improve our knowledge regarding the ecological and conservation consequences of such behaviour.

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