BEHAVIOURAL ECOLOGY AND CONSERVATION OF THE EGYPTIAN VULTURE IN HUMAN-DOMINATED LANDSCAPES: INSIGHTS FROM LONG-TERM MONITORING AND MOVEMENT ECOLOGY

PhD thesis 2022

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This Dr. Philosophy thesis, presented under the international mention from University of the Basque Country, was assessed by two scientific experts from non-Spanish research institutions:

- Dr. Maurizio Sarà, from the University of Palermo (Palermo, Italy).
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"People often say that I'm curious about too many things at once...But can you really forbid a man from harbouring a desire to know and embrace everything that surrounds him?"

-Alexander von Humboldt-

"Nature is often hidden, sometimes overcome, seldom extinguished."

-Francis Bacon-

"It's a dangerous business, Frodo, going out your door. You step onto the road, and if you don't keep your feet, there's no knowing where you might be swept off to."

- J.R.R. Tolkien, The Lord of the Rings-

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SCIENTIFIC PRODUCTION AND FORMATION

The scientific and technical material produced, and the scientific formation acquired during the period of this doctoral thesis (January 2018 - December 2021) are detailed in this section:

1. Peer reviewed publications

Publications as first author

a) **Morant, J.***, Zabala J., Martínez J. E., Zuberogoitia I. (2018). Out of sight, out of mind? Testing the effects of overwinter habitat alterations on breeding territories of a migratory endangered species. *Animal Conservation*. Vol. 21, pags: 465-473.
DOI: https://doi.org/10.1111/acv.12412

b) **Morant, J.***, López-López P., Zuberogoitia I. (2019). Parental investment asymmetries of a globally endangered scavenger: unravelling the role of gender, weather conditions and stage of the nesting cycle. *Bird Study*. Vol. 66, pags: 329-341.
DOI: https://doi.org/10.1080/00063657.2019.1688251

c) **Morant, J.***, González-Oreja J.A., Martínez J. E., López-López P., Zuberogoitia I. (2020). Applying economic and ecological criteria to design cost-effective monitoring for elusive species. *Ecological Indicators*. Vol. 115, 106366.
DOI: https://doi.org/10.1016/j.ecolind.2020.106366

d) **Morant, J.*,** Abad-Gómez, J. M., Álvarez, T., Sánchez, Á., Zuberogoitia, I., and López-López, P. (2020). Winter movement patterns of a globally

endangered avian scavenger in south-western Europe. *Scientific reports*. Vol. 10, pags: 1-11.
DOI: https://doi.org/10.1038/s41598-020-74333-0

e) Zuberogoitia, I.***** **†**, **Morant, J.*** **†**, González-Oreja, J. A., Martínez, J. E., Larrinoa, M., Ruiz, J., Aginako,I., Cinos, C., Díaz, E., Martínez, F., Galarza, A., Pérez de Ana, J.M., Vacas, G., Lardizabal, B., Iriarte, I. and Zabala, J. (2021). Management Actions Promote Human-Wildlife Coexistence in Highly Anthropised Landscapes: The Case of an Endangered Avian Scavenger. *Frontiers in Ecology and Evolution*. Vol. 491.
DOI: https://doi.org/10.3389/fevo.2021.656390

f) **Morant, J.*,** Scacco,M., Safi, K., Abad-Gómez, J.M., Álvarez, T., Sánchez, Á., Phipps W.L., Carbonell, I., García J., Prieta J., Zuberogoitia, I., López-López, P. (2021). Environmental and social correlates, and energetic consequences of fitness maximisation on different migratory behaviours in a long-lived scavenger. *Oecologia*. Under review.

g) **Morant, J.***, Arrondo E., Cortés-Avizanda A., Moleón M., Donázar J.A., Sánchez-Zapata J.A., López-López P., Ruiz-Villar H., Zuberogoitia I., Morales-Reyes Z., Naves-Alegre L., Sebastián-González, E. (2021). Factors driving large-scale ungulate carrion production in the Anthropocene. *Ecosystems*. Under review.

Publications as co-author

a) Zuberogoitia I., **Morant, J.**, Castillo I., Martínez J.E., Burgos G., Zuberogoitia J., Azkona A., Ruíz Guijarro J., González-Oreja, J.A. (2019). Population trends of Peregrine Falcon in Northern Spain – Results of a long-term monitoring project. *Ornis Hungarica*. Vol. 26, pags: 51-68. DOI: https://doi.org/10.1515/orhu-2018-0015

b) Zuberogoitia I., Burgos G., González-Oreja, J.A., **Morant, J.**, Martínez J.E., Zabala, J. (2019). Factors affecting spontaneous vocal activity of Tawny Owls Strix aluco and implications for surveying large areas. *Ibis*. Vol. 161, pags: 495-503. DOI: https://doi.org/10.1111/ibi.12684

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e) López-López P., Perona A.M., Egea-Casas O., **Morant, J.**, Urios V. (2021). Tri-axial accelerometry shows differences in energy expenditure and parental effort throughout the breeding season in long-lived raptors. Current Zoology. Pags: 1-11.
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DOI: https://doi.org/10.1038/s41598-021-84811-8

2. Publications without peer review

Morant J.* (2018). Bearded Vulture (Gypaetus barbatus) in the Basque Country. Parque Natural del Gorbea.
DOI: https://doi.org/10.5281/zenodo.5534377

3. Oral communications

Morant, J.*, Zabala J., Martínez J. E., Zuberogoitia I. (2018). Out of sight, out of mind? Testing the effects of overwinter habitat alterations on breeding territories of a migratory endangered species. Biodiversity and Nature Conservation Congress. University of Murcia. Murcia (Spain).

Morant, J.*, Abad-Gómez, J. M., Álvarez, T., Sánchez, Á., Zuberogoitia, I., and López-López, P. (2019). Winter movement patterns of a globally endangered avian scavenger in south-western Europe. European Vulture Conference. Vulture Conservation Foundation. Algarve (Portugal),

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4. Posters

Morant, J.*, Zabala J., Martínez J. E., Zuberogoitia I. (2018). Out of sight, out of mind? Testing the effects of overwinter habitat alterations on breeding territories of a migratory endangered species. I Simposium. Raptors and their habitats. Guara (Spain).

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5. Field surveys

Egyptian vulture long-term monitoring project in Biscay. Territory/Nest monitoring during breeding period of the species. Collaboration with Rangers, Stakeholders and Biscay Council managers to implement conservation measures of the species. March-September 2017-2021.

Peregrine falcon long-term population monitoring project in Biscay. Territory/Nest monitoring during breeding period of the species. Collaboration with Rangers, Stakeholders and Biscay Council managers to implement conservation measures of the species. March-September 2017-2019.

Bonelli’s Eagle long-term population monitoring project in Community of Valencia. Territory/Nest monitoring during breeding period of the species. Adult trapping and GPS tagging. Collaboration with Rangers, Stakeholders and managers to implement conservation measures of the species. January-May 2019.

JOURNAL CHARACTERISTICS

Summary of the journal characteristics in which the present thesis chapters have been published. Note that the quartile, impact factor, and journal position within the ranking corresponds to the year in which article was publihsed.

Chapter	Journal	Quartile	H-Index	Impact factor	Journal ranking
Chapter 1	Bird Study	Q2	49	0.941 (2019)	10/20
Chapter 2	Ecological Indicators	Q1	127	4.229 (2020)	49/392
Chapter 3	Animal Conservation	Q1	85	3.00 (2018)	9/58
Chapter 4	Frontiers in Ecology and Evolution	Q1	33	4.171 (2021)	40/97
Chapter 5	Scientific Reports	Q1	213	4.13 (2020)	10/33
Chapter 6	Oecologia	Q1	195	3.22 (2020)	67/163

LIST OF ABBREVIATIONS

Abbreviation	Meaning
r_s	Correlation coefficient
SD	Standard deviation
GLMM	Generalized Linear Mixed Models
AICc	Akaike Information Criterion corrected for small sample size
ΔAICc	Delta Akaike Information Criterion corrected for small sample size
$AICc_{\omega}$	Weight of Akaike Information Criterion corrected for small sample size
n	Sample size
rho	Correlation coefficient
P	Significance
W	Wilcoxon coefficient
K	Number of parameters in a model
t	t-value
m.a.s.l.	Meters above sea level
p	Detectability
ψ	Occupancy
SE	Standard Error
OR	Odds ratio
IUCN	International Union for Conservation of Nature
eDNA	Environmental Desoxyribonucleic acid
BQI	Breeding Quality Index
OHA	Overwinter Habitat Alteration
GIS	Geographic Information Systems
z	z-value
RUF	Resource Utilization Function
BMP	Basic Movement Parameter
EC	European Community
GPS	Geographic Position System
GSM	Global System for Mobile communications
ACDS	Authorized Carcass Deposition Sites
UCDS	Unauthorized Carcass Deposition Sites
KDE	Kernel Density Estimation
UD	Utilization Distribution
Chisq	Chi square
R^2 fixed	Proportion of variance explained by fixed effects
R^2 random	Proportion of variance explained by random effects
β_j	Coefficient of the resource utilization function models
Var	Variance
LCI	Lower Confidence Interval
UCI	Upper Confidence Interval
NDVI	Normalized Difference Vegetation Index

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SUMMARY

The increase in the demand for natural resources to ensure population livelihoods and the necessity to spare more time outdoors have boosted human presence in landscapes and provoked the complete transformation of ecosystems to unprecedented levels. In these human-dominated landscapes, animals have been forced to share space with human beings, which caused severe alterations in their behaviour, provoked population declines and, in the worst cases, accelerated extinction rates. However, traditional conservation approaches such as protecting large unaltered areas are not valid in such circumstances since they could potentially provoke conservation conflicts. New approaches that evaluate how human actions alter wildlife behaviour and improve human-wildlife coexistence by selecting effective behavioural targets and devising rational management and conservation measures are needed. This is particularly necessary in the case of the apex predators linked to traditional human activities like livestock husbandry that occupy a pivotal position in the food webs living in human-dominated landscapes, as vultures. Vultures, particularly Egyptian vultures, offer irreplaceable crucial ecosystem services and are considered good indicators of ecosystems health state. The steep decline in the population of this species and the increase in intensity and frequency of threats from human activities across its range has pushed it to the brink of extinction, which becomes it a conservation reliant species. The present thesis addresses how human activities may alter Egyptian vulture behaviour and design overarching conservation strategies that reconcile species conservation and human activities based on crucial behavioural indicators from long-term monitoring and GPS tracking.

Behaviour plays a fundamental role as a functional group attribute that links individuals and ecosystems. Conservation should therefore design essential behavioural targets that preserve species' long-term

population persistence (e.g., by enhancing fitness parameters) to ensure the ecosystem service that species provides. Altogether help to advise conservation planning decision process. For example, in long-lived territorial species with low productivity, such as Egyptian vulture, deciphering crucial aspects such as breeding behaviour and parental care offers valuable information about which and when vital events like incubation or hatching happen in time (Chapter 1). Furthermore, both parents in Egyptian vultures share equal effort in parental tasks, which showed that both parent efforts are necessary to raise nestlings successfully. This information is of high importance to elucidate when the species is more vulnerable and could help predict human-impacts outcomes (e.g., loss of the chick owing to nest nonattendance by parents during the first weeks of life).

Monitoring programs could also benefit from species-specific behavioural knowledge. The latter, combined with the knowledge of environmental conditions affecting species, could be used to design cost-effective monitoring programs. For example, detectability on previously occupied territories of the species could be combined with the nest site, breeding period and weather characteristics of a region to improve monitoring programs. This allows the selection of specific periods in which species is more likely to be seen/detected by investing a minimum amount of time (Chapter 2). Moreover, it makes monitoring programs more flexible and helps to adapt them depending on the financial budget available while preserving monitoring efficacy in cases of financial constrains.

Behavioural alterations also offer important insights to improve conservation programs. This holds particularly true in cases where these do not seem to pay off in terms of conservation outcomes. For instance, species do not seem to respond positively to specific actions such as temporal and spatial bans of potentially harmful human disturbances such as massive clear-cuts for wood extraction (Chapter 3). Spatiotemporal bans are habitual measures that aim to reconcile human practices and the conservation of species during sensitive periods. Data from long-term monitoring allow detecting changes in crucial behavioural indicators from breeding, such as nest use and productivity. In philopatric species such as Egyptian vultures, changes in nest use (e.g., use of nests of lower quality) due to forestry activities out of the breeding period could reduce productivity in the long term, which has detrimental effects at the population level. In such cases, the effects should be palliated by applying more strict spatiotemporal bans around nesting territories and, in some cases, taking advantage of landscape elements that reduce the effect of disturbances.

In human-dominated landscapes, however, isolated cases of human disturbances are rare, and it is habitual that species are subjected to intense disturbances regimes that vary in space and time. Specific actions are not enough in these circumstances, and more integral approaches are needed to ensure population viability. Therefore, management plans and a collaborative network between all the agents involved in species conservation are required. These actions not only help to improve crucial populations parameters such as nest/territory occupation and productivity but also help to avoid future potential disturbances in sensitive areas (Chapter 4). Moreover, collaboration among the agents involved in species conservation also enables awareness-raising by main stakeholders involved in the majority of the human disturbances (e.g., forestry). This enables the compatibilisation between human activities and species conservation in human-dominated landscapes.

Human activities in anthropised landscapes not only alter species breeding behaviour but also species movement patterns. For instance, they can favour residency in partial migratory species such as Egyptian vultures due to the increase in the predictability of food sources (Chapter 5). In particular, the changes in resource availability in farming areas could even modulate population size in unfavourable periods (i.e., winter) in which species is known to migrate to warmer areas such as African quarters. Moreover, these new human-generated favourable conditions provoked a social-mediated behavioural response in the species, forming gatherings around predictable food sources from farms (Chapter 6). Such behavioural alterations are reflected in reductions in home range areas due to the strong attraction to such places. Therefore, these areas are of particular interest for the conservation of the species.

These human-induced behavioural alterations also affect substantially species fitness; for instance, residency due to increased livestock numbers (and thus in carrion availability and predictability) increases survival likelihood but not breeding output compared to migratory individuals (Chapter 6). However, it also increases the energy costs of overwintering in the Iberian peninsula and decreases flight efficiency and activity hours. Hence, even though these behavioural changes may have contradictory effects, they seem to enhance crucial aspects such as survival which could positively affect species persistence. Nevertheless, it also highlights new conservation challenges as the numbers of the species increased, and so make the threats in Spanish wintering quarters. These results showed the complexity and extent of the effects of human activities on species behaviour. Far beyond, they emphasised the need for more in-depth research on these particular aspects to design more effective and flexible management and conservation actions that account for these behavioural changes.

The chapters included in this thesis dissertation share a practical goal as they focus on applying behaviour from data from long-term monitoring and GPS to design and assess the most effective monitoring and conservation approaches in human-dominated landscapes. Further, it helps drawing a roadmap to decipher the way and extent to which human activities could potentially alter behaviour, and advocates to create links between behavioural-based monitoring frameworks that help predict the present and future impacts of global change-related effects on vulture species worldwide.

RESUMEN

El aumento de la demanda de recursos naturales para garantizar el sustento de la población y la necesidad de pasar más tiempo al aire libre ha potenciado la presencia humana en los paisajes y ha provocado la transformación completa de los ecosistemas a un nivel sin precedentes. En estos paisajes dominados por el hombre, los animales se han visto obligados a compartir el espacio con los seres humanos, lo que ha causado graves alteraciones en su comportamiento, ha provocado el declive de las poblaciones y, en los peores casos, ha acelerado las tasas de extinción. Sin embargo, los enfoques tradicionales de conservación, como la protección de grandes áreas inalteradas, no son válidos en estas circunstancias, ya que podrían provocar conflictos de conservación. Se necesitan nuevos enfoques que evalúen cómo las acciones humanas alteran el comportamiento de la fauna silvestre y mejoren la coexistencia entre los seres humanos y la fauna silvestre mediante la selección de indicadores comportamentales eficaces y la elaboración de medidas racionales de gestión y conservación. Esto es especialmente necesario en el caso de los depredadores apicales vinculados a actividades humanas tradicionales, como la ganadería, que ocupan una posición fundamental en las redes tróficas que viven en paisajes dominados por el hombre, como los buitres. Los buitres, en particular el alimoche, ofrecen servicios ecosistémicos cruciales e insustituibles y se consideran buenos indicadores del estado de salud de los ecosistemas. El fuerte descenso de su población y el aumento de la intensidad y la frecuencia de las amenazas de las actividades humanas en toda su área de distribución han llevado a la especie al borde de la extinción, lo que la convierte en una especie dependiente de la conservación. La presente tesis aborda cómo las actividades humanas pueden alterar el comportamiento del alimoche para diseñar estrategias de conservación globales que concilien la conservación de la especie y las actividades humanas,

basándose en indicadores de comportamiento cruciales procedentes de la monitorización a largo plazo y el seguimiento por GPS.

El comportamiento desempeña un papel fundamental como atributo funcional del grupo que vincula a los individuos con los ecosistemas. Por lo tanto, la conservación debe seleccionar indicadores de comportamiento esenciales que preserven la persistencia de las poblaciones de las especies a largo plazo (por ejemplo, mejorando los parámetros de reproducción y supervivencia) para garantizar el servicio ecosistémico que proporcionan dichas especies. Estos indicadores, ayudan a asesorar el proceso de decisión de la planificación de la conservación. Por ejemplo, en las especies territoriales de larga vida y baja productividad, como el alimoche, descifrar aspectos cruciales como el comportamiento reproductivo y el cuidado de los padres ofrece una valiosa información de cuáles y cuándo se producen eventos vitales como la incubación o la eclosión en el tiempo (capítulo 1). Además, en los alimoches ambos progenitores comparten el mismo esfuerzo en las tareas parentales, lo que demuestra que los esfuerzos de ambos son necesarios para criar a los polluelos con éxito. Esta información es de gran importancia para dilucidar cuándo la especie es más vulnerable y podría ayudar a predecir los resultados de los impactos humanos (por ejemplo, la pérdida del polluelo debido a la no asistencia al nido por parte de los padres durante las primeras semanas de vida).

Los programas de seguimiento también podrían beneficiarse del conocimiento del comportamiento específico de la especie. Este último, combinado con el conocimiento de las condiciones ambientales que afectan a las especies, podría utilizarse para diseñar programas de seguimiento rentables. Por ejemplo, la detectabilidad en territorios previamente ocupados por la especie podría combinarse con el lugar de nidificación, el periodo de cría y las características meteorológicas de una región para mejorar los programas de seguimiento. Esto permite seleccionar los periodos específicos en los que es más probable ver/detectar la especie invirtiendo una cantidad mínima de tiempo (capítulo 2). Además, hace que los programas de seguimiento sean más flexibles y ayuda a adaptarlos en función del presupuesto disponible, al tiempo que preserva la eficacia del seguimiento en caso de restricciones financieras.

Las alteraciones del comportamiento también ofrecen información importante para mejorar los programas de conservación. Esto es especialmente cierto en los casos en los que no parecen dar resultados de conservación. Por ejemplo, las especies no parecen responder positivamente a acciones específicas como las prohibiciones temporales y espaciales de perturbaciones humanas potencialmente dañinas, como las talas masivas para la extracción de madera (capítulo 3). Las prohibiciones espacio-temporales son medidas habituales que pretenden conciliar las prácticas humanas y conservar las especies durante los periodos sensibles. Los datos del seguimiento a largo plazo permiten detectar cambios en indicadores de comportamiento cruciales para la cría, como el uso de los nidos y la productividad. En especies filopátricas como el alimoche, los cambios en el uso de los nidos (por ejemplo, el uso de nidos de menor calidad) debidos a las actividades forestales fuera del periodo de cría podrían reducir la productividad a largo plazo, lo que tiene efectos perjudiciales a nivel poblacional. En estos casos, los efectos deberían paliarse aplicando prohibiciones espacio-temporales más estrictas en torno a los territorios de nidificación y, en algunos casos, aprovechando los elementos del paisaje que reducen el efecto de las perturbaciones.

En los paisajes dominados por el hombre, sin embargo, los casos aislados de perturbaciones humanas son raros, y es habitual que las especies estén sometidas a regímenes de perturbación intensos que varían en el espacio y el tiempo. En estas circunstancias no bastan las acciones puntuales y se necesitan enfoques más integrales para garantizar la viabilidad de las poblaciones. Por ello, se necesitan planes de gestión y una red de colaboración entre todos los agentes implicados en la conservación de las especies. Estas acciones no sólo contribuyen a mejorar parámetros poblacionales cruciales como la ocupación del nido/territorio y la productividad, sino que también ayudan a evitar futuras perturbaciones potenciales en zonas sensibles (capítulo 4). Además, la colaboración entre los agentes implicados en la conservación de las especies también permite la sensibilización de los principales actores implicados en la mayoría de las perturbaciones humanas (por ejemplo, la silvicultura). Esto permite la compatibilidad entre las actividades humanas y la conservación de las especies en los paisajes antropizados.

Las actividades humanas en los paisajes antropizados no sólo alteran el comportamiento reproductivo de las especies, sino que también alteran los patrones de movimiento de las mismas. Por ejemplo, pueden favorecer la residencia de especies parcialmente migratorias, como el alimoche, debido al aumento de la previsibilidad de las fuentes de alimento (capítulo 5). En particular, los cambios en la disponibilidad de recursos en las zonas de cultivo podrían incluso modular el tamaño de la población en periodos desfavorables (es decir, el invierno) en los que se sabe que las especies migran a zonas más cálidas, como los cuarteles africanos. Además, estas nuevas condiciones favorables generadas por el hombre provocaron una respuesta conductual mediada por los patrones sociales de la especie, formando agrupaciones en torno a fuentes de alimento predecibles de las granjas (capítulo 6). Estas alteraciones del comportamiento se reflejan en la reducción de las áreas de distribución de los animales debido a la fuerte atracción que ejercen sobre estos lugares. Por lo tanto, la conversión de estas áreas es de especial interés para la conservación de la especie.

Estas alteraciones del comportamiento inducidas por el hombre también afectan sustancialmente al fitness de la especie; por ejemplo, la residencia debida al aumento del número de cabezas de ganado (y, por tanto, de la disponibilidad y previsibilidad de la carroña) aumenta la probabilidad de supervivencia, pero no el rendimiento reproductivo, en comparación con los individuos migratorios (capítulo 6). Sin embargo, también aumenta el coste energético de la hibernación en la Península Ibérica y disminuye la eficiencia del vuelo y las horas de actividad. Por lo tanto, aunque estos cambios de comportamiento pueden tener efectos contradictorios, parecen mejorar aspectos cruciales como la supervivencia, lo que podría afectar positivamente a la persistencia de la especie. No obstante, también ponen de manifiesto nuevos retos en la conservación al aumentar el número de ejemplares de la especie y, por tanto, las amenazas en los cuarteles de invernada peninsulares. Estos resultados muestran la complejidad y el alcance de los efectos de las actividades humanas en el comportamiento de las especies. Más allá, enfatizan la necesidad de investigar más a fondo estos aspectos particulares para diseñar acciones de gestión y conservación más eficaces y flexibles que den cuenta de estos cambios de comportamiento.

Los capítulos incluidos en esta tesis doctoral comparten un objetivo práctico, ya que se centran en la aplicación del comportamiento a partir de los datos procedentes del seguimiento a largo plazo y del GPS para diseñar y evaluar los enfoques de seguimiento y conservación más eficaces en los paisajes dominados por el hombre. Además, ayudan a trazar una hoja de ruta para descifrar la forma y el grado en que las actividades humanas podrían alterar el comportamiento y aboga por crear vínculos entre el seguimiento basado en el comportamiento que ayuden a predecir los impactos presentes y futuros de los efectos relacionados, y el cambio global en las especies de buitres de todo el mundo.

GENERAL INTRODUCTION

Almost 75% of the world's landscapes has been altered sometime by humans, while 50% of the landscape has been transformed for human needs during the last 12,000 years (Ellis et al., 2011, 2021). Only 20-40% of the earth surface is under low-human influence (Figure 1; Riggio et al., 2020). Industrialisation and massive urbanisation, coupled with big agricultural changes to fulfil ongoing human population growth, are among the main drivers of these global anthropogenic transformations (see also Ellis et al., 2021). Such landscapes acquired the name of anthropogenic landscapes since they encompass human settlements of different entities and subsistence activities (Chase and Chase, 2016). Under this scenario, the room for wild areas has been notably reduced. This is reflected in the low percentage of unaltered ecosystems nowadays (<3%; Plumptre et al., 2021). Therefore, it is evident that the majority of ecosystems and ecological communities that these landscapes (hereafter human-dominated landscapes) encompass are, to a greater or lesser extent, under the influence of human activities.

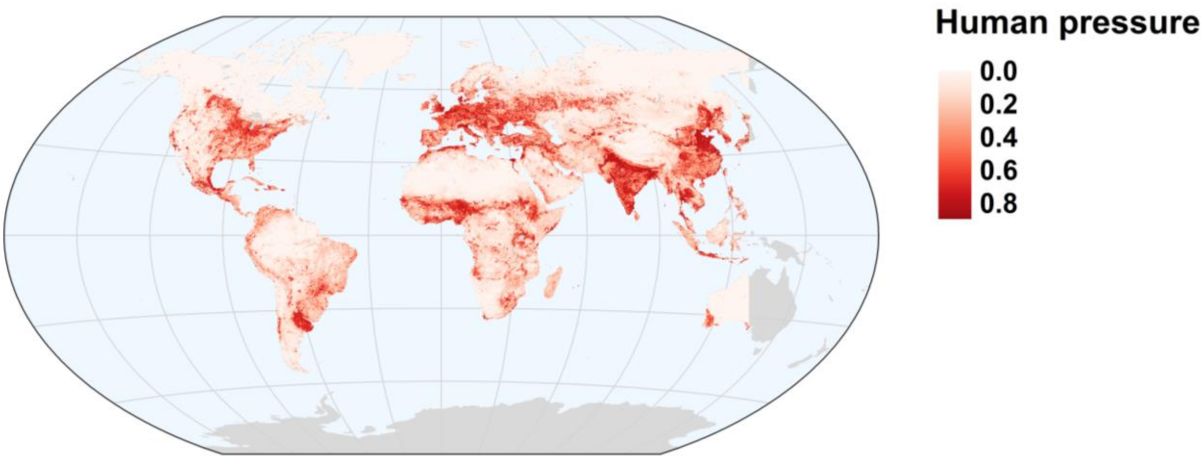

Figure 1. *Map of the human pressure worldwide shows the proportion of the landscape modified based on modeling the physical extents of 13 anthropogenic stressors and their estimated impacts using spatially-explicit global datasets with a median year of 2016. Adapted from Kennedy et al., 2019.*

Human-dominated landscapes encompass a wide variety of anthropogenic activities mainly related to extraction of resources (e.g., forestry, mining, agriculture), services (e.g., roads, power lines) and recreational activities (e.g., hiking, hunting) that are consumed to fulfil human necessities (Chase and Chase, 2016). These activities could generate disturbance that have lethal (e.g., direct mortality) and non-lethal (e.g., behavioural alterations) impacts on wildlife. Likewise, the extent of the effects could vary from large scale to local. Some activities could act as bottom-up effects on populations by directly changing the physical environment in which species inhabit. For instance, the development of energy and transportation infrastructures at large scale could have a direct impact on wildlife by inducing direct mortality due to collisions with human-made infrastructures and vehicle collisions (Northrup and Wittmeyer, 2013; Torres et al., 2016; Cirlo et al., 2020; Hill et al., 2020). Other activities such as long-term land-use change could alter species behaviour, translating into changes in distribution and diversity at broad scales (Sirami et al., 2017; Newbold et al., 2018). Human activities could also exert top-down effects by potentially altering species behaviour at large and local scales in response to human presence (Wilson et al., 2020). For instance, human disturbances during critical periods (i.e., breeding period) or in sensitive areas could alter. parental care patterns, affecting reproductive outcomes (e.g., loss of chicks; Wilson et al., 2020). Animals may also respond by altering their movement patterns (e.g., increasing their home range areas) during periods of high-human pressure, such as weekends (e.g., Perona et al., 2019). The latter is particularly pervasive due to rising recreational activities in natural areas (Larson et al., 2016; Watson et al., 2016). Human may also alter species behaviour by providing stable and predictable food sources during long-time periods (Oro et al., 2013; López-López et al., 2014b). These changes could provoke shifts in large scale movement patterns such as migrations on opportunistic social species (e.g., Gilbert et al., 2016). Moreover, human-driven climate change could alter the physical environment and induce alterations in animal movement (Beever et al., 2017). All these behavioural changes may have a profound effect on both population dynamics (Katzner et al., 2020) and ecosystem functioning, such as seed dispersal, nutrient cycling, primary production and pathogen transfer (Tucker et al., 2021; Leroux et al., 2015; Schmitz et al., 2008; Hawley et al., 2011), among others.

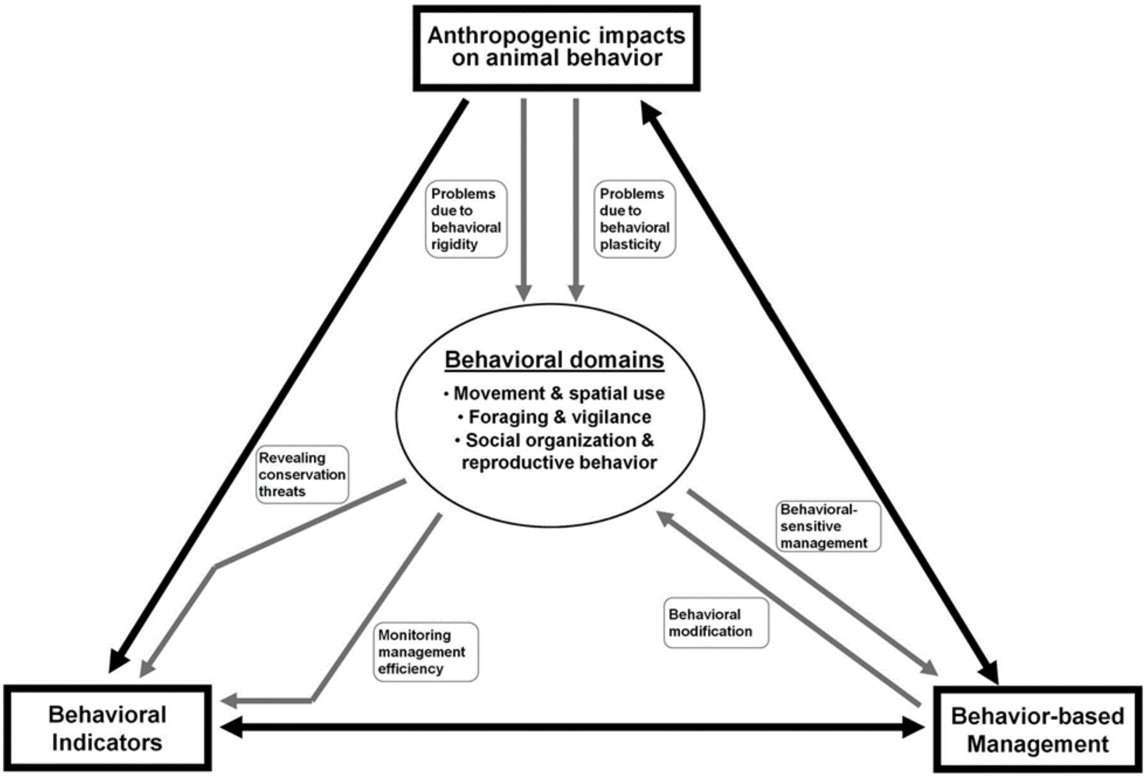

Figure 2. *The conservation behaviour framework is composed of 3 basic interrelated conservation themes: 1) Anthropogenic impacts on animal behaviour; 2) behaviour-based management; and 3) behavioural indicators. The black arrows represent interactions between the conservation themes. Gray arrows represent the pathways that connect each theme to the behavioural domains. Adapted from Berger-Tal et al., 2011.*

Assessing and palliating the effects of human activities requires basic knowledge of species-specific behavioural traits, which could be used as ecological indicators (hereafter behavioural indicators). Behavioural indicators could be classified into those involving different behavioural domains such as 1) foraging ecology, 2) social organization and breeding behaviour, and, 3) species habitat selection and movement patterns (see Figure 2; Berger-Tal et al., 2011). Gaining knowledge of these three behavioural domains could help to assess survival and fitness and provide invaluable information on populations and community dynamics (Bro-Jorgensen et al., 2019). Furthermore, integrating the use of such indicators in species conservation and management is crucial for evidence-guided decision making. For example, they could be used to 1) monitor the effects of anthropogenic impacts on species fitness (Wilson et al., 2020), 2) test the effectiveness of management programs or measures (e.g., Margalida et al., 2016), and 3) evaluate the success of a management program at its early stages (e.g., before population, or ecosystem-level responses become evident; Lindell et al., 2008). Moreover, behavioural indicators such as movement patterns may be crucial for the delineation of protected areas (Caro and Berger, 2019), increase the extent of existent ones (Coristine et al., 2018) or even help to reduce human-wildlife conflicts (Melzheimer et al., 2020).

BOX 1. Long-term monitoring projects are crucial for the correct assessment of the ecosystems and animal populations status (Marrugan et al., 2010; Mills et al., 2015, 2016) and have become invaluable tools for species conservation worldwide (Conde et al., 2019). Despite the coupled financial constraints usually linked to such projects (Cauglan and Oackley, 2001; Birkhead 2014), the benefits in the advances in ecology and evolution largely overcome the economic costs. For instance, such projects are particularly relevant in long-lived species whose pace of life would make it impossible to obtain relevant data on species behaviour, demography, population growth rate, and fitness (White, 2019). This knowledge is necessary to implement or improve management plans that match species-specific ecology (Yoccoz et al., 2001). Long-term monitoring account for the heterogeneity and variation in population response to a variety of environmental determinants and help to assess the effects of human impacts at local and global scale (Reinke et al., 2019). The latter also enables testing the effectiveness of current conservation measures, informing proportionate policy responses, and correcting budget allocation (Lindenmayer et al., 2012; Hughes et al., 2017). Finally, long-term monitoring could help to improve the social perception of species in anthropised landscapes. For instance, by implementing measures based on palliating the effects of a specific behaviour of target populations could promote coexistence and alleviate conservation conflicts (e.g., Nakamura et al., 2021).

The first fundamental step to select informative behavioural indicators is, therefore, to assess focus species behaviour. In this context, monitoring, and particularly, long-term monitoring, is a powerful tool for understanding species' basic behavioural traits such as species occupancy or breeding behaviour (BOX 1). Long-term monitoring could also be combined with new GPS monitoring techniques to reliably and accurately assess species use of space and foraging habits, among others (BOX 2). The use of both tools gains significant relevance in the study of long-lived threatened species, playing a crucial role in ecosystems such as apex predators. Among apex predators, raptors (e.g., hawks, harriers, kites, eagles, falcons, and vultures) offer invaluable ecosystem services, serve as cultural symbols to humans, and are usually considered sentinels of biodiversity and environment due to their high ecological requirements (Donázar et al., 2016; McClure et al., 2018). Moreover, raptors have the potential to structure communities due to their high-trophic level (e.g., Sergio et al., 2007; Donázar et al., 2016). However, this fact makes them particularly sensitive, even more than other bird species, to innumerable direct and indirect anthropogenic threats, ranging from resource extraction to poisoning (Sergio et al., 2008; McClure et al., 2018). In fact, 18% of raptors (N=557 species) are threatened with extinction, and 52% of raptors have declining global populations (McClure et al., 2018). Among them, Old World vultures are by far the most threatened bird guild worldwide, with 11 of 16 species categorised as endangered by the IUCN (McClure et al., 2018), thus requiring particular attention from the scientific community to implement adequate management and conservation plans to reverse this situation (Buechley et al., 2019).

BOX 2. The advance in tracking technologies has permitted the study of the movement of hundreds of organisms, varying from centimetres and seconds to thousands of kilometres during their whole lives (Kays et al., 2019). The development of such technology has enabled researchers to untangle why, how, when and where species move (Nathan et al., 2008). In particular, the emerging use of miniaturized tracking devices and coupled Big data analytical procedures has helped to shed light on previously unanswered questions in contemporary ecology (Wilmers et al., 2015; López-López, 2016). For example, how individuals use social cues during long-distance migrations, the potentiality of species to disperse seeds at a global scale or to uncover unexpected transcontinental migratory routes in insects and birds (López-López et al., 2010; Flack et al., 2018; Tucker et al., 2021 and Phipps et al., 2019). Moreover, it has allowed identifying crucial abiotic (e.g., productivity; Dodge et al., 2014), biotic (e.g., age, sex and intraindividual effects; Spiegel et al., 2016) and human related factors (e.g., human pressure, Tucker et al., 2018; Magioli et al., 2019) affecting species movement. Importantly, the potential of this technology has also contributed to species conservation; for example, by reducing human-wildlife conflicts, identifying potential risks and even delineating effective conservation areas basing on species airspace/space use (Allen and Singh 2016; Arrondo et al., 2021; Caro and Berger. 2019). More recently, calculations of movement costs are also possible thanks to the biologging devices such as accelerometers attached to GPS tags (Wilson et al., 2019). The data derived from these devices could be used to estimate the energy expenditure from different behaviours (e.g., flapping flight) as it has never before (e.g., Williams et al., 2020), finding links between behaviour and fitness (Grémillet et al., 2018), or even using such information to elucidate optimal energy use of animals in both terrestrial and marine environments (e.g., Masello et al., 2021; Papastimatiou et al., 2021).

As sole obligate scavengers, vultures have a unique role in ecosystems by removing carrion from carcasses, which becomes crucial in ecosystems functioning and balance (Gangoso et al., 2013; Moleón et al., 2014). Moreover, vultures also contribute to human well-being by controlling the spread of potentially harmful diseases and facultative scavengers that could prejudice humans (Ogada et al., 2012; O'Bryan et al., 2018). Vultures may also contribute to reducing the gas emission that incineration of carcasses entails (Morales-Reyes et al., 2015, 2017) and provide non-material (e.g., cultural inspiration and recreational activities; Natividad et al., 2020) and material ecosystem services (e.g., economic;

García-Jiménez et al., 2021). Non-natural mortality from humans is among the most threatening factors for Old World vultures, including poisoning, electrocution, and collisions with human-made infrastructures such as roads or wind farms (Murn and Botha, 2018; Carrete et al., 2009). Moreover, their link to human activities such as extensive and intensive livestock (Mateo-Tomás and Olea, 2009) makes them particularly vulnerable to alterations in their primary resources (i.e., dead livestock carcasses). For instance, feeding on carcasses from intensive livestock farming could expose them to the ingestion of harmful pharmaceutics (Blanco et al., 2019).

Although significant advances have been made in the conservation of vultures, most of them are still based on species presence or distribution data (e.g., Santangeli et al., 2019), and often lack the particular realities at the local scales (Effrat et al., 2020). Moreover, the applicability of broad scales conservation and management (i.e., by virtually protecting large areas) is hampered by various factors, such as the anthropization of landscapes in which species inhabit. Conservation in human-dominated landscapes is particularly challenging due to increased human recreation activities and resource extraction that could affect species breeding ecology (e.g., Zuberogoitia et al., 2008; Donázar et al., 2002a). Furthermore, change in resource availability due to implementing different regulations in such landscapes could potentially alter species use of space (e.g., López-López et al., 2014; Margalida et al., 2016; Arrondo et al., 2018). Although these factors could not be considered as harmful as others, like non-natural mortality, they may also alter species behaviour with profound implications at the population level (e.g., Margalida et al., 2011). Management and conservation of vultures require the knowledge of vulture behaviour (e.g., particular social habits, breeding ecology, movement patterns) to better understand how species responds to human disturbances or anthropogenic changes and persist in human-dominated landscapes (van Overveld et al., 2020a,b). Therefore, filling the gaps between vulture behaviour and effective population management and conservation requires high-monitoring effort, and the use of new tracking technologies which could either improve monitoring programs (Perrig et al., 2019; Alarcón and Lambertucci, 2018).

AIM, OBJECTIVES AND THESIS STRUCTURE

The main aim of the present thesis is to build links between species ecological knowledge and effective management and conservation by using a set of behavioural indicators (i.e., occupancy, breeding behaviour and movement behaviour) obtained from long-term field and GPS monitoring. Specifically, this thesis intends to understand how human activities could potentially alter species behaviour, particularly those with delicate conservation status, such as Egyptian vulture Neophron percnopterus, and transform such information into effective and feasible conservation targets that could harmonise vulture conservation and human activities in human-dominated landscapes.

The current dissertation is divided into two well-defined blocks (see Figure 3 for a comprehensive assessment of the theoretical framework). In the first block, two sets of behavioural indicators derived from long-term monitoring are used, namely; breeding and occupancy/detectability data, to assess species breeding ecology (Chapter 1), design cost-effective monitoring programs (Chapter 2), and implement conservation and management measures (Chapters 3 and 4). The second block uses the combination of movement data indicators and population monitoring to assess resource utilization by the species and the influence of trophic resources provided by humans (Chapter 5) and evaluate causes and consequences of change in species migratory behaviour (Chapter 6).

Due to the disparate questions and methodologies used to address the above-mentioned objectives, the thesis is divided into six different chapters. Each of them is presented as an individual scientific article with its own introduction, methodology, results and discussion. This may inevitably provoke a certain overlap in the information of some sections (e.g., introduction) between chapters.

Chapter 1 evaluates the species' breeding ecology through the study of parent care of the species, and measures the effect of environmental variables such as weather, period and sex differences in parental tasks.

Chapter 2 develops a cost-effective monitoring program, based on species-breeding ecology and environmental characteristics, to be implemented in the national and regional census and conservation programs.

Chapter 3 measures the effects of anthropogenic habitat alterations on species occupancy and breeding biology, and evaluates the current mitigation measures for species conservation in human-dominated environments.

Chapter 4 investigates the effects of long-term management measures on species persistence in anthropogenic environments, and evaluates the success of protocols that ensure human-wildlife coexistence.

Chapter 5 assesses the winter population structure, evaluates how individual traits affect winter movement patterns, and measures the influence of factors, such as food provided by humans, on species space use during winter.

Chapter 6 explores the effect of environmental (food and temperature) and social factors on wintering population size as the main drivers of migratory behaviour change, and the trade-off between different fitness components and energetic consequences between migrant and resident individuals.

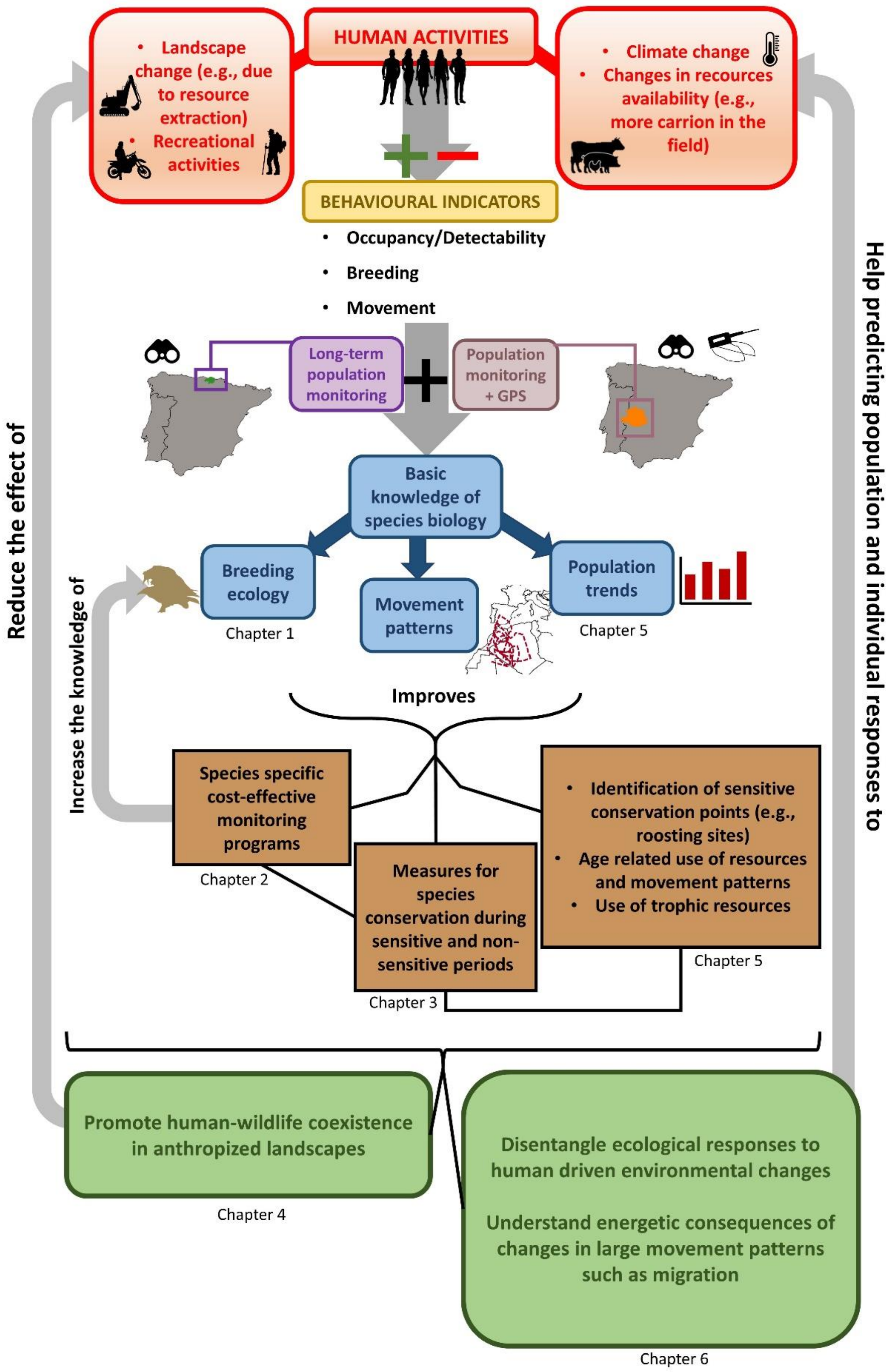

Figure 3. *Theoretical framework of the current thesis dissertation. Note that the footnotes indicate the article to which the corresponding box alludes. Silhouettes were obtained free of royalties from https://www.freepik.com/free-photos-vectors/silhouettes and https://all-free-download.com/free-vector/silhouette.html.*

STUDY AREA AND TARGET SPECIES

The study area encompasses two provinces of mainland Spain, one located on the North and the other on the South-West (Figure 4A). The northern study area occupies the whole province of Biscay (Basque country; Figure 4B), a mountainous area characterised by temperature oscillation of almost 12ºC between the coldest and hottest months, and mean annual rainfall ranging from 1200 to 2000 mm (Euskalmet, 2020). The province has undergone strong industrialisation and ongoing urbanisation during the last three decades, being one of the most densely populated regions in Europe, with 520 inhabitants/km2 (Eustat, 2020). The landscape is mainly occupied by extensive urban and industrial areas located in valley floors and gentler slopes. Agriculture, mainly extensive livestock farming, was the main activity in the region experiencing a substantial decline in the last decades in favour of forestry plantations of Pinus radiata covering almost 45% of the province (Euskadi.eus, 2019).

The south-western study area includes the province of Cáceres (Extremadura; Figure 4C). The region exhibits a typical Mediterranean climate with mild winter temperatures all year round. Average monthly temperature ranges between 7.8 – 26.2 °C in the coldest and hottest periods, respectively, and the mean annual rainfall is 551 mm (AEMET, 2021). Flat and wide valleys characterise the orography, with a mean altitude of 440 m.a.s.l (Felicísimo, 2001). Human population density is one of the lowest in Europe, with 54.8 inhabitants/km2 (CIESIN, 2020), and the majority of the region is markedly rural with scarce industry development. It is recognised as one of the major biodiversity hotspots of the Mediterranean region (López-López et al., 2011), with more than 6.9% and 31% of the land covered by Natural Protected Areas network and Natura 2000 network, respectively (Traba et al., 2007). Landscape is mainly occupied by the so-called “Dehesa” or “Montado” (Peinado and Rivas-Martínez, 1987), an agro-grazing system alternating open areas and holm oak (Quercus ilex) and corn oak (Quercus suber) forests which were progressively thinned until forming wood-pasture used for animal grazing and foraging plus crop production. This particular agrobiome is dedicated mainly to agriculture, combining extensive and intensive livestock rearing.

The focus species is the Egyptian vulture (Neophron percnopterus), a medium-sized (~ 2 kg), long-lived monogamous migratory avian scavenger (Forsman, 2020). This species exhibits a slow life-history, deferred maturity, low fecundity (0–2 fledglings per breeding attempt; Serrano et al., 2021) and a very long lifespan, reaching almost 30 years (Donázar and Margalida, 2021). The species is widely distributed across much of southern Europe, northern Africa, the Middle East and Central and South Asia (BirdLife International, 2020). The species population comprises both migratory and sedentary populations. Spain is home to 40% of the European breeding population, which is made of ca. 3,000-4,700 pairs (Birdlife International, 2019). Migratory Egyptian vultures regularly travel >4,000 km between northern breeding and southern wintering grounds and use several distinct migratory flyways, visiting up to 28 countries (Phipps et al., 2019). European populations winter in sub-Saharan Africa within the 14°–17°N belt and the Arabian Peninsula, with juveniles often remaining in the winter range for more than a year after their first migration (Donázar et al., 2002b; García-Ripollés and López-López, 2011; Oppel et al., 2015). Sedentary populations are found in Mediterranean islands (i.e., Menorca) and Macaronesian islands (Canary Islands, Cape Verde, Oman, Socotra and Ethiopia), and non-migratory breeding populations in sub-Saharan Africa (Donázar et al., 2002b; Freitas et al., 2020). There are also wintering individuals in Southern and South-Western Spain, being the former documented in the early eighties and the latter at the end of the XX century (García et al., 2000; Javier prieta pers. com.), and more recently in Sicily (see Di Vittorio et al., 2016).

The species experienced a sharp decline during the 20th century (Birdlife International, 2020). High adult mortality due to poisoning (Cortés-Avizanda et al., 2009; Hernández and Margalida, 2009; Sánz-Aguilar et al., 2015a), collisions with artificial infrastructures such as wind farms or power lines (Carrete et al., 2009; García-Alfonso et al., 2021), habitat loss (Velevski et al., 2015), habitat change (Mateo-Tomás and Olea, 2015), food shortages, and human disturbance at breeding sites are among the main causes of this decline (Zuberogoitia et al., 2008, 2014; Margalida et al., 2012; Donázar et al., 2016). Additionally, other indirect effects are also considered as a potential threat for the species, such as those derived from the consumption of carcasses from intensive livestock farming (Blanco et al., 2019), lead poisoning from game hunting carcasses (Arrondo et al., 2020) and exploitation of artificial food sources (Tauller et al., 2018; Ortíz-Santaliestra et al., 2019).

The current thesis uses data from two populations. The first one, of northern Spain in Biscay, encompassed a mean number of 23 breeding pairs. This population has been intensively monitored every breeding season, between February and the end of September from 2000 to the present-day (Chapters 1-4). The second population, of South-Western Spain in Cáceres is a wintering population, which was monitored every wintering season between November and February from 2006 to 2019 in (Chapters 5 and 6). In the latter, besides the field monitoring data, 15 non-migrant individuals were tagged with GPS devices to track their movement. Movement data were used in the elaboration of Chapters 5 and 6. Additionally, movement data from another 24 GPS tagged Egyptian Vultures from Salamanca, Douro, Guadalajara and Castellón were used for Chapter 6.

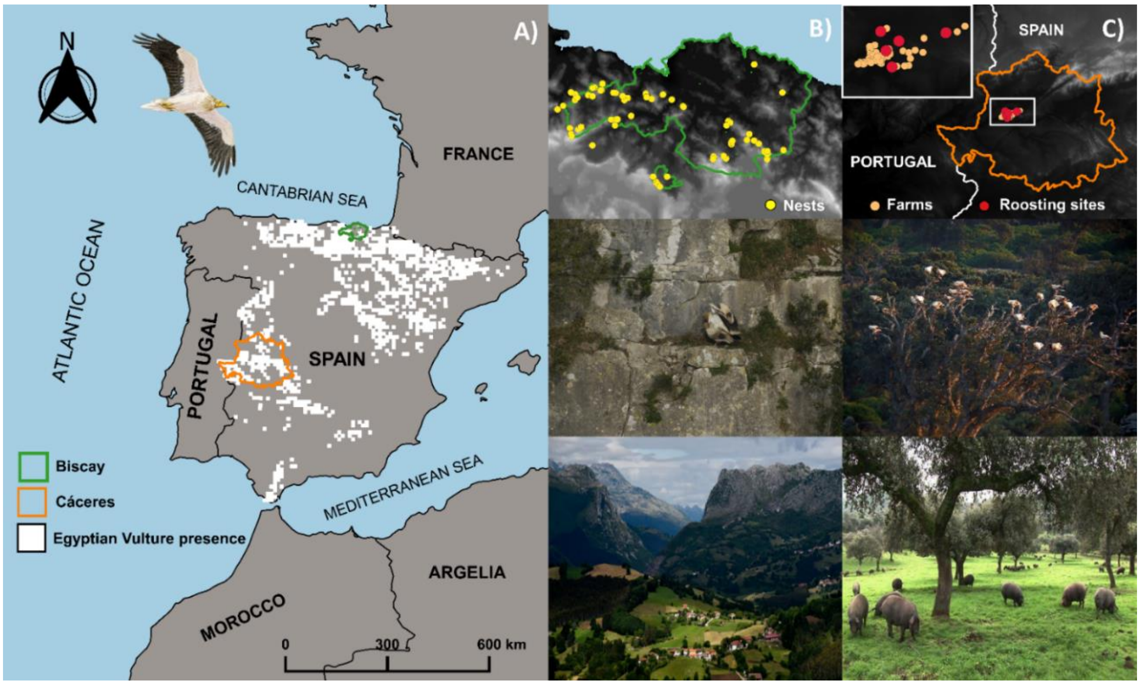

Figure 4. *Locations of study areas of Biscay (Basque country) and Cáceres (Extremadura), and the distribution of Egyptian vulture in UTM grid of 10x10 km in peninsular Spain (A). The column B) shows (from up to down) the locations of nesting sites (between 2000 and 2020) of Egyptian vultures in the study area of Biscay, a typical scene of an Egyptian vulture pair copulating in one of the cliffs where they usually breed and a picture representing the landscape in which agricultural mosaic of grasslands, monoculture woodlands and calcareous cliffs in which the species usually breed could be observed. In column C) (from up to down) the locations of wintering roosting sites used by Egyptian vultures and nearby livestock farms, one of the trees in which vultures usually rest and the typical landscape of the so-called Spanish savannah find in the study area of Cáceres are represented. Photo credits; Egyptian vulture pair picture- Dr Iñigo Zuberogoitia, Egyptian vultures at the roosting site-José Juan, landscape pictures obtained from internet license-free. Egyptian vulture illustration by Juan Varela Simó. Distribution of Egyptian vulture in peninsular Spain was obtained freely from MITECO(2021;https://www.miteco.gob.es/es/biodiversidad/temas/inventariosnacionales/inventario-especies-terrestres/inventario-nacional-de biodiversidad/bdn-ieet-atlas-vert-aves-n.aspx).*

CHAPTER 1

Parental investment asymmetries of a globally endangered scavenger: unravelling the role of gender, weather conditions and stage of the nesting cycle

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1.1. ABSTRACT

Capsule: In Egyptian Vultures *Neophron percnopterus*, both sexes invested similar parental effort throughout the breeding period. However, there was variation in the degree of intensity of parental care during some stages of the breeding period, suggesting that sex-role specialization exists for some activities.

Aims: To quantify parental care behaviour of Egyptian Vultures for the first time and to examine the role of sex, weather conditions, and stage of nesting cycle on breeding ecology.

Methods: We monitored 15 nests of Egyptian Vultures to analyse parental care investment. We collected data on nine different behavioural parameters/activities per sex, which were recorded throughout the entire breeding period. Variation in parental investment was analysed using generalized linear mixed models.

Results: Females invested more effort in incubation/brooding (61.45% for females and 31.54% for males) and egg turning (0.45 events/h for females and 0.37 events/h for males) while males contributed more to nest material delivery to the nest (0.67 deliveries/h for males and 0.14 deliveries/h for females). Conversely, both sexes invested the same effort in nestling attendance (21.89% for females and 21.21% for males) and food provisioning (0.28 items/h for females and 0.25 items/h for males). Furthermore, parental investment was not affected by weather, especially during critical moments such as incubation/brooding, however, changeover rate was positively related to temperature.

Conclusion: Our results suggest that, in the Egyptian Vulture, one sex is not entirely responsible for a particular task and the compensatory effort of the other mate is required. Finally, our findings indicate that major events such as incubation onset and hatching caused important shifts in the patterns of parental investment.

1.2. INTRODUCTION

Reproduction is one of the most critical stages of the annual cycle for most animals (Barta, 2016) and attributes linked to physiology (e.g., hormone levels), morphology (e.g., body size) and behaviour (e.g., parental care) are the most likely to have an impact during this phase of the life history. Of these, parental care is closely related to successful offspring rearing (Kokko and Jennions, 2008; Hoeck et al., 2015), with important effects on individual fitness (Clutton-Brock, 1991) and population viability (Cruz-López et al., 2017). There is considerable variation in parental care strategies across animal taxa. Birds exhibit huge diversity in parental care behavioural strategies across the altricial-precocial spectrum with regard to the amount of care provided, for example in tasks such as nest building, incubation and offspring attendance (Balshine, 2012). There are two well-distinguished patterns in parental care behaviour (Royle et al., 2012, Remeš et al., 2015): (1) both male and female are engaged in rearing their brood (perhaps with different degrees of involvement), namely bi-parental care and (2) total involvement by one of the parents during the entire breeding period, namely uni-parental care.

Among birds providing care for their offspring, birds of prey (Accipitriformes, Falconiformes and Strigiformes) are well known for their asymmetric parental care roles. In fact, in most birds of prey, females usually incubate, brood and provision nestlings, whereas males normally hunt, assisted by females only during the latter part of the nestling period, if at all (Newton 1979, 1986; Cramp and Simmons, 1980; Cramp, 1985; Wiehn and Korpimäki, 1997; Eldegard et al., 2003; Eldegard and Sonerud, 2012). The effects of diet in sex-role asymmetry (Sonerud et al., 2014a, 2014b), and factors affecting the duration of the post-fledging period, are well known (Arroyo et al., 2002; Tarwater and Brawn, 2010; Muriel et al., 2015). However, other aspects linked to the influence of the stage of the nesting cycle, the parents' sex and environmental conditions on the level of parental investment remain poorly understood (but see Lens and

Dhondt. 1994; Sánz et al., 2003). In fact, although the trade-offs between components of parental care are tightly linked to breeding performance (Monaghan and Nager, 1997; Byholm et al., 2011; Mariette and Griffith, 2015), other operating factors also affect breeding strategies in many ways. In particular, abiotic factors, such as temperature and precipitation, affect egg turning rates and nest attentiveness (Cresswell et al., 2003; Kovarik et al., 2009). Furthermore, environmental conditions fluctuate throughout the day and during the course of the breeding season. Hence, the costs of parental care and self-maintenance are also likely to vary (e.g., costs of thermoregulation, Piersma and van Gils, 2010). On the other hand, biotic factors such as predation risk, food availability, the stage of incubation, adult and nestling age, and individual behavioural differences also affect incubation routines and nest attentiveness (Smith et al., 2012; Cole and Quinn, 2014; Bulla et al., 2016; Zuberogoitia et al., 2018). These factors remain poorly understood in determinate groups, particularly in old-world vultures (but see Margalida and Bertran 2000, Xirouchakkis and Mylonas, 2007; Bassi et al., 2017; Holland et al., 2017).

Parental care investment and factors determining why, how and by whom care is provided are of crucial importance in long-lived monogamous, monomorphic species with slow life-history strategies. In fact, these species usually exhibit low fecundity rates (commonly one fledgling per year) and extended breeding periods. This has been demonstrated for large avian scavengers (vultures and condors, Accipitridae and Cathartidae; De Magalhaes and Costa 2009). Vultures are typically long-lived, monomorphic monogamous species that provide biparental care for their offspring and in which pair-bonds are maintained from one year to another (Newton 1979, Cramp and Simmons 1980). Furthermore, the peculiar foraging habits of this group (i.e., exploitation of scarce and unpredictable resources) obligate parents to spend long periods away from the nest (Jackson et al., 2008, Deygout et al., 2010). This is the case for the Egyptian vulture Neophron percnopterus, a globally endangered scavenger. Many aspects of the breeding ecology of this species remain unknown (but see Donázar and Ceballos 1989, Donázar et al., 1994). Our understanding of essential aspects of the breeding biology of this long-lived species is therefore of importance. Moreover, such data could be used as a conservation tool to promote effective management actions (Brooker et al., 2016, Merrick and Koprowski 2017), thus benefiting wildlife managers concerned with reducing vulture-related conflicts (Zuberogoitia et al., 2008, Avery et al., 2011), particularly in those populations subjected to high levels of human pressure.

In this study, we use data from a breeding population of Egyptian Vultures that has been the subject of a long-term monitoring programme (2000–2018) in Northern Spain, in order to: (1) describe behavioural patterns during the breeding period; and (2) assess the effects of sex, breeding stage and weather on parental investment in all activities. Given the lack of size dimorphism and the foraging ecology of the Egyptian Vulture, we expect that parental expenditure would be equally divided between both breeding adults and, furthermore, that both sexes would be equally involved in the various breeding activities. Therefore, we do not predict any sex-specific role specialization. We also analyse the effect of weather conditions on the amount of care provided during certain critical phases of the breeding cycle such as incubation onset and offspring hatching.

1.3. MATERIALS AND METHODS

Study area

The study was conducted in the administrative region of Biscay (northern Spain; surface area 2384 km2; coordinates from 43°11'00" to 43°12'70"N and from 3° 12'70" to 2°13'10"W). Barely 50 km separate sea level from the highest altitude (1480 m above sea level). The relief of the study area is abrupt and characterized by the presence of extensive urban and industrialized areas. More than 50% of the area is dedicated to forestry, at the expense of traditional, small-scale farming. A wet and warm Atlantic climate strongly influences the weather conditions. The average annual temperature is around 14°C and the mean annual precipitation fluctuates between 1,200 and more than 2,000 mm/m2 (Euskalmet, 2017), making this one of the highest rainfall areas in Europe (NOAA, 2016).

Study species

The Egyptian vulture is a medium-sized, long-lived, monogamous, trans-Saharan migratory raptor (Ferguson-Lees and Christie 2001). Continental Western European populations of Egyptian vultures spend the wintering season (and usually their first year of life) in the sub-Saharan Sahel region (García-Ripollés et al., 2010, López-López et al., 2014a). The European population is estimated at between 3,300 and 5,050 breeding pairs (BirdLife International, 2018), of which 1,270–1,300 pairs are found in the Iberian Peninsula (Iñigo et al., 2008). The European population has experienced a severe decline in the past few decades, mainly due to non-natural mortality caused primarily by poisoning (BirdLife International 2018). As with other long-lived scavengers, Egyptian vultures are highly philopatric to their breeding territories (Donázar 1993; Carrete et al., 2007). They breed in cavities and on cliff ledges located in open landscapes, usually in rugged, arid regions (Cramp and Simmons 1980; Donázar 1993). In our study area, the species inhabits mountainous areas, far from towns and villages, where extensive cattle farming and timber extraction are the main economic activities. The diet is based mainly on sheep and goat carcasses, and small or medium-sized animals, mostly road-killed mammals and passerines (Hidalgo et al., 2005). The main threat to the species in our study area is human disturbance associated with leisure activities and forestry during the breeding season (Zuberogoitia et al., 2008). However, these activities have been partially banned during this period thanks to the proposed effective mitigation measures outlined by Zuberogoitia et al., (2014).

Field procedure and data collection

We developed an intensive monitoring programme to study the breeding pairs from 1 February to 30 September 2017, thus covering the whole breeding period. During this time, we monitored five nesting sites intensively. The remaining Egyptian vulture breeding pairs (n = 15) were monitored intermittently, due to financial and logistic constraints. The five intensively monitored nests were observed weekly, with visits to each of the five nests at least once a week from the arrival of the adults at the breeding grounds until the departure of the offspring, while the remainder were monitored less frequently than the previous five (from 1 to 29 visits/nest), in order to assess breeding performance. Following Zuberogoitia et al., (2008), we monitored nest sites from vantage points that were situated far enough away to avoid disturbance, using 20–60x telescopes. We monitored the nests in all weather conditions. Overall, we spent 583.94 h monitoring the nests (n = 20) on 141 different days during the study period, with an average of 4.30 h/day (sd = 2.02, range = 1–9.42 h) being spent at each nest. One researcher (JM) carried out the intensive monitoring from sunrise to dusk, randomly visiting the five nests during mornings and afternoons throughout the study period. The non-intensive monitoring of the remaining 15 nests was performed from sunrise to dusk by four additional researchers who spent on average 3.91 h/day (sd = 1.75, range = 1–7.35 h) at each nest. At each viewpoint, we conducted intensive monitoring of nesting sites and their surroundings, both to detect individuals and to record their behaviour. We noted the location of every individual with regard to the nest. We also recorded the time (starting time and duration) of the arrivals and departures of each member of the pair to the nest; the behaviour of each target individual, as described below; and the location and behaviour of its mate. Gender identification was determined by using facial marks and facial cere colours, which are usually orange in males and yellowish in females (Negro et al., 2002, Margalida et al., 2012b). This feature was more evident when both members of a pair were together. We took photographs of each bird during the initial monitoring visits, recording facial marks, individual variation in the colour of the greater coverts and flight feathers, including their moult pattern, and colour rings from our long-term ringing project (Zuberogoitia et al., 2018). Gender identification was confirmed later by observing the position of partners during copulatory behaviour. Five of the 20 territorial pairs did not lay eggs. From the 15 pairs that started breeding, only 1 of them raised 2 fledglings and 10 raised 1 fledgling. Two of the intensively monitored pairs failed at an earlier incubation stage, whereas nestlings of another two intensively monitoring pairs died at an advanced stage of growth.

To analyse parental care investment, we collected data on nine different behavioural variables/activities per sex, which were recorded throughout the entire breeding period. We calculated the ratio of each activity as the number of times or percentage of time that the event was observed and the total hours of observation per day. The recorded activities were: (1) material deliveries: the number of times that material was carried to the nest; (2) nest arrangement: the number of times that adults arranged newly added or existing material in the nest; (3) incubation and nestling brooding: the percentage of time invested by adults in incubation and nestling brooding; (4) nestling attendance: the percentage of time invested by adults in offspring attendance; (5) egg turning: the number of times that eggs were turned; (6) changeovers: the number of times each parent was replaced by the other at the nest; (7) food provisioning: the number of times that food was provided to the nest; and (8) nestling feeding: the number of nestling feeding events (feeding events are particular behaviours, not necessarily occurring on every event of food provisioning).

The breeding season was divided into four different stages (see Zuberogoitia et al., 2008 for more details):(1) courtship period (February–March): including nest repair/construction, copulation and egg laying; (2)

incubation period (April–May): in our study area incubation started on average on 17 April 2017 (sd = 11.44 days, range = 1 April–14 May, n = 15) and spanned 42 days from incubation onset to hatching date; (3) nestling period (May–August): from the hatching date to the first fledging; and (4) fledging period (August–September): from the first fledging until departure from the breeding site.

We considered the week relative to (1) incubation onset and (2) nestling hatching as independent variables in order to test the effects of time on parental care. Likewise, this latter unit represents the breeding stage (i.e., from the hatching week until the end of the fledging period). We also recorded the mean temperature (°C), precipitation (mm), insolation (w/ m2) and humidity (%) relative to the surveyed hours in each day from the nearest meteorological stations of the Basque Meteorological Agency (n = 17 stations) (www.euskalmet.euskadi.net) (Zuberogoitia et al., 2014).

Statistical analysis

To analyse parental behaviour, we ran generalized linear mixed models (GLMM) with a Gaussian distribution, using the nine behavioural parameters as response variables. We considered the gender, period (week), and the four weather variables as independent variables. Gender was entered as a factor in the models. Territory was included as a random factor, to account for multiple measurements of the same breeding pairs. To avoid collinearity, we preliminarily calculated the Spearman's correlation coefficients (rs) for all pairs of variables using the 'rcorr' function implemented in the R package 'Hmisc' (Harrell 2013).

When two variables were highly correlated (rs > 0.5), we dropped collinear covariates, and the less biologically significant variable was consequently excluded from further analyses (Dormann et al., 2013). Thereby, we removed from the models insolation (w/m2), given its high correlation with temperature.

We computed all models, fitted by maximum likelihood methods, using the Laplace approximation, using the 'lmer' function as implemented in the 'lme4' package (Bates et al., 2015) for R (R Core Team 2016).We used the Akaike Information Criterion corrected for small sample size (AICc) for model comparison (Burnham and Anderson 2002). We used standard model selection procedures to interpret ΔAICc and AICc ω (weight) among competing models and considered models within 2 AICc units as having substantial empirical support (Burnham and Anderson 2002).

1.4. RESULTS

Copulatory behaviour

During the breeding season, we observed a total of 24 copulations, including both the intensively and intermittently observed pairs (n = 20). The mean distance of copulation attempts to the nest was 146.62 m (sd = 155.19 m, range = 0–530 m). The average copulation duration was 13.09 s (sd = 6.05 s, range = 0.5–25 s). After each copulation attempt, most pairs remained together (n = 18) and performed mutual preening. Copulations reached their maximum level one week before the onset of incubation and sharply decreased after this date (Spearman correlation test; rho = 0.545, P = 0.005, Figure 1.1).

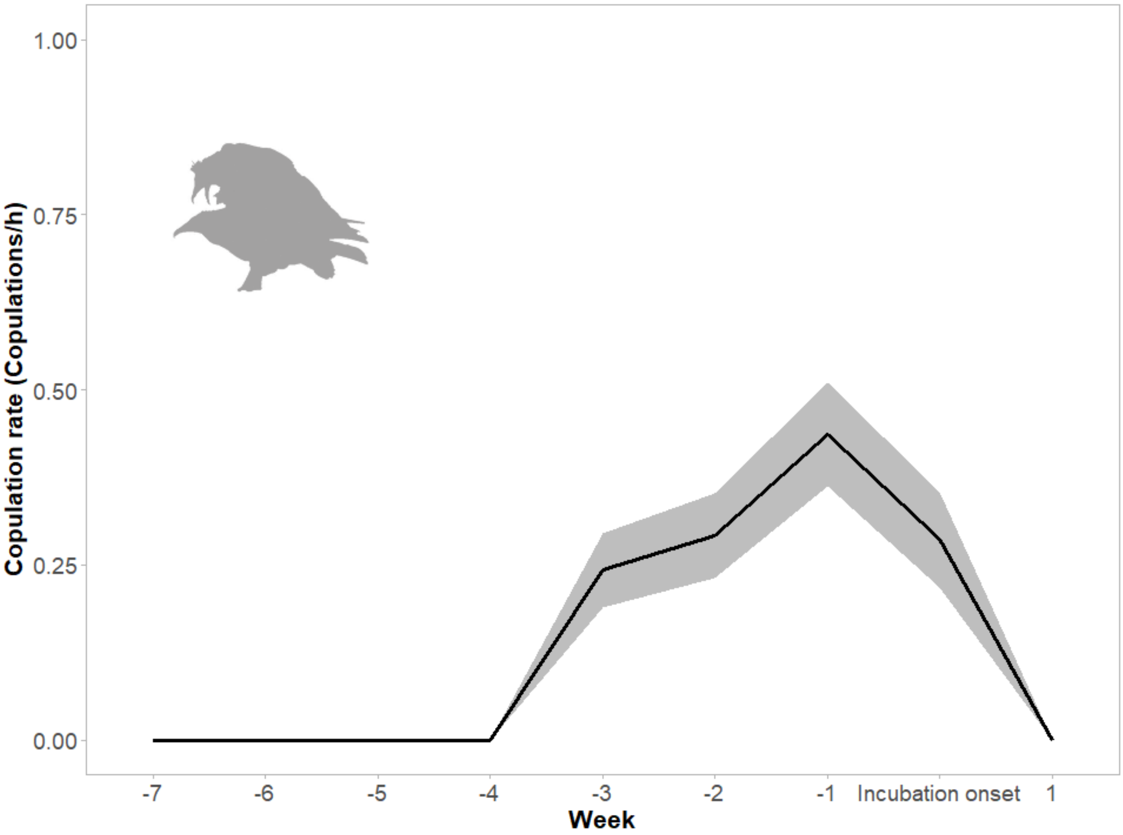

Figure 1.1. *Mean rate of copulations per week relative to the onset of incubation (week 0). The shaded area represents ± se.*

Nest building and maintenance

Egyptian vultures started to deliver material to the nest three weeks before incubation onset, reaching peak activity just one week before incubation started (Figure 1.2(A)). Material selected for nest construction was transported using the talons or the beak. During the nest-building period, males showed higher material delivery effort (0.67 deliveries/h, sd = 0.78, range = 0–2.75) than females (0.14 deliveries/h, sd = 0.07, range =0–0.37; Table 1.1; Figure 1.2(A)). However, results for the material delivery models showed a weak support for 'sex', which was included in the best model, but only at 1.5 ΔAICc to the null model. Both sexes invested a similar effort in nest arrangement (0.58 events/h, sd = 0.54, range = 0–2.5, for males; and 0.63 events/h, sd = 0.51, range = 0–2.14, for females; Wilcoxon test, W= 521, P = 0.54), not only during the nest-building phase, but also during incubation and the first weeks of nestling attendance (Tables 1.1 and 1.2, Figure 1.2(B)). We observed that nest arrangement consisted mainly of moving and resettling items that were carried to the nest during nest building or were left over from the previous breeding season. This activity peaked before the onset of incubation, and then decreased gradually before reaching a second peak around hatching time.

Incubation/brooding and nestling attendance

During incubation both males and females covered the clutch continuously, except for a few interruptions that occurred during mate changeovers and egg turning. Females invested significantly more time in egg incubation (61.45%, sd = 35.78, range = 13.7–93.9%) than males (38.54%, sd = 32.68, range = 0–100%, Table 1.1, Figure 1.3(A)). Brooding effort dropped after the third week of life of the nestlings, although adults continued brooding nestlings until the fifth week. Both sexes invested almost equal time in nestling attendance (females: 21.89%, sd = 27.40, range = 0–97.2%; males: 21.21%, sd = 26.97, range = 0–89.42%; Table 2.1, Figure 1.3(A)), although it decreased over time (Tables 1.1 and 1.2, Figure 1.3(B)).

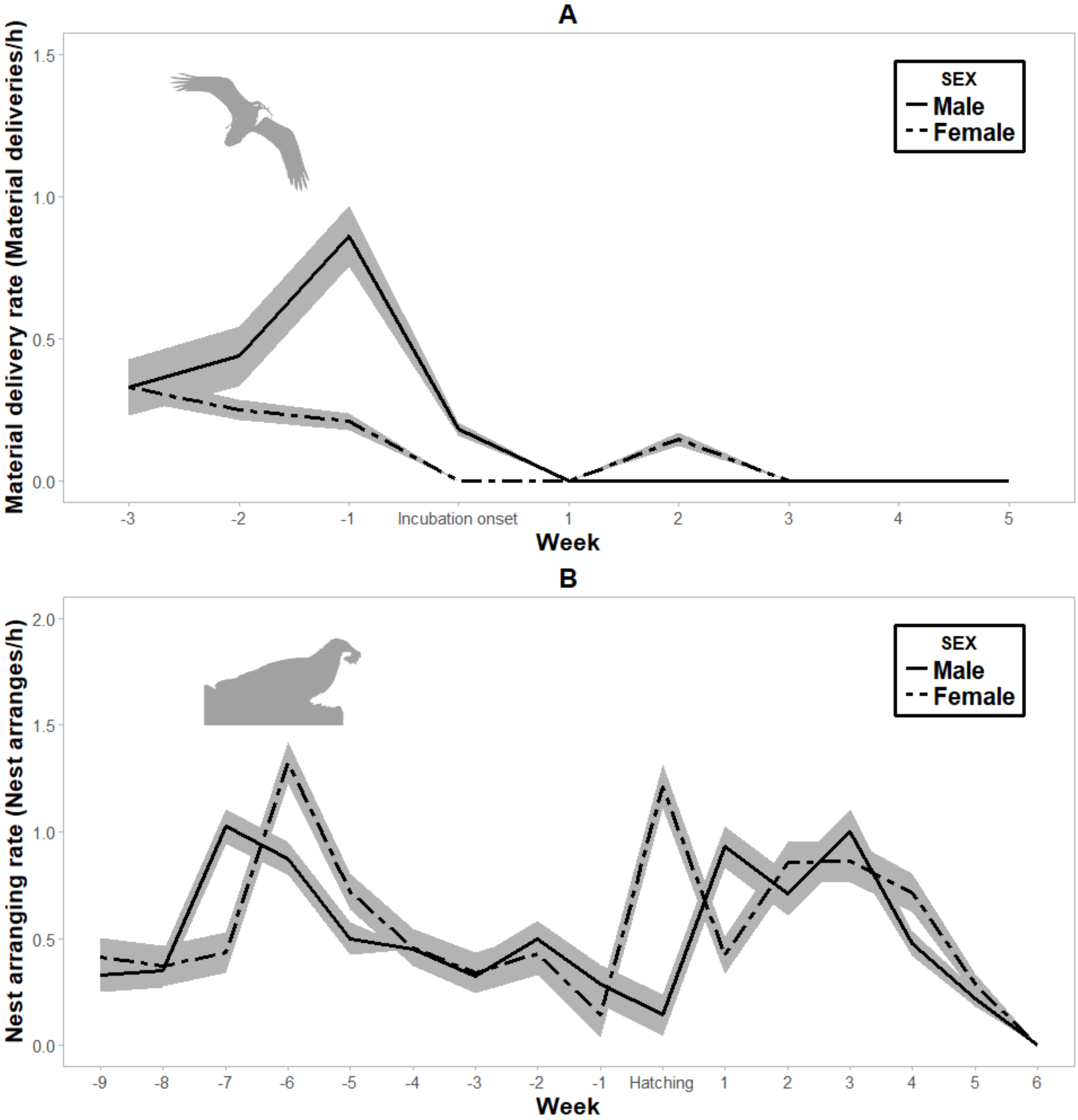

Figure 1.2. *Mean rate of delivery of material to the nest per week relative to incubation onset (week 0) (A). Mean nest arrangement rate (B) per week in relation to hatching week (week 0). The shaded areas in both graphs represent ± se.*

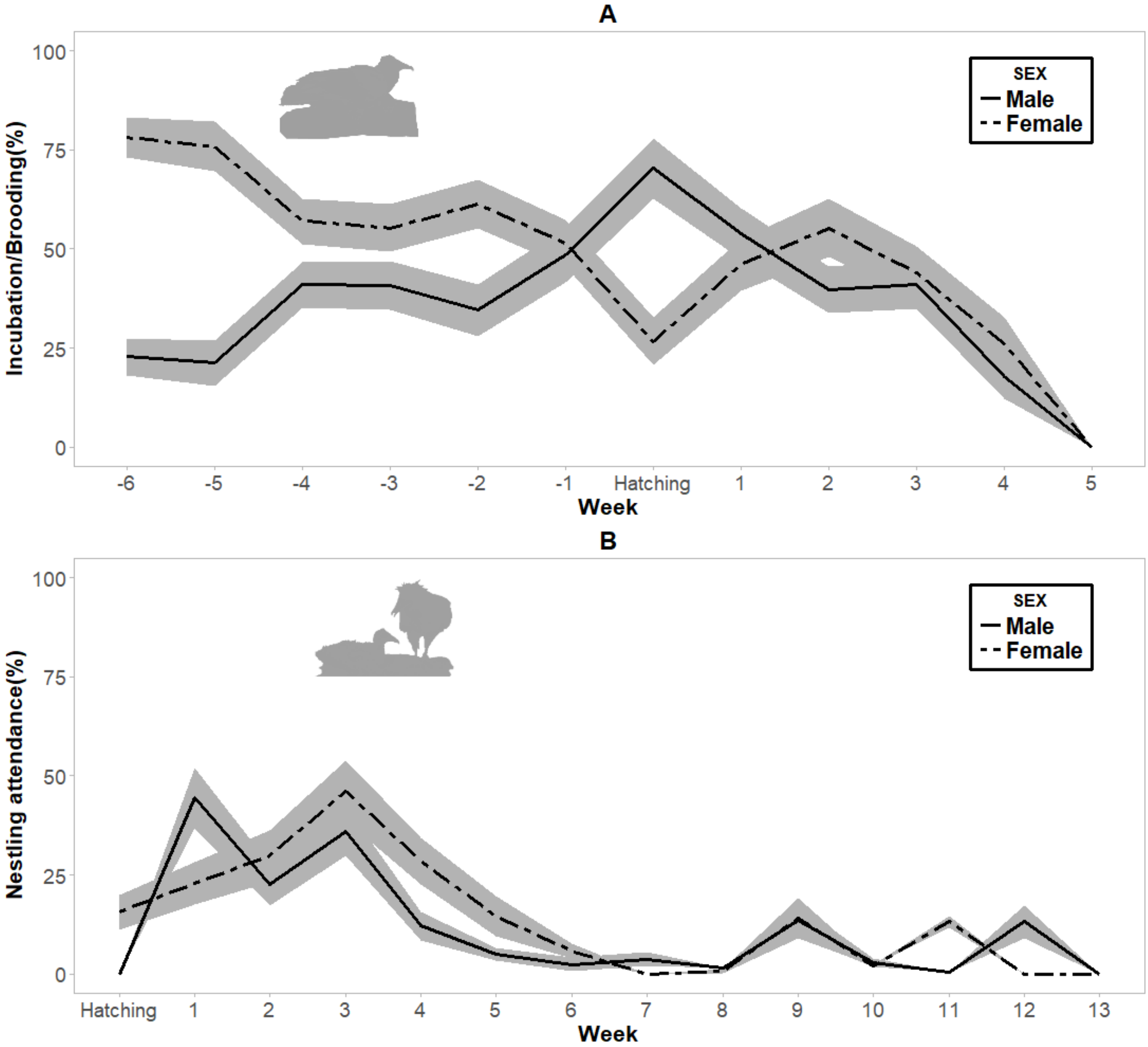

Figure 1.3. *Incubation and brooding investment (A) and nest attendance investment (B) per week in relation to hatching date (week 0). Values are expressed as a percentage of time. Shaded areas represent ± se.*

Table 1.1 *Results of the GLMMs for each behaviour recorded in Egyptian vulture pairs (n = 20) in northern Spain.*

Activity	Variables	AICc	ΔAICc	AICcW	*K*
Material delivery	Weather+Sex+Period	79.9	39	0.00	5
	Weather+Sex	65.6	24.7	0.00	4
	Weather+Period	67.5	26.6	0.00	4
	Sex+Period	44.6	3.7	0.15	2
	Weather	62.7	21.8	0.00	3
	Sex	**40.9**	**0.0**	**0.70**	**1**
	Period	44.6	3.7	0.11	1
	Null model	**42.4**	**1.5**	**0.00**	**-**
Nest arrangement	Weather+Sex+Period	136.1	31.4	0.00	5
	Weather+Sex	129.3	24.6	0.00	4
	Weather+Period	106.1	1.4	0.29	4
	Sex+Period	109.1	4.4	0.07	2
	Weather	124.7	20	0.00	3
	Sex	124	19.3	0.00	1
	Period	**104.7**	**0.0**	**0.59**	**1**
	Null model	107.6	2.9	0.00	-
Incubation/Brooding	Weather+Sex+Period	987.5	2	0.06	5
	Weather+Sex	988.6	3.1	0.03	4
	Weather+Period	995.6	10.1	0.01	4
	Sex+Period	985.8	0.3	0.21	2
	Weather	996.8	11.3	0.00	3
	Sex	**985.5**	**0.0**	**0.68**	**1**
	Period	994.1	8.6	0.00	1
	Null model	993.9	8.4	0.00	-
Egg turning	Weather+Sex+Period	55.5	41.4	0.00	5
	Weather+Sex	43.9	29.8	0.00	4
	Weather+Period	52.9	38.8	0.00	4
	Sex+Period	17.5	3.4	0.15	2
	Weather	45.3	31.2	0.00	3
	Sex	**14.1**	**0.0**	**0.79**	**1**
	Period	19.7	5.6	0.05	1
	Null model	25	10.9	0.00	-
Nestling attendance	Weather+Sex+Period	800.1	2.9	0.13	5
	Weather+Sex	808.5	11.3	0.00	4
	Weather+Period	802.7	5.5	0.00	4
	Sex+Period	**797.2**	**0.0**	**0.49**	**2**
	Weather	811.3	14.1	0.00	3
	Sex	804.9	7.7	0.00	1
	Period	799.9	2.7	0.35	1
	Null model	807.8	10.6	0.00	-
Changeovers	Weather+Period	**-41.8**	**0.0**	**0.83**	**4**
	Weather	-33.7	8.1	0.02	3
	Period	-38.5	3.3	0.16	1
	Null model	-38.6	1.2	0.00	-
	Weather+Sex+Period	-18.6	28.6	0.00	5
	Weather+Sex	-34.7	12.5	0.00	4
	Weather+Period	-36	11.2	0.00	4

Food provision	Sex+Period	-40.1	7.1	0.01	2
	Weather	-41.7	5.5	0.03	3
	Sex	-45.8	1.4	0.24	1
	Period	**-53.7**	**0.0**	**0.67**	**1**
	Null model	-47.2	6.5	0.00	-
Nestling feeding	Weather+Sex+Period	-40.1	24.1	0.00	5
	Weather+Sex	-41.3	22.9	0.00	4
	Weather+Period	-53.5	10.7	0.00	4
	Sex+Period	-56.6	7.6	0.02	2
	Weather	-48.7	15.5	0.00	3
	Sex	-51.5	12.7	0.00	1
	Period	**-64.2**	**0.0**	**0.97**	**1**
	Null model	-58.86	5.3	0.00	-

Notes: Models are listed from the most saturated to the simplest, including combinations of variables. For each model, the differences of AICc values (ΔAICc) concerning the best model and the number of parameters (K) are shown, as well as their relative weight (AICcw). The best models are highlighted in bold.

Table 1.2. *Results of GLMMs for the most parsimonious model for each breeding behaviour of Egyptian vultures.*

Values	**Estimator**	**St. Error**	***t***	***P***
	Material delivery			
Intercept	0.15	0.24	0.61	0.56
	Nest arrangement			
Intercept	0.35	0.17	2.07	0.06
Period	0.36	0.15	2.33	0.02
	Incubation/Brooding			
Intercept	51.22	10.90	4.78	**<0.001**
Factor(Sex)M	-14.82	6.64	-2.23	0.02
	Egg turning			
Intercept	0.29	0.06	4.77	**<0.001**
Factor (Sex)F	-0.21	0.06	-3.20	**0.002**
	Nestling attendance			
Intercept	-1.63	52.75	-0.03	0.97
Factor(Sex)	1.52	4.58	0.33	0.74
Period	-4.75	1.32	-3.58	**<0.001**
	Changeovers			
Intercept	0.03	0.20	0.16	0.87
Temperature	0.11	0.06	-1.53	0.03
Relative humidity	$5.14e^{-04}$	0.01	0.32	0.74
Precipitation	$2.93e^{-05}$	$9.96e^{-05}$	0.29	0.65
Period	$-6.38e^{-03}$	0.01	0.45	**0.001**
	Food provision			
Intercept	0.06	0.03	2.06	0.051
Period	0.01	0.01	2.31	0.02
	Nestling feeding			
Intercept	0.34	0.05	7.34	**<0.001**
Period	-0.02	0.01	-3.68	**<0.001**

Note: Significant values are highlighted in bold.

Egg turning

We observed a total of 61 egg turning events during incubation. Eggs were turned using the beak and the talons. Females invested more effort (0.45 events/h, sd =0.27, range = 0–0.83) than males (0.37 events/h, sd = 0.33, range = 0–1.16) in egg turning. This differential rate was consistent over time (Tables 1.1 and 2.1, Figure 1.4(A)).

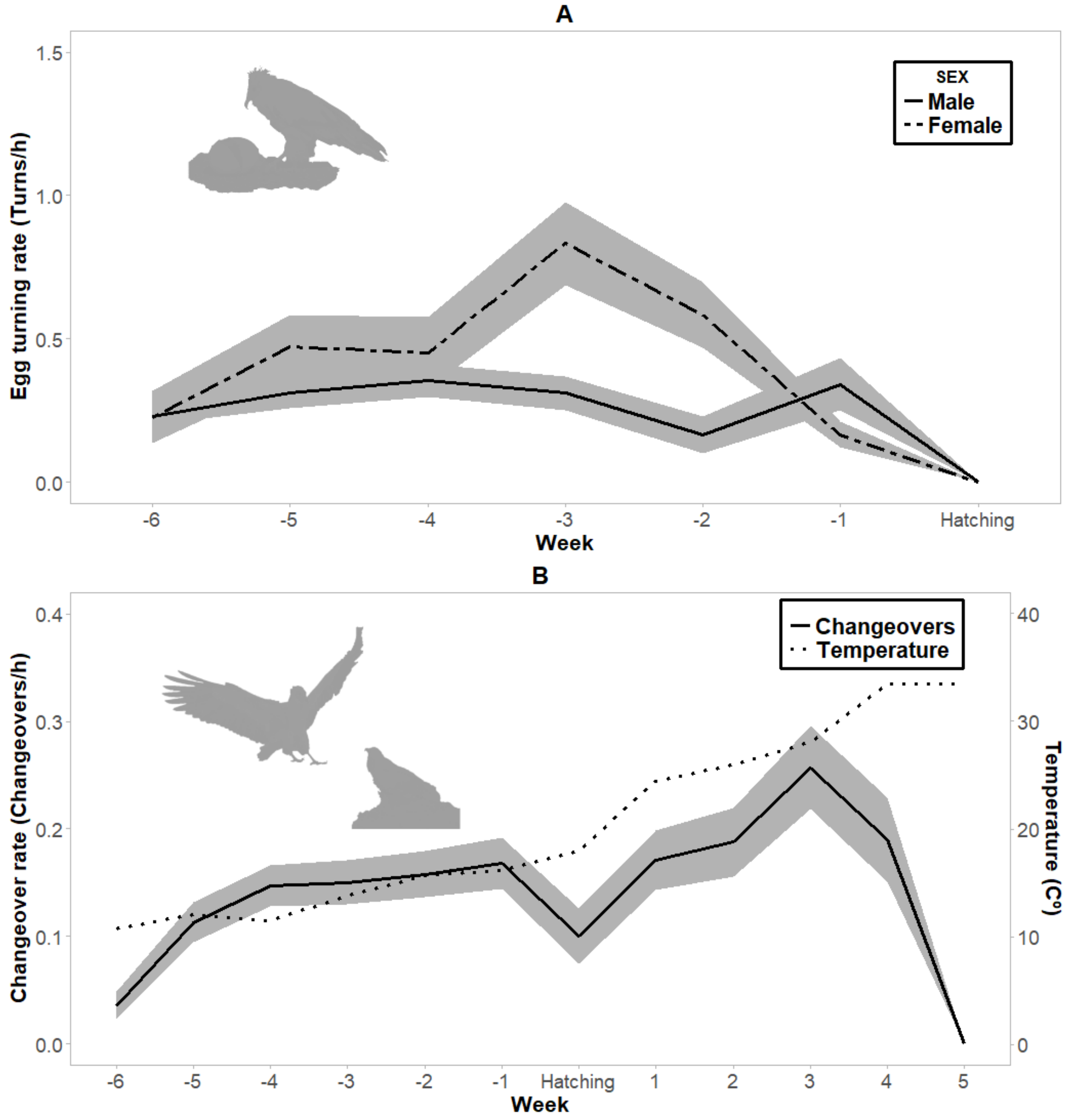

Figure 1.4. *The mean rate of egg turning (A) and mean changeover rate (B) per week in relation to hatching date (week 0). Temperature is expressed in degrees Celsius. Shaded areas in both graphs represent ± se.*

Changeovers

Egyptian Vultures carried out 0.16 changeovers/h (sd = 0.12, range = 0–0.375) during incubation and 0.17 changeovers/h (sd = 0.14, range = 0–0.5) during the brooding period. The changeover rate was related to weather and stage of the nesting cycle, although models showed a weak support (1.2 ΔAICc to the null model; Table 1.1). Changeover rates were low during the first stages of incubation, when temperatures were lower than those recorded later in the spring. Changeover rates increased from the hatching date onwards, until the nestlings were in their third week, but dropped afterwards when continuous brooding was unnecessary (Figure 1.4(B)).

Food provision and nestling feeding

Overall, we observed 56 food provisions and 42 feeding events. Adults always carried the food in the beak and there was no regurgitation of food to feed offspring. Once in the nest, adults prepared the food items, breaking them up to facilitate ingestion. The average food provision rate was 0.25 items per hour for males (sd = 0.15, range = 0–0.75) and 0.28 items for females (sd = 0.16, range = 0–0.67), and there were no significant sex differences (Table 1.1). There were no sex differences in feeding rate (0.24 events/h for males; sd= 0.16, range = 0–0.75 and 0.26 events/h for females; sd= 0.11, range = 0–0.5, Table 1.1). However, both provisioning and feeding rates decreased over time (Tables 1.1 and 2.1), being higher during the first weeks after hatching and slightly decreasing as nestlings grew (Figure 1.5(A,B)). Adults still fed juveniles occasionally even when they were ready to fly.

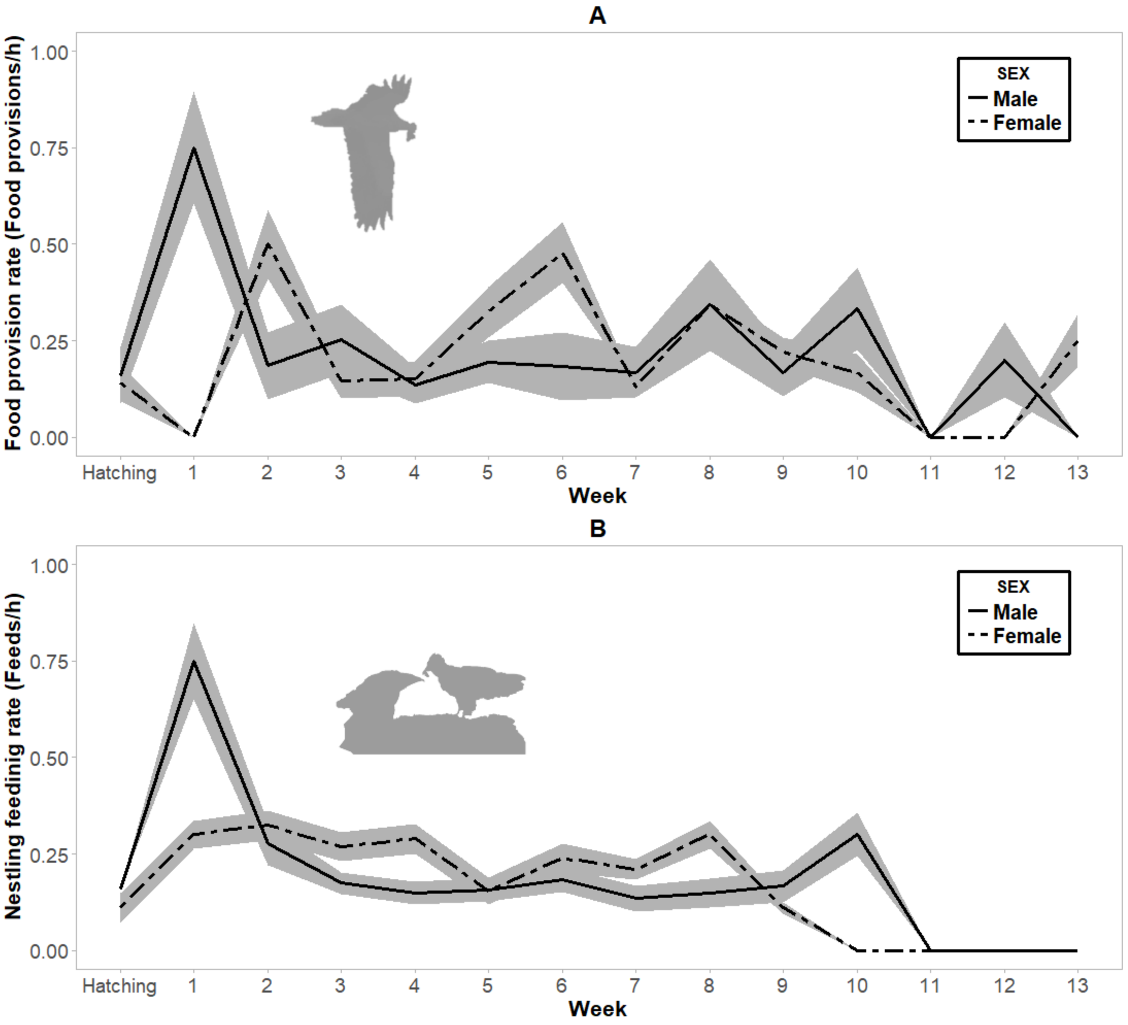

Figure 1.5. *Mean food provisioning rate (A) and mean nestling feeding rate (B) per week in relation to hatching date (week 0). Shaded areas in both graphs represent ± se.*

1.5. DISCUSSION

Our results showed that the Egyptian vulture exhibits biparental care throughout its extended breeding period of approximately 24 weeks. However, we observed behavioural asymmetries in the parental investment of each sex depending on specific activities. Furthermore, we found that parental investment type changed over the course of the breeding period in both sexes with regard to almost all activities.

Surprisingly, although weather conditions might constrain optimal embryo development and thus increase parental care by mates (Bulla et al., 2015), we found that weather did not influence parental investment during critical stages, for example, during incubation and brooding. Normally, Egyptian Vultures use cavities and holes for nesting and hence nests are protected from meteorological events (i.e., rain and storms). This could help to maintain an adequate environment for eggs and nestlings by reducing temperature variation.

The breeding cycle of the Egyptian vulture starts with nest repair (in the case of reusing a nest site, Donázar 1993) or new nest building, and courtship. We observed that both activities took place simultaneously, which suggests a common stimulus (i.e., sperm viability and the fertile female period; Donázar et al., 1994). Egyptian vultures started copulating 25 days before the onset of incubation, showing a peak one week before. This suggests that copulations outside the fertile period could be related to pair bonding, mate assessment and territorial behaviour (Newton 1979, Negro and Grande 2001). The maximum peak in copulation rate occurred a few days before the laying of the first egg and continued after the laying of the second egg and the onset of incubation (Egyptian vultures usually lay two eggs, with an interval of 3–4 days; Donázar 1993, Margalida et al., 2012a). Copulation activity and nest material delivery took place at the same time and followed similar trends during the weeks before incubation onset.

After the onset of incubation, both sexes shared the incubation effort. From incubation to the early stages of the post-hatching period, both sexes continuously covered the clutch or nestlings, except for the time spent in changeovers, egg turning and nest repairing activities. The regular presence of one of the adults at the nest during incubation and brooding may be necessary to protect the eggs or nestlings from low temperatures, insolation and predation (Al-Rashidi et al., 2010, Bulla et al., 2014, Deeming and Reynolds 2016 and references therein). However, our results showed sex asymmetry in incubation behaviour, with females spending significantly more time incubating and egg turning, although there was compensation by each mate in nest attendance (Figure

1.3(A)). Given that incubation and brooding are energy-demanding activities (Bulla et al., 2014), compensation during incubation may be necessary for Egyptian Vultures to deal with: (1) the difficulty in searching for carrion, which is a spatially and temporally unpredictable resource (Deygout et al., 2010, Monsarrat et al., 2013, López-López et al., 2014b) and (2) the excessive costs of continuous incubation by only one parent (Brunton 1988). In fact, our results showed that males progressively invested more effort in incubation, from 25% of the time during the first week to 70% during the hatching week. Nonetheless, the low variability explained by sex in our model (only 4%; Table 1.1), suggests that other factors such as individual traits (e.g., age, experience and personality; Sanz-Aguilar et al., 2017, Zuberogoitia et al., 2018) and those related to nest structure and specific micro-environmental characteristics of nest placement could also affect behavioural differences during incubation (Deeming and Reynolds 2016). Similarly, we also observed differences between sexes in other activities associated with incubation, like egg turning. Egg turning is crucial for maintaining embryo development and presenting the chick in the correct position for successful hatching (Deeming 2002, Wilson et al., 2003). Given the importance of this activity, the higher investment of females and the absence of partial or total compensation by males might suggest sex-role specialization (Figure 1.4(A)).

All activities related to the rearing of nestlings until the fledging stage were carried out by both parents and decreased in parallel with the growth of the nestlings, as described in other species of the same guild (Donázar 1993, Margalida and Bertran 2000). During the first month of life, nestlings were continuously accompanied by one parent because of their limited thermoregulatory capacity and to reduce predation risk (Hohtola and Visser 1998, Deeming 2002, Margalida et al., 2007). A reduction in the time spent in nestling attendance occurred from the third week onwards, corresponding with the moment at which nestling energy requirements and thermoregulation ability increases (Newton 1979, Komen 1991). This pattern is also related to the increase in foraging time and to the rise in the number of prey delivered to the nest (Margalida and Bertran 2000, Holland et al., 2017). Other factors, such as lower predation risk and better meteorological conditions as the breeding season advances, could also explain our results (Dodge et al., 2014). During the final days of nest attendance, parental care was reduced to only food provisioning and some flights in front of the nest.

Species-specific life-history traits, in addition to ecological and environmental conditions, also influence parental care (Klug et al., 2013). In this context, our results showed that changeovers were not only dependent on the breeding stage but also on particular environmental conditions, mainly temperature. During incubation and offspring rearing, changeovers are necessary to share breeding costs (Marasco and Spencer 2015), and to fit parental effort to the nestlings' development requirements. This explains observed differences in changeovers during the preand post-hatching period. During the nestling stage, the changeover rate increased in parallel with temperature over time (Figure 8(B)). In fact, the poikilothermic-homeothermic transition of nestlings elicits changes in the amount of care provided. Moreover, changeovers are related to the rate of successful foraging (Newton 1979, Cresswell et al., 2003, Rollack et al., 2013), which is also related to food availability (Donázar 1993, Monsarrat et al., 2013, Cortés-Avizanda et al., 2016).

According to the pattern observed in similar species with biparental care (Margalida and Bertran 2000), food provisioning and feeding rates were equally divided between both mates throughout the nestling period. During the first weeks after hatching, we observed that the feeding rate by adults was probably a response to the increasing food requirements of nestlings (Newton 1979) and also to other processes affecting food availability in the surrounding area (Bruun and Smith 2003). In subsequent weeks the provisioning rate decreased since the increasing demand of nestlings obliges adults to increase the quantity of food supplied on each visit to the nest. This suggests that adults were forced to expend more time foraging. Furthermore, this could explain the lower contribution of both mates to brooding and nestling attendance. Similarly, the nestling feeding rate decreased with time because the young birds became more skilled at dealing with prey items, and most of the food was self-consumed (Watson 2010, Sonerud et al., 2014a, Bassi et al., 2017). During the final weeks before fledging, food provisioning was maintained but no feeding occurred. This coincided with less time expenditure in food preparation by adults, which suggests an increase in the ability of nestlings to manipulate prey remains. This also compensated for the increased parental effort in searching for food, since the adults spent less time feeding their offspring (Deeming and Reynolds 2016). Likewise, this fact could also prevent any conflict between offspring and parent requirements as other authors have previously assessed (Royle et al., 2012, Iserbyt et al., 2015).

Overall, our findings suggest that Egyptian vultures invested similar parental effort during the breeding period, although with different degrees of intensity depending on the stage of the cycle were observed. This suggests that biologically relevant events, such as incubation and hatching date, could drive parental investment (Royle et al., 2012). This is of key importance in explaining observed behavioural patterns in this species. Our results showed that parental care was similar with regard to certain activities, such as nest arrangement, nestling attendance, food provisioning and nestling feeding. However, sex-specific roles were observed for some activities. Females contributed more to incubation, brooding and egg turning activities, while males participated more actively in other tasks such as the delivery of material to the nest. In fact, similar results were found in the bearded vulture Gypaetus barbatus (Margalida and Bertran 2000, Bassi et al., 2017) and griffon vulture Gyps fulvus (Xirouchakkis and Mylonas 2007). The absence of apparent differences in both sex roles suggests a balanced distribution of parental care effort, which implies that neither sex could meet nestling requirements alone without help from the mate. Finally, the number of changeovers observed over time suggests that particular environmental conditions and the breeding stage could also explain variation in parental care in long-lived species

CHAPTER 2

Applying economic and ecological criteria to design cost-effective monitoring for elusive species

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2.1. ABSTRACT

Monitoring programs of long-lived and elusive species often incur high costs in terms of field effort and economical budget, but both components are often considered separately. Also, there is scant information on the use of reliable detectability estimates under imperfect detection conditions based on environmental factors, which is key to accurately estimate financial costs and define optimum monitoring strategies. In this study, we use an intensive survey program (2017–2018) of the Egyptian vulture *Neophron percnopterus* population in Bizkaia (northern Spain) to model detectability at nests taking into account imperfect detection. Our main goal is to estimate both the number and timing of surveys, and the allocation of survey effort/costs, in order to design cost-effective monitoring programs. Firstly, throughout the breeding seasons, we used focal sampling methods on 19 nesting territories historically occupied by the study species. Then, we employed single-season occupancy models to assess detectability considering different levels of effort (from 1 to 5 h) at each nest, including both species breeding phenology and environmental covariates that could modify detection probabilities. Our results showed that the species was more likely to be detected in dry years and when the nest was visible during the nestling period, investing five hours of the survey. The optimal number of monitoring days required to account for 95% of false negatives for a single nest was eight days, investing one hour per breeding stage. The optimal monitoring cost was reached in dry years when the nest was visible, investing one hour per breeding stage (ca. 242 €/nest). The cost of monitoring was highest in rainy years when the nest was not visible (ca. 1954 €/nest). The cost of monitoring entire occupied nesting territories without accounting for covariates was of 23,294 € (n = 19). In order to offer reliable species assessments, design rigorous surveys and accurately estimate monitoring costs, studies should account for imperfect detection, particularly for long-lived vertebrates. Here, we show that monitoring

programs ought to (a) consider the effort necessary to detect the species while accounting for species-specific breeding ecology and, (b) adjust field effort based on lower costs and environmental conditions. Our results provide simple and practical guidelines for the efficient allocation of human and economic resources, which could be of interest to those practitioners involved in the regular monitoring of elusive species.

2.2. INTRODUCTION

Long-term monitoring protocols are critical to establishing baseline data for the evaluation of conservation and management actions (Nichols and Williams, 2006; Lindenmayer and Likens, 2010; Lindenmayer et al., 2012; Bal et al., 2018). Long-term surveillance programs provide ecological insights by indicating the directionality and magnitude of temporal trends in biodiversity (Wintle et al., 2010). Moreover, monitoring programs provide essential information on site occupancy by gathering detection and non-detection data across space and time (MacKenzie et al., 2018), which is essential for the adequate management of most endangered species. Most of the key research areas in conservation biology depend on occupancy data (Richardson and Whittaker, 2010), which can be difficult to obtain because of the imperfect detection of the study species during monitoring surveys (MacKenzie et al., 2006; Wintle et al., 2012). Detectability studies are often used to interpret observational data and determine, with confidence, whether a species is present at a given site when not detected (i.e., false negative). This could help to understand the relationship between species occurrence and their environment (MacKenzie et al., 2006).

Monitoring programs do not always adequately consider when or how much monitoring effort should be invested (Yoccoz et al., 2001). This can lead to the gathering of information eventually irrelevant to management (McDonald-Madden et al., 2010), and the misclassification of the threat/conservation level for rare, cryptic and elusive species (see also Refsnider et al., 2011; McGrath et al., 2015; Barata et al., 2017). Moreover, although most of the monitoring programs are underresourced (Lindenmayer et al., 2012) and the largest portion of a monitoring program budget is spent on data collection (Caughlan and Oakley, 2001), they do not usually consider and report economic costs or constraints (but see Carlson and Schmiegelow, 2002; Field et al., 2005; Pollock, 2006). In these cases, misallocation of available resources could occur (Bailey et al., 2014). Therefore, decision making in endangered species management requires a combination of ecological knowledge with knowledge of time and financial constraints (Maxwell et al., 2015). Occupancy/detectability studies that take into account imperfect detection are useful to reduce management uncertainties and to determine the most cost-effective actions (i.e., when, and how much, to survey) in terms of the optimal monitoring strategy (MacKenzie and Royle, 2005; Sewell et al., 2012; Runting et al., 2013).

The importance of accounting for imperfect detection in assessing spatiotemporal changes in occupancy and detection has been demonstrated in previous studies, mostly for threatened and elusive species (Karanth et al., 2011; Sunarto et al., 2012; Srivathsa et al., 2018). Longterm monitoring programs grounded on simple and cost-effective methods (like visual surveys) are useful when attempting to minimize subjectivity (e.g., estimating the prior probability of occupancy; Blanc et al., 2014). This is the case for many reptiles and amphibians (Mazerolle et al., 2007; McGrath et al., 2015), plants (Chen et al., 2013), large mammals (e.g., Foose and van Strien, 1997) and birds (Einoder et al., 2018). Among birds, vultures have received particular attention due to their globally endangered status and for being crucial ecosystem services providers (e.g., Buechley and Şekercioğlu, 2016; Mateo-Tomás et al., 2017; Safford et al., 2019; Sebastián-González et al., 2019). Although the Egyptian vulture (Neophron percnopterus) has been studied throughout its breeding range including Bulgary, Macedonia, Greece, Italy, Sicily, France, Portugal and Spain (Del Moral and Martí, 2002; Del Moral, 2009; BirdLife International, 2020), its low density, elusive behavior, and secretive habits make this a difficult-tomonitor species (Badia-Boher et al., 2019; Olea and Mateo-Tomás, 2011). Few studies have explored the ability to detect changes in trends and occupancy rates in the breeding populations of this elusive bird (Olea and Mateo-Tomás, 2011) and, to the best of our knowledge, none has examined the economic costs needed to inform monitoring programs.

In this paper, we take advantage of a long-term (2000–2018) monitoring program of the Egyptian vulture population in Bizkaia (northern Spain). Here we assume that optimal effort-cost relation is that which is efficient in terms of minimum monitoring cost and invested effort (Bailey et al., 2014) while accounting for biologically significant variables. In this context, our goals are: (1) to estimate the effect of sampling effort, breeding stage and environmental covariates on species' detectability and, (2) to optimize monitoring protocols by accounting for imperfect detection in surveys including both economic and ecological criteria.

2.3. MATERIALS AND METHODS

Study species

The Egyptian vulture is a medium-sized, long-lived, and long-distance migratory scavenger (Ferguson-Lees and Christie, 2001). Western European populations spend the wintering season (and usually their first years of life) in the sub-Saharan Sahel region (Grande et al., 2009; López-López et al., 2014). It is listed as globally endangered due to severe declines experienced throughout its range (BirdLife International, 2020). It breeds in cavities and on ledges on cliffs located in open landscapes, usually in rugged and arid regions (Phipps et al., 2019; Cramp and Simmons, 1980). Breeding pairs arrive from their winter grounds in Africa in late February and early March and remain in their territories until mid-September/October (López-López et al., 2014). During this period, they usually rear one or two chicks. They generally reuse the same nest unless they are disturbed during sensitive phases, or the nest area is altered (Zuberogoitia et al., 2008; Morant et al., 2018). In our study area, the species inhabits mountainous landscapes, far from towns and villages, where extensive cattle farming and timber extraction are the main economic activities.

Study area

The study was conducted in Bizkaia (northern Spain; area 2384 km2; coordinates from 43°11'00" to 43°12'70" N and from 3°12'70" to 2°13'10" W; Figure 2.1). Barely 50 km separate sea level from the highest altitude (1352 m.a.s.l). The relief is abrupt and characterized by the widespread presence of urban and industrialized areas. More than 50% of the area is dedicated to coniferous forestry for timber harvesting, at the expense of traditional, small-scale farming. The weather is dominated by a wet and warm Atlantic influence and is included within the rainiest regions of Europe (www.climate-charts.com/ World-Climate-Maps.html). The mean annual precipitation ranges from approximately 1200 to 2000 mm, and the annual mean temperature is 14 °C (Euskalmet, 2018).

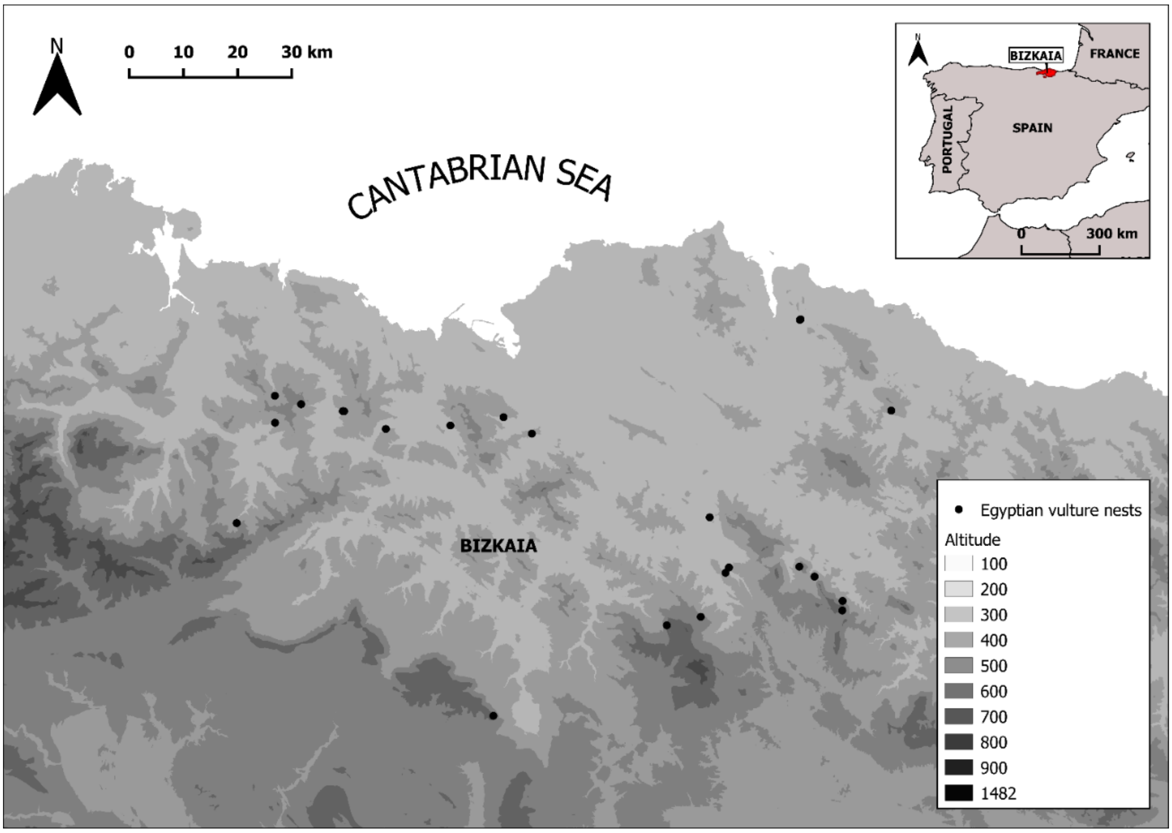

Figure 2.1. Location of the study area (upper right) including Egyptian vulture occupied nests (n = 23; black dots) during the study period (2017–2018).

Field procedure and data collection

Every year, from 2000 to 2018, we carried out surveys from February to September to determine the location of all territories and nests and to examine changes in occupancy, breeding parameters, and population trends. From 2000 to 2016 we identified 23 territories and 70 used nests within them (mean ± SD = 3.04 ± 1.43 nests/territory, range = 1–6). During this period, pairs that established a nest within a territory remained until the end of the breeding seasons regardless of breeding failure (see Morant et al., 2018 for further details). Based on previous knowledge, we designed an intensive survey schedule in 2017 and 2018. We took advantage of the knowledge of previous laying dates, nest/territory availability, individual preferences, and behaviour to assure the programmed objectives. Two of the authors, experienced observers (JM and IZ), carried out all the fieldwork, using all the daylight period and changing the monitoring timetable of each territory from one day to another (e.g., one day during the first hours after sunrise, another during afternoon). We used 20–60 × telescopes to observe nests from vantage points located far enough to minimize disturbance to the breeders (mean distance: ca. 1000 m; range: 442–2826 m; for more details, see Zuberogoitia et al., 2008). Surveys, which were divided into periods of one hour, lasted up to five hours or until we assured detection of the species using the nest (e.g., carrying material, incubating, feeding nestlings). We did not consider observations of individuals flying or perched until they used the nest since there is an abundant floater population in the study area. Therefore, our response variable was the positive/negative observation of at least one adult in the nest, developing the expected behaviour in each breeding stage.

Surveys completed in empty territories allowed us to confirm vacancies; nevertheless, these surveys were not taken into account in detectability analysis. We only used known, occupied territories that were later confirmed; thus, we focused data on the 19 target nesting territories in both years. We must consider that among the monitored nesting territories, seven pairs changed the nest from one year to another, one pair did not breed one year, and another pair did not breed the two years, although these two pairs remained in their territories. We suspected that the probability of detection could vary all over the breeding cycle related to changes in breeding behaviour (e.g., during incubation regular changeover rate is expected, or during nestling phase adults must invest a great effort to take care of and feed chicks). To model the possible influence of stage of the breeding cycle in detection probability, we divided each breeding stage into three periods of unequal length because they depicted behavioural phases rather than time (Tapia and Zuberogoitia, 2018; Morant et al., 2019). These periods were: (1) courtship: including nest repair/construction, copulation, until egg-laying (March-April); (2) incubation (April-June): in our study area, incubation started on average on April 17th (range = 1st April-14th May, n = 23 between 2017 and 2018) and spanned 42 days until hatching date; and (3) nestling period: from the hatching date to the first fledging (June-September).

Data analysis

We estimated the probability of detecting Egyptian vulture nests (p) following methods developed by MacKenzie et al., (2002; 2006) and implemented in the PRESENCE software (Hines, 2006; MacKenzie et al., 2018). The model assumes that the population is closed, referred to as the closure assumption. The monitored territories of Egyptian vulture remained stable, and territories did not change throughout the study period. Therefore, there were no changes in occupancy (ψ) at the surveyed sites. Known territories were treated as sample sites and each survey as an independent sample. Covariates were incorporated in the logit models for modeling detection probability (MacKenzie et al., 2002; 2006). Detection probability was modeled as a function of either site-specific or survey-specific covariates (Bailey et al., 2007). To identify the source of variation in detection probability, and based on previous studies (Olea and Mateo-Tomás, 2011; Zuberogoitia et al., 2008), we selected five covariates (for further details see Table 1). We used descriptors of nests and surrounding areas as site-specific covariates; and variables changing in time as survey-specific covariates (Bailey et al., 2007). Sitespecific covariates included: (1) area of the visual basin at an angle of 180° (km2), centered in the observation sites towards nesting cliff (VIEWSHED); (2) nest visibility from the observation sites (VISIBILITY: yes/no), and (3) a proxy of annual weather condition (WEATHER, dry/ rainy: 2018 was a particularly rainy year, whereas 2017 was a dry one) (Table 1). Survey-specific covariates included: (1) breeding stage (PERIOD), a categorical covariate with three levels (i.e., courtship, incubation, and nestlings), and (2) survey effort (EFFORT), a categorical variable (from 1 to 5 h) (Table 2.1).

We ran single-season models, instead of multi-season models, because we considered inter-year weather variability as a site-specific covariable (WEATHER). We built a set of models in which occupancy was constant, ψ(.), and the logit link was used to model detection probability against the 28 possible combinations of the covariates, including the null model (ψ(.)p(.)) (MacKenzie et al., 2006). To reduce the number of models, we grouped PERIOD and EFFORT and analysed them as a single covariate with three and eight levels respectively (see Olea and Mateo-Tomás, 2011, for a similar approach).

We compared models using the Akaike Information Criterion, corrected for small samples (AICc; Burnham and Anderson, 2002). We used standard model selection procedures to interpret changes in AICc (ΔAICc), and considered models within two AICc units of the best model as having substantial support (Burnham and Anderson, 2002). Taking advantage of the balanced representation of variables in the set of models, we calculated AICc model weights (AICc ωi) and the multimodel averaged relative importance value of each variable, as the sum of the AICc ωi of all the models including that variable (Burnham and Anderson, 2002; Giam and Olden, 2016). We also reported the parameter estimates and standard errors (SEs) from the model with the highest AICc weight within the set of candidate models. For each covariate in the best model, we calculated their corresponding odds-ratio (OR), which measures the direction and magnitude of discrepancy between proportions (Nad'o and Kaňuch, 2018). Recall that the logit-link is the natural logarithm of the odds of a 'successful' event (in this case, the observation of adults in the nest), and that to calculate an oddsratio, we can take the inverse-logarithm of the beta parameter (MacKenzie et al., 2018). The model fit and overdispersion were assessed by a goodness-of-fit test (MacKenzie and Bailey, 2004), based on parametric bootstrapping

Minimum number of surveys required to determine absence with 95% confidence

Following previous works, we obtained absence probability (1-p), which would be the detection probability of true absence that, in our case, would be zero (e.g., Olea and Mateo-Tomás, 2011; Zuberogoitia et al., 2011). The probability pn of detecting a species at least once after (n) repeated visits (or surveys) to an occupied site is given by $pn = 1 - (1 - p)n$, where p is the per-visit detection probability of the species (MacKenzie et al., 2006). We also considered corrections proposed by Kéry (2002) and Wintle et al., (2012), although, in our case, prior occupancy was 1. From these predicted detection rates, we estimated the number of surveys needed to obtain 95% confidence in occupancy determination.

Table 2.1 *Covariates considered in detectability models.*

Variables	Definition	Method	Hypotheses
VIEWSHED	The visual basin of each observation point measured in square kilometers (km^2).	We used observation points recorded in a shapefile and DEM (25m resolution) to calculate the total area (km^2) that is covered from each observation point at an angle of 180 degree (Visual basin). Analyses were carried out by using observer points tool implemented in ArcGIS 10.5 for analysis (ESRI, 2016).	The probability of detecting species can vary between observation points. (i.e., open areas with wide visual basin could facilitate detection).
VISIBILITY	The nest was visible or not (0/1) from the observation points.	We specify whether the nest was visible or not from observation points during courtship, incubation or nestling period.	The visibility of the nest can affect detectability of the species. In some cases it is possible to see the nest but some other nests are hidden in caves or behind vegetation, and it is needed longer surveys to assure breeding status.
WEATHER	Differences between two survey years with totally different weather conditions (Rainy year/Dry year).	We divided two survey years into rainy year (monthly mean of 2018 = 79.23 mm, SD = 70.71 mm, range = 8.5 - 219.8 mm) and dry year (monthly mean of 2017 = 56.06 mm, SD = 18.17 mm, range = 20.3 - 81.8 mm) with respect to monthly average precipitation (mm) throughout the species breeding period (from February to September) of the study area in the last ten years (monthly mean of 10 years period = 72.6 mm, SD = 61.04 mm, range =4.4-301.3 mm) (http://www.euskalmet.euskadi.net).	Since our data suggest that precipitation is one of the main factors affecting breeding success and it determines breeding failures (Zuberogoitia et al., 2014), and therefore during rainy years the increased number of failures may negatively affect detectability throughout the breeding season and significantly affect the detection capability of the observers (Ilknayan et al., 2013).
PERIOD	Breeding period when surveys were conducted; (1) Courtship, (2) Incubation and (3) Nestlings.	We divided breeding into three phases according to the breeding phenology of the species (see methods).	The species is more likely to be detected during some phases of the breeding period due to specific behaviours at each stage (e.g. when mates spend more time at nest feeding offsprings; Donázar, 1993; Tapia and Zuberogoitia, 2018).
EFFORT	Time (hours) invested in each survey/nest (1-5 hours).	We divided monitoring into 1, 2, 3, 4 and 5 hour periods.	In elusive species as Egyptian vultures, we may expect that the longer the survey, the higher the detectability is (Olea and Mateo-Tomás, 2011).

Estimation of monitoring costs

To estimate monitoring costs, we divided costs into three elements: (1) costs of a field-work by a skilled technician, (2) travel expenses, and (3) cost of displacement. We computed total costs as (1) + (2) + (3) (for details, see Appendix A Supporting information A.1). Once we obtained the total cost for each case, we assessed the optimal monitoring cost as the lowest value in terms of both effort and money. Finally, we applied this optimal cost to estimate the cost of monitoring the total number of occupied nesting territories (n = 19).

2.4. RESULTS

In 2017, we completed 211 surveys, which summed to 838 h; and, in 2018, 155 surveys and 469 h. We detected Egyptian vultures in their nests in 20% of the surveys completed during the courtship stage, in 61% of the surveys completed during incubation, and in 75% of the surveys completed during nestling. The naïve occupancy value for the best model was 0.86, whereas the estimated occupancy (ψ) was 0.88. The best model included two site-specific variables (VISIBILITY, YEAR) and two survey-specific variables (PERIOD, EFFORT) (Table 2.2). Detectability was highest when the nest was visible (AICc ωi = 0.98), in the dry year (AICc ωi = 0.9), and it increased throughout the breeding period (AICc ωi = 0.98) and with monitoring effort (AICc ωi = 0.96) (Figure 2.2). The probability of detecting the species was almost ten times higher during the nestling period than during courtship (see OR in Table 2.3). Likewise, the highest detection probability was reached by investing five monitoring hours whatever the breeding phase (Figure 2.2). The only variable excluded from the best model was VIEWSHED. The models, including this variable, only had 0.48 of the total weight. AICc increased by 0.06, where VIEWSHED improved the model by 1.94 units, not enough to improve the two penalty units (Burnham and Anderson, 2002; Arnold, 2010). The best model fitted correctly ($\chi 2$ = 181.5, p = 0.69) and showed no overdispersion ($\hat{c}$ = 0.81, 1000 bootstrap samples).

Table 2.2. *Summary of the best models (up to two AICc units from the top-ranked model) obtained in the model selection procedure for estimating detectability in the Egyptian vulture. Model AICc values, the relative difference in AICc units compared with the top-ranked model (ΔAICc), AICc model weights (ωm), twice the negative loglikelihood (-2l), and a number of covariates (k) are shown.*

Ranking	Models	AICc	ΔAICc	ω_m	-2l	*k*
1	ψ (.),*p*(VISIBILITY+YEAR+PERIOD+EFFORT)	1408.73	0.00	0.45	1386.73	11
2	ψ (.),*p*(VIEWSHED+ VISIBILITY+YEAR+PERIOD+EFFORT)	1408.79	0.06	0.43	1384.79	12
3	ψ (.),*p*(VISIBILITY+PERIOD+EFFORT)	1413.43	4.70	0.04	1393.43	10
4	ψ (.),*p*(VIEWSHED+ VISIBILITY+PERIOD+EFFORT)	1414.10	5.37	0.03	1392.10	11
5	ψ (.),*p*(VIEWSHED+ VISIBILITY+YEAR+PERIOD)	1415.17	6.44	0.02	1403.17	6
6	ψ (.),*p*(VISIBILITY+PERIOD+EFFORT)	1415.19	6.46	0.01	1401.19	7
31	ψ (.),*p*(.)	1633.49	224.76	0.00	1629.49	2

Table 2.3. *Parameter estimates and standard error (SE), detection probability (p) with standard error (SE) between brackets, and odds ratios (OR) for the effect of the covariates of the best model on detectability.*

	β	S.E.	*p* (S.E.)	OR
ψ	1.99	0.53	0.88(0.05)	-
p(VIEW)	0.95	0.10	0.72(0.02)	2.23
p(YEAR)	-0.98	0.37	0.27(0.07)	0.37
PERIOD				
p(COURT)	-0.39	0.78	0.40(0.18)	0.67
p(INCUBATION)	1.71	0.90	0.84(0.11)	5.53
p(NESTLINGS)	2.26	0.91	0.90(0.07)	9.6
EFFORT				
p(1 hour)	-1.15	0.55	0.24(0.10)	0.32
p(2 hour)	-0.96	0.55	0.27(0.11)	0.41
p(3 hour)	-0.48	0.56	0.38(0.13)	0.61
p(4 hour)	-0.31	0.57	0.42(0.14)	0.73
p(5 hour)	0.04	0.59	0.51(0.15)	1.04

Monitoring costs

To assure occupancy (or absence) when no other variable and breeding stage were considered, the optimal number of surveys per site (hours × monitoring days) would be: 1 h × 7, 2 h × 6, 3 h × 5, 4 h × 5, or 5 h × 4 (Figure 2.3a). If we account for the breeding stage, the optimal monitoring cost is reached by investing several surveys of one hour in the three breeding stages instead of a few surveys of five hours (see Appendix A Table A.1). As a direct consequence of the lower probability of detection, the total cost of detecting 95% of false negatives is higher during the courtship than during incubation and nestlings (Figure 2.3b; Appendix A Table A.1). If we want to consider the basic monitoring of breeding territories throughout the whole breeding season (i.e., firstly assure nest occupancy during courtship, secondly assure incubation and thirdly assure productivity and fledgling success) investing one hour, we estimated a maximum cost of 1,226 € per nest (Appendix A Table A.1). The estimated cost of monitoring all the occupied nesting territories was 23,294 € (n = 19). Total monitoring costs differed when we included environmental variables in our models, and ranged from 242 €/nest (a visible nest in a dry year) to 1,954 €/nest (a non-visible nest in a rainy year). Total costs were similar throughout all breeding phases for visible nests in rainy years (514 €/nest on average) and non-visible nests in dry years (512 €/nest on average) (Figure 2.3b; Appendix A Tables A.3 and A.4).

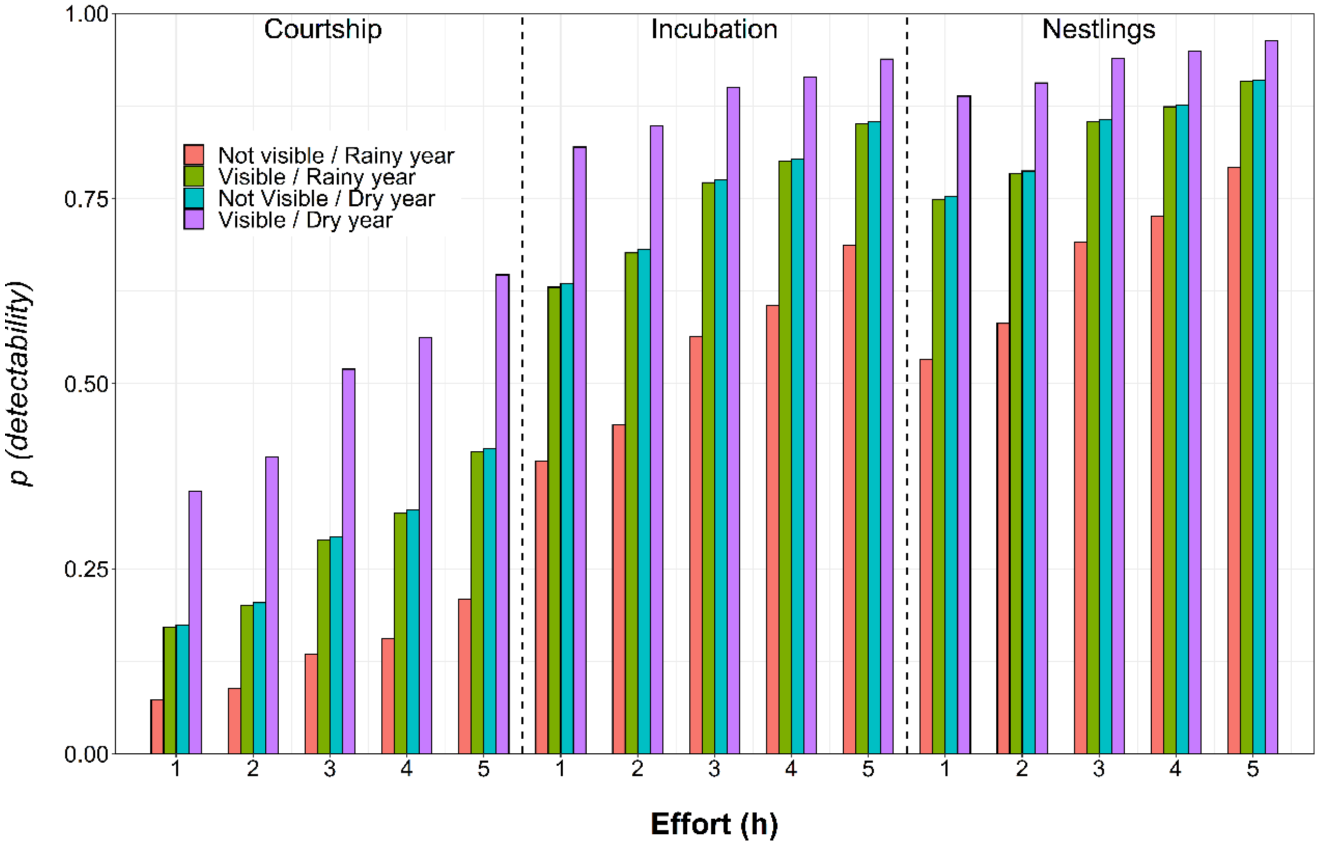

Figure 2.2. *Detection probability of Egyptian vulture (from 0 to 1) at intervals of five sampling hours throughout the breeding season (i.e., courtship, incubation, and nestlings) considering nest visibility and annual average weather conditions during the study period (2017–2018).*

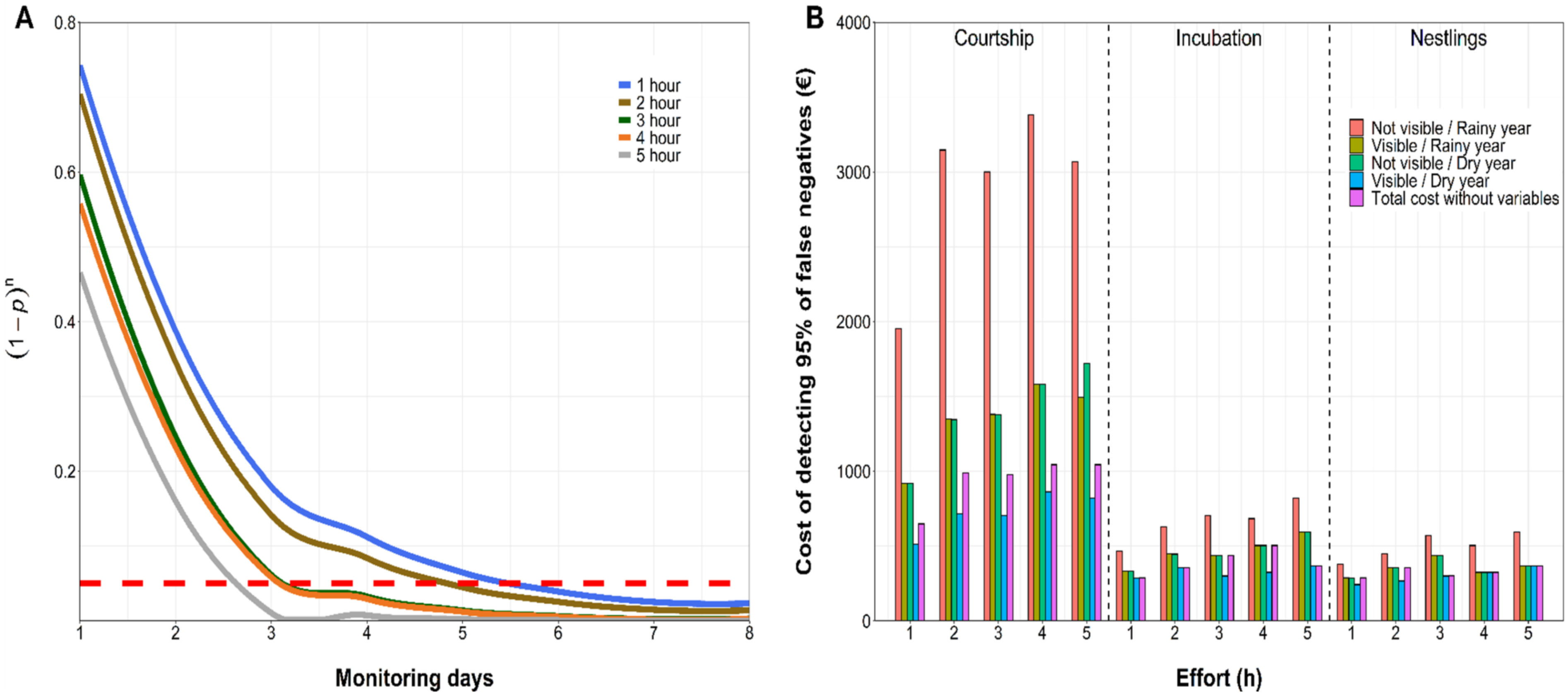

Figure 2.3. *Monitoring days (n) necessary (without considering covariables) to detect 95% of false negatives $(1-p)^n$ for a single nest investing from 1 to 5 hours effort .The dashed red line is the probability (0.05) of species is not truly present at 95% C.I. (a). Total cost of monitoring based on Equation 4 (see Methods section) for a single nest without considering covariates, and considering nest visibility and annual average weather conditions at intervals of five sampling hours at each breeding phase (b).*

2.5. DISCUSSION

Our results reveal the importance of using biological and environmental information when assessing monetary costs in biodiversity monitoring programs, especially for those species whose elusive behaviour makes them difficult to detect (Thompson, 2013). In our case, the long-term monitoring of the Egyptian vulture in the study area helped us to distinguish between breeding stages, and to better explain changes in detectability within different phases. Detectability changed with the breeding stage and increased during incubation and the nestling period (see León-Ortega et al., 2017 for similar results). On the one hand, the Egyptian vulture exhibits secretive behaviours during courtship, which results in a higher effort needed to assure occupancy. On the other hand, detectability increases during incubation, when adults center their activity around the nests, and the regular rate of changeovers (the change of the adult that is incubating by its partner) is expected to occur (Tapia and Zuberogoitia, 2018; Morant et al., 2019), and even more during the nestling phase (when adults must carry food to feed nestlings regularly) (Donázar et al., 1994; Tapia and Zuberogoitia, 2018; Morant et al., 2019). Accounting for detectability in early breeding stages is critical for study design and monitoring planning. Generally, during the courtship period, individuals tend to adjust nest site selection; thus, more reliable information becomes available within this breeding stage (Dall et al., 2005). Our results showed that if detectability is low during this period, the location of active nests is difficult, and observers can spend hours, even days, in front of a nest without clear evidence of occupancy (Olea and Mateo-Tomás, 2011). This could affect the monitoring of the study population from erroneously estimating the number of breeding pairs, or the percentage of breeding failures, to inadequate management decisions. Taking into account that the Egyptian vulture is an endangered species, more efforts are needed during the early phases of reproduction to detect breeding attempts (see Badia-Boher et al., 2019; Zuberogoitia et al., 2014). Otherwise, in the absence of sightings, conservation practitioners might stop surveying too early (Stokstad, 2007; Fisher and Blomberg, 2010) in areas where breeding failures are high and many hazards affect the normal breeding cycle of the species (e.g., timber and leisure activities in nest site surroundings; Morant et al., 2018).

Our analyses revealed that detectability increases when the nest is visible, making accessible the monitoring of breeding pairs in those places where observers can see the nests. However, this is not so evident during courtship, when nest activity increases close to laying dates but remain at a low level some weeks before. The knowledge of the laying dates in each study site would help to avoid wasting time and resources surveying in early dates. However, it requires an in-depth knowledge of the population based on long-term monitoring efforts. Otherwise, a surveyor could waste his/her time visiting an empty nest until assuring occupancy, as our results reveal. Later, after the first egg is laid, occupancy is confirmed just in a first sight during the rest of the breeding season. This, moreover, facilitates the early detection of failures on the monitoring throughout the breeding cycle.

Differences in detectability throughout the breeding season and the amount of field effort needed to detect the target species also depended on environmental weather conditions. We know that a high amount of precipitation during incubation or the first weeks of nestling development causes many failures; in fact, only an average of 41.7%±31.4% (mean ± SD) (range 0–92.3%) of the breeding attempts per territory was successful in rainy years (Zuberogoitia et al., 2014). Detection rates varied from one rainy season to another dry season. This is not related to the ability of the observer to detect Egyptian vultures on rainy days since surveys are usually developed in dry conditions. The low rate of detectability is related to the increased likelihood that the monitored nest failed during the incubation or nestling phase. We found that breeding success was 62.5% in 2017, a relatively dry year, and 55.5% in 2018, a rainy year. This is not a problem when the nest is visible, but it requires a survey effort to ascertain the true stage of the nest when the observer cannot access to see the nest (Figure 2.2).

Interestingly, the lack of differences in detectability between dry years when the nest is not visible versus rainy years when the nest is visible suggests a trade-off between weather conditions and factors affecting nest visibility (Figure 2.3b). Although monitoring programs use standardised field methods (Li et al., 2010), they do not still guarantee constant detectability across sites (Thompson, 2002). Particularly, in the case of species that breed in both dry and temperate areas throughout its distribution range. Our results suggest that a more considerable survey effort is needed to guarantee detectability in temperate regions with regular unfavourable climatic conditions and a rugged topography. This highlights the need to account for variation in detectability across different climatic regions. Therefore, there is a need to adapt monitoring schemes adequately and to cautiously analyse and interpret recorded data (i.e., raw data counts).

In occupancy-detectability studies, not accounting for “false absences” might lead to underestimating the actual level of occupancy and are a potential source of bias (Wintle et al., 2012). To account for the effect of imperfect detection and minimize the possibility of a false absence, one solution is to conduct multiple surveys within a relatively short timeframe (MacKenzie and Royle, 2005). Here we show that accounting for imperfect detection is useful to define the optimal survey strategy (i.e., when, and how much, to survey), as well as to reliably assess monitoring costs. Our study indicated that, without previous environmental or biological information, eight hours/nest/survey should be invested to account for 95% of false negatives. This contrasts with other authors who found that a minimum of five visits are required to be 95% certain that an average territory of the species is truly unoccupied (Olea and Mateo-Tomás, 2011). However, the main difference between similar works and ours is that we worked with an already known occupancy data. Thus we knew when false negatives occurred. The naïve occupancy was very close to the estimated occupancy, suggesting that the species had been detected in most occupied sites. This gains major relevance in several censuses and long-term monitoring programs of threatened species where the species are known to be present but are not detected — thus helping to assess only for detectability of species while controlling for occupancy. For instance, in the case of large carnivores surveys where one site that was occupied once, is usually considered to remain occupied throughout all monitoring period (Blanc et al., 2014).

Although some studies offer different practical methods to explicitly compute monitoring costs (Gálvez et al., 2016; Lieury et al., 2017), few estimates monitoring costs while accounting for conventional statistical errors (e.g., Type I errors; see details in Field et al., 2005) understandably and straightforwardly for conservation practitioners. Here, we calculate the optimal cost of monitoring, accounting for imperfect detection. This is a tool for developing cost-efficient designs for a broad application to other species and geographical contexts (MacKenzie and Royle, 2005; Guillera-Arroita et al., 2010). Our estimates of optimal costs showed that monitoring the species investing one hour during several surveys in a single nest in each breeding stage when variables are and are not considered would be the most cost-effective option for managers. However, the variation in time to be spent, depending on the phase of the breeding period, should also be considered, e.g., during courtship, ten surveys of one hour or four surveys of five hours are needed to assure occupancy (Table A.1). Usually, national censuses of the species do not include environmental factors that affect detection (see Del Moral, 2009) and do not invest so much effort to assure occupancy during the first stages of the breeding season when detecting breeding pairs is crucial for conservation purposes at a national scale. If we consider the optimal budget to confirm reliable occupancy in our known nesting territories (1226 €/nest when no variables were considered), we would need 23,294 € per year, without considering the effort needed to check other empty territories or new evidence. This budget would be the maximum required to assure all the false negatives, and it might be adjusted yearly depending on the increased experience of observers and knowledge of the nesting territories and laying dates. We think this is a large budget for long-term monitoring programs or those at a national scale, and a considerable number of volunteers are needed to reach monitoring objectives with much lower and realistic budgets. In this sense, we encourage wildlife managers and policymakers to take into consideration the real cost of obtaining High quality data of elusive endangered species and the effort done by field workers to reach primary objectives.

Management and conservation implications

Nowadays, the vast majority of conservation and monitoring projects are underfunded, and less than 25% of the funding needed just for imperiled species recovery has been provided overall (Gerber, 2016). It is, therefore, necessary to rank which species to monitor and which not (Wilson et al., 2015), and more importantly, how much must be invested in such monitoring programs. The precipitous, global declines of most vulture populations highlight the relevance of range-wide and long-term monitoring programs (Jachowski et al., 2015). For this reason, transboundary conservation actions targeted at vulture populations have been established (Multi-species action plan to conserve African-Eurasian vultures, Botha et al., 2017). This program relies on demographic parameters to evaluate the achievement of settled conservation goals. However, for many species, standardised monitoring protocols using non-invasive methods are generally lacking (Perrig et al., 2019). In this context, our study helps to settle guidelines to know when and how much to monitor while addressing both weather conditions and species-specific biological and ecological traits. This is especially relevant for monitoring large territorial carnivores (Blanc et al., 2014), amphibian (Tanadini and

Schmidt, 2011) and philopatric species like most of the vultures. Our study might be of help for managers and conservation practitioners to assess the feasibility of monitoring programs in their initial stages and their re-assessment regarding the available budget, given that financial constraints impose practical limits to conserve threatened species (Santika et al., 2015), notably in underdeveloped countries.

In the end, some points should be considered regarding the applicability of our results to other threatened species and geographical contexts. Since one in six species on the IUCN Red List is currently classified as Data Deficient (due to lack of information on their taxonomy, population status, or impact of threats), the first limitation comes from the lack of information available of each species-specific behavioural traits. For instance, differences in detectability among sexes, ages, and body sizes have been reported for several species (e.g., Pickett et al., 2012). Furthermore, variation in home range area or density at the species, population, and individual levels can also influence detection (Latif et al., 2018; Schlossberg et al., 2018). Sampling methods and survey effort should also be taken into consideration. Many elusive species, like mammals, require more sophisticated or combined methods (i.e., eDNA, Dorazio and Erickson, 2018) to obtain presence data (which increases the effort and costs to ensure the detection and occupancy). Moreover, even species known to occupy a certain patch could go undetected, generally because the surveys do not target periods when detectability is likely to be high (Sewell et al., 2010) or the monitoring schedule is not the most appropriate (i.e., short-term monitoring and irregular censuses among years). Finally, although we deemed landscape as constant in this study, climate and land cover changes could also drive spatiotemporal occupancy patterns of species (Kalle et al., 2018), which could be an important issue when estimating the costs of long-term monitoring projects and obtaining precise and accurate occupancy estimates.

CHAPTER 3

Out of sight, out of mind? Testing the effects of overwinter habitat alterations on breeding territories of a migratory endangered species

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3.1. ABSTRACT

Anthropogenic activities are one of the main threats to species living in human-dominated landscapes and can promote behavioral changes in birds. This paper presents a novel approach to test how a migratory species responds to habitat alterations occurring in nesting territories during winter, when the species is absent. From 2000 to 2016, we collated territory and nest monitoring data for the endangered Egyptian vulture *Neophron percnopterus* in the north of Spain, to test the effects of overwinter habitat alterations (OHA) around breeding territories on the species reproductive output. We monitored 70 different nest sites and observed OHA around the nesting area in 39 cases. Probability of switching to another nesting site almost tripled after OHA. Pairs that switched experienced substantially decreased breeding success and avoided reusing the nest for 4.8 ± 4.64 years. The presence of determinate landscape elements that provide screening, such as forest patches, increased nest reoccupancy probability after OHA by more than 0.3, to 0. 55 (compared to 0.24 when no screening was present). We also found that the distance and the situation of the OHA were critical factors explaining reproduction probabilities at nest sites. Our results demonstrate how OHA can strongly impact the breeding behaviour of long-lived species. This highlights the need to examine the long-term impact of OHA rather than focusing only on disturbances during sensitive periods, as is often the case with habitual mitigation measures.

3.2. INTRODUCTION

Human activities can impact wildlife directly (e.g., by persecution and harvesting) or indirectly, via effects on the quantity, quality, or configuration of the landscape and consequently on the habitats that it contains (Hollander et al., 2011; Kamp et al., 2016). Landscape changes are by far the most important cause of habitat loss and fragmentation in modern times (Kerr and Deguise, 2004; Newbold et al., 2015; Fardila et al., 2017). These alterations are believed to negatively affect, to a greater or lesser extent, virtually all animal taxa including: birds and mammals (Andrén, 1994; Johnstone, Lill and Reina, 2014), reptiles (Gibbons et al., 2000), amphibians (Stuart et al., 2004) and invertebrates (Didham et al., 1996). They have therefore been the focus of many conservation biology and landscape ecology studies over the last century (Tscharntke et al., 2012; Driscoll et al., 2013).

Changes are frequent in human landscapes and species living in these environments are also exposed to various types of human disturbance (George and Crooks, 2006; Zuberogoitia et al., 2008; Ordiz et al., 2016). Species differ greatly in both their behavioral and reproductive responses to human disturbance and landscape changes, as well as to the relationships between these two variables (Beale and Monaghan, 2004; Finney et al., 2005; Guénette and Villard, 2005; Carrete et al., 2013). Landscape modification may lead to local or regional declines (see Zabala et al., 2003; Furrer et al., 2016), and ultimately extinction (McCarthy et al., 1997). Identifying the effects of landscape changes on species is critical for the development of efficient and effective conservation strategies (Lindenmayer and Fischer, 2006). Research has revealed the great susceptibility of many species to disturbances and human activities during particularly sensitive phases of their life cycles, such as reproduction. For instance, the disturbance of nesting birds can have a variety of direct effects, ranging from changes in behaviour to complete desertion of a nest site (Newton, 1979; Zuberogoitia et al., 2008; Francis and Barber, 2013; Cartwright et al., 2014). A common management approach to combine wildlife conservation and human activities is the imposition of temporary bans during periods of high sensitivity. This approach is underpinned by the assumption that species respond to the direct disturbance, but will not be affected by the consequences of the action if it takes place outside sensitive periods and does not modify key structures within their habitat (e.g., does not destroy nest sites or key feeding areas). However, this assumption remains, to the best of our knowledge, untested.

Raptors are good study subjects for this topic as they are sensitive to environmental disturbance (Sergio et al., 2008). Vultures, in particular, are vulnerable to human disturbances and habitat loss resulting from forestry and other land-use practices (Fargallo et al., 1998; Donázar et al., 2002a; Arroyo and Razin, 2006; Margalida et al., 2011). Among them, the Egyptian vulture Neophron percnopterus is a suitable candidate for testing the assumption that species are unaffected by the consequences of major human disturbances that take place outside sensitive periods. The species is distributed mainly across southern Europe, Africa and the Indian subcontinent. It is a migratory bird that abandons its European breeding areas between September and February (Ferguson-Lees and Christie, 2001). European populations winter in sub-Saharan Africa, within the 14°–17°N belt (Donázar et al., 2002b; García-Ripollés and López-López, 2011). During the 20th century, the population of this long-lived scavenger has steadily declined across large parts of its European and African range (Carrete et al., 2007). The causes of this decline are diverse: high adult mortality due to poisoning (Cortés-Avizanda et al., 2009; Hernández and Margalida, 2009); collisions with man-made infrastructures (wind turbines and power lines; Carrete et al., 2009); electrocution; habitat loss (Velevski et al., 2015); habitat change (Mateo-Tomás and Olea, 2015); food shortages; and human disturbance at breeding sites are among the main threats to the species (Margalida et al., 2012; Sanz-Aguilar et al., 2015; Donázar et al., 2016). In the north of its Spanish distribution range the species breeds in an oceanic landscape, on cliffs surrounded by dense forests, far from built-up areas. Extensive cattle farming and timber extraction are the main activities in this region (Zuberogoitia et al., 2008), and in fact the target population breeds in a managed forest landscape. Timber activities here have been developed over decades, with activity peaking from the 1950s onwards, when there was a great increase in timber plantations to the detriment of oak woods and grassfields (Michel, 2006). Moreover, during the last decade, economic interests associated with large forests and the accompanying market-orientated changes have favored the gradual replacement of pines by eucalyptus (Zuberogoitia et al., 2011). Egyptian vultures in our study area are very sensitive to disturbances. During the breeding season, interventions such as forestry practices near nesting areas result in the immediate failure of the clutch and abandonment of the nest site (see Zuberogoitia et al., 2008). Consequently, temporary bans on potentially disturbing practices have been imposed during the breeding cycle of the species (Zuberogoitia et al., 2014). This assumes that Egyptian vultures can tolerate some level of habitat alteration near nest sites if the activity takes place when the vultures are at their wintering grounds.

However, it remains untested whether breeding pairs react to landscape alterations occurring during the non-breeding season, thus the efficacy of these bans is unknown. Specifically, it remains to be seen whether vultures returning from their winter areas in sub-Saharan Africa react to alterations in non-key elements of their habitat caused by anthropogenic activities during the winter period. Our main objective was therefore to evaluate the efficiency of temporary bans in relation to sensitive species, by examining the response of the Egyptian vulture to the alteration of non-key habitat elements in the area surrounding the nest site, occurring during the absence of the species. We assessed the effect of such habitat alterations, due to forestry and other land-use practices, on the nest-site reoccupancy and reproductive success of Egyptian vultures in northern Spain.

3.3. MATERIALS AND METHODS

Study area

The study area was the Biscay region (Basque Country, northern Spain; 2384 km2; 43°12'00''N 3°13'00''W). The territory is hilly and steep, with only 50 km separating the sea from the highest altitude (1480 m). Man-made forests, pastures, small villages and densely populated cities make up the bulk of the province. More than 50% of the area is dedicated to forestry, mainly plantations of Pinus radiata and Eucalyptus sp. These forests have been created at the expense of traditional small-scale farming. The area has a temperate climate, with an annual rainfall of 1000–1300 mm and mean annual temperatures of 11–12°C.

Field procedure

We surveyed the Egyptian vulture population in Biscay systematically, from 2000 to 2016. The number of breeding territories ranged from 18 to 22 during the monitoring period. Nests were located by observing individuals displaying near the cliffs where they eventually breed. We defined territories as being the exclusive nest sites plus the surrounding areas and resources defended by territory holders against intruders. Breeding territories encompassed several nests (from 1 to 6, Zuberogoitia et al., 2008), which were monitored from February to September each year in order to obtain data on: the number of territorial pairs, number of pairs which start reproduction, nest location, laying date, breeding success, number of fledglings and causes of clutch loss. We visited the nesting area from March to April, in order to detect Egyptian vultures entering the nest site with material for building the nest or to relieve the mate during the first stages of incubation. According to Olea and Mateo-Tomas (2011) the

Egyptian vulture has relatively low detectability (the probability of detecting the species is less than 50% during surveys performed at occupied sites). Therefore, we visited the territories as many times as needed to confirm unequivocal occupation or abandonment, and breeding success (e.g., in the 2016 breeding season we conducted 123 monitoring events, which took a total of 333.75 h, visiting each territory a mean of 6.45 times and taking an average of 153.6 min per visit). Once we had ascertained the onset of incubation, we continued monitoring until the fledglings left the nests. To minimize the effect of inter-annual variability on breeding success, we created a Breeding Quality Index (BQI). The BQI was defined as the difference between the number of offspring of a particular territory and the average number of offspring of the entire population in the same season (e.g., Zabala and Zuberogoitia, 2014).

We defined Overwinter Habitat Alterations (OHA) of the nesting area as those interventions that: (1) resulted in noticeable changes in the landscape/vegetation structure within a 1 km radius of the nest site, and (2) took place between late September and early March, when the species was absent. OHA were mainly due to forestry operations, that is, clear-cuts (n = 30) and opening of forest tracks (n = 3). Other incidences included construction (1), quarry filling (1), bike trail creation (1), gas pipeline deployment (1), industrial park construction (1), and erection of observation platforms (1). We discarded those actions that caused only subtle changes (e.g., forest thinning and plantations). To obtain measures of OHA we combined our own field data with historic orthophoto sequences from Google Earth (Google Inc., 2016) and Quantum GIS software (QGIS Development Team, 2016), using digital land-use maps, topographic maps and satellite imagery at a scale of 1:5000, available as free data source on the Basque Government website (GeoEuskadi, 2013).

Data analysis

We investigated possible responses to OHA by breeders in two steps. Firstly, we assessed response to OHA in terms of nest site selection, and secondly we assessed possible consequences of remaining in the affected nest site on breeding success. To model the response of the species to habitat alteration we considered two response variables: (1) Nest reoccupancy – taking as a reference the nest occupied in the year prior to OHA, with the pair either reusing the previous year's nest or switching to another nest, and (2) Reproduction – the pair remain at the same nest site and either reproduce in the previous year's nest or do not breed. We considered four predictive variables: On the one hand we looked at two continuous variables represented by: (1) Distance – measured as the distance (m) between the nest and the nearest point of habitat alteration, and (2) Area – the forest surface removed as a result of each type of action (m2). On the other hand we considered two fixed, qualitative factors: (3) Screening – the presence or not of a screen between the nest and the OHA (i.e., a landscape feature precluding visibility of the intervention; normally mature forest patches), and (4) Situation – the location of OHA in relation to the nest (above, front, side, or behind). Lastly, in order to account for possible correlations due to repeated observations within same breeding sites, we included territory identity as a random factor in the models. To elucidate the effect of predictors over response variables, the two response variables were subjected to model selection using generalized linear mixed models (GLMM) (McCullagh, 1984). All possible models, from the most general, were performed (including noted explanatory variables) through 'glmer' function, implemented using the 'lme4' package for R version 3.3.2 (R Development Core Team, 2015), and evaluated using Akaike Information Criterion (AIC, Burnham et al., 2011). On the basis of the above, the model that showed the lowest AIC value was selected, in order to examine and analyse the effects of predictor variables.

To analyse the effect of switching the nest site on productivity, we applied a GLMM using Breeding Quality Index (BQI) as a response assuming a normal distribution. We used a binomial variable as a predictive factor to discriminate between switched nests and habitual nests. In the first case, we considered switched nests as those cases where Egyptian vultures changed the nest site after OHA, whereas habitual nests were those used by Egyptian vultures for at least three consecutive years. To account for the possible non-independence, territory identity was included as a random factor. We used the 'glmer' and 'Anova' functions implemented in the 'lme4' (Bates et al., 2015) and 'car' (Fox and Weisberg, 2011) packages for R (R Core Team, 2015).

3.4. RESULTS

During the study period (2000–2016), we monitored 277 breeding attempts in 70 different nest sites, located in 23 territories (3.04 ± 1.43 nests/territory, range = 1–6). We observed OHA around the nest area in 39 cases in 22 nest sites. Egyptian vultures switched nests on 72.79% of the occasions when OHA took place in the nest surroundings (perimeter range = 10–1055 m). This was almost triple the rate observed for vultures with no OHA (26.90%; n = 197). The average distance between the two nest sites (before and after the OHA) was 1182 ± 1146 m (range = 10–5871 m) and 542.24 ± 795.18 m (range = 3–4487 m) in those cases without OHA (Mann–Whitney Test; U = 283, P = 0.01). Vultures responded to OHA in the proximity of their nest by switching nests significantly more often than other pairs (GLMM: Estimate = 1.4376, S.E. = 0.4935, t value = 2.973, P = 0.002; Figure 3.1).

Table 3.1. *Results of the procedure referring to selection of developed models for determining the variables affecting nest reoccupancy and reproduction in Egyptian Vultures when Overwinter Habitat Alteration (OHA) has taken place during the study period (2000-2016) in Biscay, northern Spain. The models are list ed from the most saturated to the simplest, including combinations of variables. For each model, the differences of AIC values (ΔAIC) with respect to the best model (AIC=0) and K (number of employed parameters in each model) are shown, as well as their relative weight (AICw). The best models are highlighted in bold.*

	Nest reoccupancy			**Reproduction**			***K***
Variables employed in each model	AIC	ΔAIC	AICw	AIC	ΔAIC	AICw	
Distance+screen+situation+surface	54.82	3.02	0.04	45.34	2.51	0.09	4
Distance+screen+situation	53.52	1.72	0.08	**42.83**	**0**	**0.34**	**3**
Distance+screen+surface	**52.24**	**0.44**	**0.15**	47.94	5.11	0.03	**3**
Distance+situation+surface	54.32	2.43	0.05	45.85	3.02	0.08	3
Screen+situation	55.64	3.84	0.03	47.41	4.58	0.03	2
Distance+screen	**51.80**	**0**	**0.19**	45.90	3.07	0.07	**2**
Distance+situation	54.31	2.51	0.05	**43.42**	**0.59**	**0.25**	**2**
Distance+surface	53.94	2.14	0.06	50.62	7.79	0.006	2
Situation+surface	57.36	5.56	0.01	50.46	7.63	0.007	2
Screen+surface	54.07	2.27	0.06	49.74	6.91	0.01	2
Situation	54.31	2.51	0.05	48.52	5.69	0.02	1
Distance	55.04	3.24	0.03	48.99	6.16	0.015	1
Screen	**52.18**	**0.38**	**0.15**	47.83	5	0.02	**1**
Surface	56.21	4.41	0.02	53.03	10.2	0.002	1

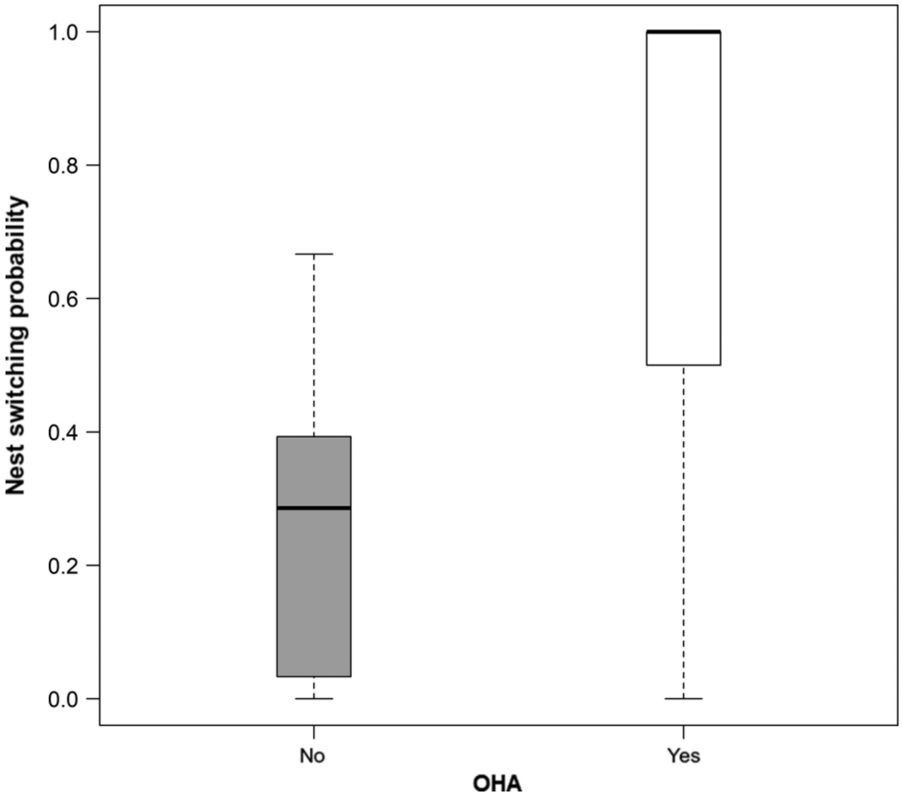

Figure 3.1. *Tukey box plot showing nest switching probability by Egyptian vultures after OHAs (Overwinter Habitat Alteration)s around the nest during the reported period (2000–2016), in Biscay, northern Spain.*

Nest reoccupancy after OHA in the territory was conditioned by the presence of a screen between the nest site and the OHA and, to a lesser degree, the distance from and the area of the OHA (Table 3.1). Although distance and area were selected into the most parsimonious models (Table 3.1), their relative importance was low, due to high variability in the response of territorial birds (Table 3.2). Screens significantly isolated nest sites from the OHA area and reduced the probability of the pair moving to another nest (Figure 3.2a).

The distance of the OHA from the nest site was a determining factor conditioning reproduction (Tables 3.1 and 3.2). The next most important factor was the situation of the OHA, and to a lesser extent the presence of a forest screen. The area of the OHA did not affect reproduction probability, since even small changes were enough to cause nest switching. OHA located in front of the nest caused reproduction probability to be low at distances of less than 600 m. In contrast, when

OHA were located above, to the side, or behind the nest, the probability of reproduction substantially increased (see Figure 3.2b).

Table 3.2. *Results of GLMM for the most parsimonious model for Nest Reoccupancy and Reproduction models (Table 3.1). The values of the estimator, standard error, z and probability are shown. Significant values are highlighted in bold.*

	Estimator	St Error	z	*P*
Values	**Nest reoccupancy**			
Intercept	-1.8599	0.740	-2.51	**0.01**
Distance	0.0022	0.001	1.49	0.14
Factor(Screening)1	1.7346	0.778	2.23	**0.03**
	Reproduction			
Intercept	-2.7480	1.472	-1.87	**0.06**
Distance	0.0062	0.003	2.02	**0.04**
Factor(Screening)1	1.6827	1.083	1.55	0.12
Factor(Situation)front	-3.746	2.060	-1.82	0.06
Factor(Situation)side	0.2229	1.322	0.17	0.86
Factor(Situation)opposite	-1.8779	2.031	-0.92	0.26

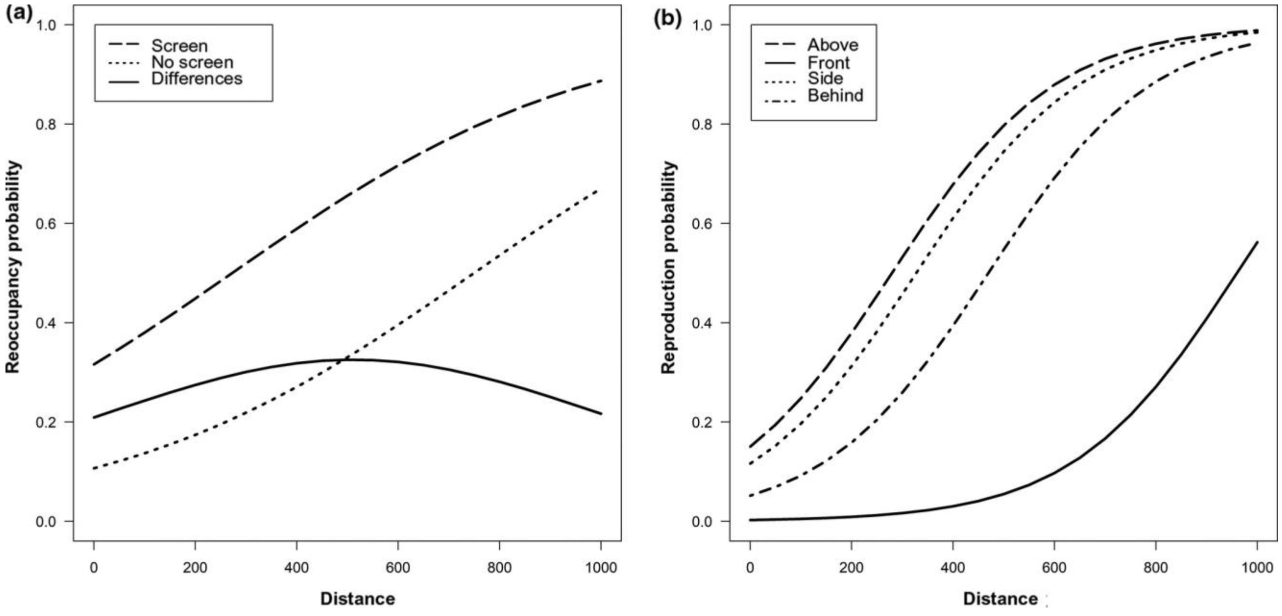

Figure 3.2. *Plot (a) shows Egyptian vulture reoccupancy probability (obtained from the model 6) in function of the distance of OHA when a screen was or was not present, and the differences between these two (i.e., the variation in the screen effect with distance to OHA). Plot (b) indicates the reproduction probability (obtained from the model 2) in relation to location of the OHA in reference to the nest-site (above, front, side and behind) and the distance (as meters between OHA and nest sites).*

After OHA, abandoned nest sites were not re-used for 4.8 ± 4.64 years (range=1-14 years; n = 20). Ten nests were never used again, seven were reoccupied after 2.86 ± 3.24 years, and the remainder suffered OHA more recently, hence insufficient time has passed to permit the effects to be correctly evaluated. Two territories had only a single nest site so breeders were forced to remain in the same nest even though OHA had occurred. In such cases, the pair did not reproduce for years, despite using the same nest site. Finally, two territories systematically suffered OHA near the nest sites, which led to abandonment of the breeding area. Furthermore, pairs that switched nests as a consequence of OHA had reduced productivity compared to that observed in their habitual nests (GLMM: Estimate = 0.4797, S.E. = 0.1427, t value = 3.362, P < 0.001; Figure 3.3).

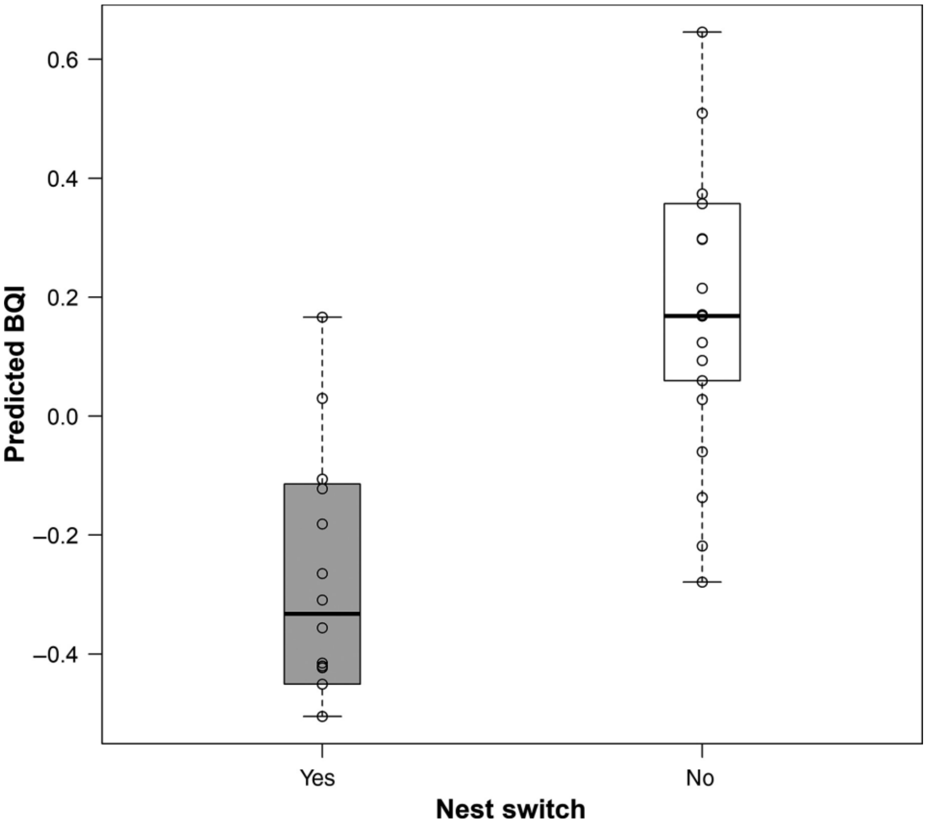

Figure 3.3. *Model predicted values for BQI (Breeding Quality Index) of Egyptian vultures that switched nest site in response to OHA (Overwinter Habitat Alterations) compared to BQI in the habitual nests (those in which vultures bred for at least three consecutive years previous to OHA), during the study period (2000–2016) in Biscay, northern Spain.*

3.5. DISCUSSION

Our results show that the performance of temporary bans is lower than expected, even if direct impact on Egyptian vultures' breeding success was prevented by forcing potentially disturbing activities to take place outside the breeding season. Indeed, nest switching by Egyptian vultures was strongly correlated with OHA near nest sites, despite the OHA taking place in periods when the species is not present in the territory. Furthermore, nest switching as consequence of OHA resulted in comparatively reduced breeding success in subsequent years.

Previous studies carried out in the same target population showed negative consequences of human disturbances on breeding performance (Zuberogoitia et al., 2008, 2014). Thus, Egyptian vultures are able to actively prevent possible threats by avoiding breeding in altered environments (or disturbed areas), and so it is not surprising that human activities limit the distribution of the species by altering nest site selection patterns (Sen, Tavares and Bilgin, 2017). However, it is not easy to detect indirect effects on the ecology of a species when there is no obvious disruption of biological routine (i.e., no reproductive abandonment) in the studied population. Moreover, subtle, indirect effects, such as those reported in this study, are normally obscured by other hazards (e.g., direct mortality) that threaten the survival of the species (Cortés-Avizanda et al., 2009; Hernández and Margalida, 2009). In addition, other unmeasured factors, such as temporal trends in food availability, might obscure our results. In fact, the temporal relationship between variations in trophic diversity and productivity may suggest a causal link between variation in diet and reproductive output (Margalida et al., 2012). In our case, long-term monitoring data allowed us to discriminate the subtle effect of OHA.

Although species of medium size, such as Egyptian vultures, are less constrained than larger species by the availability of a suitable substrate for nesting (Newton, 1979), our results suggest that they are probably obliged to move to other unaltered but usually low-quality nest sites nearby, as has been reported for other raptors (e.g., Rodríguez-Estrella et al., 1998). In our study area, Egyptian vultures showed a tendency to reuse affected nest sites after a medium-term period. However, some nest sites were not reused even after 14 years and two territories disappeared putatively due to continuous habitat alterations. This could have effects on population size and dynamics (see Gill, 2007). Furthermore if, as suggested by our results, alternative sites are of lower quality, this leads to reduced reproductive success in subsequent nesting events. The productivity in habitual nests was much higher than that registered in alternative nests (Figure 3.3), which is coherent with reports of other raptors forced to use lower quality nest sites (Ferrer and Donazar, 1996; Mooney and Taylor, 1996; Krüger et al., 2015). Thus, it is necessary to develop buffer areas around habitual nest sites, in the hope that such planning measures will minimize disturbance impacts and promote population persistence in nesting areas (McCarthy et al., 1997; Donázar et al., 2002a; Koch and Paton, 2014).

In relation to buffering, we found that the presence of a screen isolated nest sites and muffled the effect of OHA, thus increasing the probability of nest reoccupancy. Forest patches were of great importance when they were located between the OHA and the nest site, whereas the size of the altered area (e.g., tree felling zone) and its distance from the nest site were relegated to second place. Nevertheless, these results must be interpreted carefully since the degree of cover, the surface area involved, and the location of the screen should also be considered. OHA close to the nest (Figure 3.2B) always resulted in abandonment of the nest site, and the same effect was noted when works produced large, empty areas.

An open question is why OHA result in nest switching. Surprisingly, OHA across very small areas (i.e., 0.13 ha) resulted in switching of the nest site in some cases. Egyptian vultures are extremely cautious when they approach the nest, and if there is any disturbance in the surroundings during the breeding period they tend not to enter until the disturbance ends (Zuberogoitia et al., 2008). A greater distance between the alteration and the breeding site increased the probability of laying eggs in the affected nest. However, not all altered locations in relation to the nest site had similar effects. This might be explained by the degree of visual impact when birds arrived at the nest site or when they were sitting on the nest, and could explain why alterations located in front of, and at distances of less than 600 m from the nest, significantly decreased reproduction probability. Other intrinsic, and as yet unexplained, characteristics relating to the situation of OHA are likely to be responsible for unfounded differences when OHA were located to the side of the nest. Our results suggest that tolerance to disturbance decreases when the stimulus is closer and thus more focused (Russell, 1980; Holmes et al., 1993; Morán-López et al., 2006). In this context, it is logical to think that species may perceive OHA as a source of hazard around their nesting territories, and consequently adopt avoidance strategies to reduce the effect of determinate human activities (see Morán-López et al., 2006). It is possible that OHA zones have higher human frequentation during subsequent years (e.g., afforestation activities, recreation activities favoured by open areas) that are more visible after the affection, and thus there is a higher probability of anthropogenic disturbances during the subsequent breeding seasons. We must also stress that individual differences may condition the magnitude of the effect. Some individuals may be more tolerant than others to OHA, and the effects of the latter may also depend on the degree to which the birds are accustomed to human activities around the nesting area. There is growing evidence for differences in personality in animals, affecting their response to cues such as human presence (Carere and Maestripieri, 2013; Haage et al., 2017). Likewise, nest site quality and environmental variability could affect the variability in Egyptian vulture response to OHA. Individuals in territories of higher quality (i.e., with more and better nest sites available) could be more resilient to OHA.

Implications for management

Some management actions only aim to palliate specific problems faced by the species (Carrete et al., 2007). For example, temporary bans issued during critical periods (i.e., nest building, incubation and chick raising) to reduce the likelihood of nest abandonment (Harness, 2007). Zuberogoitia et al. (2014) found that the ban on habitat alterations during the breeding season precluded direct impacts on breeders and nesting failure but did not prevent effects in the following years. Our results show how the modification of non-key habitat structures in the proximity of the nests triggers responses in the subsequent breeding season, resulting in displacements to lower quality habitat and decreased productivity. In order to guarantee the persistence of pairs in nests and reproduction, some actions must be implemented. We suggest first assuring a buffer area with forest patches (screen) around the nest site in order to achieve reoccupancy of the previous year's nest. Second, any OHA in front of the nest should be avoided at distances of less than 800 m. Third, those OHA located above, behind, or to the side of the nest should be carried out beyond a 600 m radius, thus obtaining an 80% probability of reproduction. We recommend that management models to assure Egyptian vulture conservation should consider the following six points: (1) the number of nest sites per territory, (2) the importance of the nest site for the territory (habitual or alternative nest), (3) the number of years that the nest has been used in the last decade, (4) the synergic effects of different OHA in the nest sites of a territory during the last decade, (5) the position of the evaluated OHA and (6) the presence of a screen between nest site and evaluated OHA. Furthermore, temporary bans are common practice in conservation biology yet their performance has rarely been critically analyzed. Our results suggest that such bans ameliorate impacts but do not completely avoid them. Consequently, we encourage further testing of their performance on other endangered species.

CHAPTER 4

Management actions promote human-wildlife coexistence in highly anthropised landscapes: the case of an endangered avian scavenger

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4.1. ABSTRACT

Anthropised landscapes are characterised by various human activities related to resource extraction, recreational activities, and urbanization, among others. Conservation of species living in such landscapes is challenging due to the lack of compatibility between wildlife and human needs, which can create win-lose scenarios for target species. Therefore, adequate management practices are necessary to reduce conflicts and promote coexistence between wildlife and human beings. Here, we test the effectiveness of management measures on the productivity of an Egyptian vulture population living in an anthropised region of Northern Spain by using long-term monitoring data (2000–2020). During the first decade, we demonstrated that disturbance events negatively affected the species reproduction. Therefore, in 2010 we started a management plan in which we first established a basis for the species protection, and second we developed management actions to avoid or reduce the impact of potential disturbance events on the Egyptian vulture' breeding. We observed that almost half of the disturbances detected after the management was related to resource extraction activities such as forestry (40.6%). Management measures effectively increased productivity (84 vs 137, chicks fledged successfully before and after, respectively) and the breeding success of the pairs in which the disturbances were detected and stopped (66.7%) was much higher than those non-managed and non-stopped in time (17.4%). Moreover, we estimated that 44 nestlings (32.1%) would have died without management actions during the second decade. Overall, our work demonstrated that collaborative networks can design and implement effective management measures for endangered territorial species, taking into account all agents involved (policymakers, rangers, stakeholders, general public, and researchers) in the conservation area. Thereby, it alleviates conflicts in human-dominated ecosystems and generates a balanced scenario that favours long-term sustainable human-wildlife coexistence.

4.2. INTRODUCTION

As human population increases, so does the impact caused on ecosystems and species living on them (Venter et al., 2016). Currently, only 42–50% of the Earth's surface could be considered free or exhibiting low levels of human disturbances (Riggio et al., 2020). In fact, 20% of the planet's terrestrial surface is classified as built-up or cropland (Defourny et al., 2017), but only 15% of Earth's land surface is formally under protection (UNEP-WCMC, IUCN, and NGS, 2019). This means that majority of the taxa are now living in environments under moderate and high human pressures (O'Bryan et al., 2020). Such environments, namely anthropised landscapes, are characterized by intense and abrupt land-use changes derived from different human activities (e.g., resource extraction activities, recreational activities, agriculture, hunting, among others) and urban development (Newbold et al., 2015). Therefore, the organisms inhabiting anthropised landscapes have had their behaviour, physiology, phenology, and life history traits negatively altered (Gaynor et al., 2018; Sanders et al., 2020; Wilson et al., 2020), which can in the worst cases ultimately result in population declines and extinctions with severe ecological impacts (Wilson et al., 2020).

Management of threatened and endangered species requires decision making in the face of uncertainty (Runge, 2011). Complex management decisions necessitate a management approach that supports effective decision-making and incorporates practitioner knowledge changes as management progresses (Dreiss et al., 2017). Usually, management actions are based on measures in which actions focus only or mostly on target species and do not consider humans inhabiting the same areas. This leads to conservation conflicts in which one of the relevant parties is excluded from the conservation and management participatory processes (Redpath et al., 2013). Conservation in anthropised landscapes could be particularly challenging since it requires knowledge not only of the "how" and "where" some species thrive and persist but also of the social, cultural, and economic context themselves (Blackwell et al., 2016). However, in some cases, human intervention takes more weight at the time of reversing population declines or palliating the effects of different human impacts (Bolam et al., 2020). To improve conservation planning in such conditions or environments, both the spatial variation in causes generating the conflicts and the target species' particular requirements must be identified (Ferrier and Wintle, 2009). This holds especially true for territorial species with high ecological requirements and slow reproductive rates which are frequently on the brink of extinction and involved in most conservation conflicts (Ripple et al., 2014; van Eeden et al., 2018).

Raptors are declining quicker than other birds, with 52% of species in decline and 18% currently classified as threatened with extinction. Vultures, and particularly Old-World vultures, are by far the most threatened group within them, with 12 of 16 species listed as Endangered or Critically Endangered (McClure et al., 2018; BirdLife International, 2020; McClure and Rolek, 2020). Deliberate or unintentional poisoning events (Plaza et al., 2019; Aresu et al., 2020), conflicts with farmers depending on regional differences of livestock management (Margalida et al., 2014; Duriez et al., 2019), and low survival probability due to accidents with infrastructure, such as electrocution and collision with power lines and wind turbines (e.g., Donázar et al., 2002; Ogada et al., 2016; Badia-Boher et al., 2019; Arrondo et al., 2020) are among the main hazards for this avian group worldwide. Their particular biology and life history (delayed sexual maturity and low productivity, Donázar, 1993), together with the above-mentioned threats, caused vulture populations to plummet worldwide (Ogada et al., 2012). This situation urged scientists to delineate priority areas for conservation based on species-level risk assessment (Santangeli et al., 2019). Nevertheless, problems identified at broad scales might not reflect local-level factors (Efrat et al., 2020). Vulture populations in Europe are threatened by several hazards, that greatly vary among socio-economic and political situations of different countries or, even, within countries (see for example Olea and Mateo-Tomás, 2014). In highly anthropised landscapes, setting aside large areas of land for conservation might not be feasible due to intensive uses for recreational or economic activities. Further, usually there are areas or locations of high conservation value (e.g., nest sites, feeding sites) that are dispersed outside protected areas, often close to cities and villages, and subject to unique and variable pressures. These sites can support, altogether, a relevant part of the population and their dynamic management is needed to make conservation compatible with other uses, and enhance conservation efforts focused on protected areas. In order to improve conservation measures and reduce conservation conflicts, based on sound scientific evidence, the participation and coordination of authorities, managers, ecologists, and other social actors is needed (Redpath et al., 2013).

The Egyptian vulture (Neophron percnopterus) is a medium-sized, long-lived, monogamous, scavenger (Ferguson-Lees and Christie, 2001). Western European mainland populations spend the winter (and usually their first year of life) in the sub-Saharan Sahel region (Phipps et al., 2019), although a non-migrant population was detected in South-western Spain (Morant et al., 2020a). It is listed as globally endangered due to severe declines experienced throughout its range (BirdLife International, 2020). This is a species with a slow life-history, showing deferred maturity, and low fecundity (0–2 fledglings per breeding attempt; Serrano et al., 2021). They breed in cavities and on ledges on cliffs located in open landscapes, usually in rugged, arid regions (Donázar, 1993). Breeding pairs arrive from their winter grounds in Africa in late February and early March and remain in their territories until mid-September/October (Phipps et al., 2019). They generally reuse the same nest unless they are disturbed during sensitive phases, or the nest area is altered (Zuberogoitia et al., 2008; Morant et al., 2018).

The Egyptian vulture population in Biscay, northern Spain, is made up of 18–25 occupied territories. It occupies mountainous landscapes, far from towns and villages, where extensive cattle farming and timber extraction are the main economic activities. Breeding success and productivity in this population are affected by adverse weather conditions (mainly rainfall, Zuberogoitia et al., 2014), but mostly by disturbance derived from human activities (Zuberogoitia et al., 2008). In fact, the population suffered a severe decline in productivity during the first decade of 2000s, mainly due to the direct impact of recreational activities and forestry during the breeding period (see Zuberogoitia et al., 2008; 2014). In order to revert this situation, we started a management program in 2010 aimed at reducing the impact of human activities on Egyptian vultures' breeding success and hence, increasing population viability (Zuberogoitia et al., 2014). This program, which was ongoing at writing this paper, has been designed to reconcile conservation pactices that account for crucial species requirements with human activities (see, for instance, McCarthy and Possingham, 2007). In our study area, these activities include outdoor sports, recreational activities, road-works, and impacts associated with quarries, among others. In this study, we show how management measures have successfully helped to solve conservation conflicts in landscapes subjected to several human activities. Using long-term monitoring data (2000–2020), we test the effectiveness of management measures on the Egyptian vulture population inhabiting a highly human-modified area. Here we assess whether these management actions on breeding territories subjected to various disturbance regimes have effectively benefited the study population. Finally, we discuss future directions and challenges to mitigate vulture-human conservation conflicts.

4.3. MATERIALS AND METHODS

Study Area

The study was conducted in Biscay (northern Spain; area 2,384 km2; coordinates from 43°11′00″ to 43°12′70″ N and from 3°12′70″ to 2°13′10″ W). It has an Atlantic climate and mild temperatures with a thermic oscillation of 12°C from the coldest to the hottest months and 1,200–2,000 mm of rainfall distributed throughout the year (Euskalmet.eus, 2021). The landscape is mountainous and densely populated (520 inhabitants/km2; Eustat.eus, 2020), with extensive urban and industrial areas, mainly located in valley floors and on the gentler slopes, while mountain areas support semi-natural landscapes and wildlife. Overall, 79% of the area is dedicated to forestry (Euskadi.eus, 2019). Forestry plantations (Pinus radiata and Eucalyptus spp.) have become widespread in the last 80 years, gradually replacing grazing land for extensively reared livestock, traditional agricultural activities, as well as a few remnants of native forest.

Field Work and Data Collection

Annually, between 2000 and 2020, from February to September, we surveyed and monitored known and possible breeding areas to determine the location of all territories and nests of Egyptian vultures (between a minimum of 18 and a maximum of 25 territories per year). From 2000 to 2020, we identified 25 different breeding territories and monitored 86 nest sites within them (mean ± s.d., 3.44 ± 1.61 nest sites per territory, and range = 1–7), that were used at least once in these 21 years. Although Egyptian vultures had several nest sites in each territory, they normally used one or two as preferred nests (Morant et al., 2020b). We examined changes in occupancy, breeding parameters (breeding success and productivity), and population trends (number of territories and breeding pairs per year). We used 20 × 60 telescopes to observe nests from vantage points located far enough to preclude disturbing the breeders (mean distance: ca. 1,000 m; range: 442–2,826 m; Zuberogoitia et al., 2008).

Monitoring also included the assessment of disturbances within breeding territories from the last weeks of February to middle September. Disturbance variables were measured in a 1,000 m radius around the occupied nest sites (Zuberogoitia et al., 2008; Morant et al., 2020b). On average (s.d.), 13 (3.7) experienced observers spent 265.5 (77.1) survey hours in 107.4 (162.2) survey days per year. Human activities observed in the vicinity of the nest site that could disturb vultures during reproduction were: forestry works (cuts, clear-cuts, afforestation, and opening of new forest tracks); operation of quarries; public works (building or maintenance of roads, electric lines, and gas pipelines); cars, motorcycles and tractors passing or parking in the vicinity of the nest sites; climbers, hikers, mountain bikers, helicopters, paragliders, photographers, and birdwatchers; illegal hunting; outdoor sports (pedestrian and mountain bike racings); and fire. We considered the alert behaviour (when a at least one vulture was prevented from entering its nest and flew around the cliff in apparent uneasiness, Zuberogoitia et al., 2008) and the reproductive parameters (incubation, changeover rate, feeding rate, and others, Morant et al., 2019) to asses the intensity of disturbing events. According to their duration and frequency, disturbances were classified into: (1) low: low level, specific, non-recurring disturbances (i.e., occasionally detected and did not cause an evident alert behaviour and did not alter the normal reproductive behaviour of the Egyptian vultures; e.g., people practicing sports or forestry and farming works for short periods (less than 1 or 2 h) and far from the nest site (>600 m, considering the 1 km radius); (2) medium: one-off high level or medium-level disturbances (i.e., when disturbance duration extended for several hours; e.g., multitudinous races during one whole day, large vehicles, or machines working for several hours); and (3) high: chronic and high-level disturbances (i.e., detected through all day, or during several days, or when the effect was permanent; e.g., forestry activities, works related to the construction of new infrastructures and actions which produced direct disturbance, permanent alert behaviour of the adults and negative changes in the expected rate of reproductive parameters, during the entire activity period). High-level disturbances can carry on temporal (e.g., machines and vehicles working) or permanent habitat changes (e.g., opening of new roads, trails and paths close to nests, or forest cuts which eliminate protection patches of vegetation around the nests) and, consequently, they can influence nesting in the future (Morant et al., 2018). Further, considerable modification of areas surrounding nesting sites (permanent habitat changes), even if they take place during the winter –when breeders are absent from the area–, can push adults to move to alternative, less preferred or lower quality sites, resulting in higher chances of failure in subsequent nesting events (Morant et al., 2018).

Establishing the Basis for the Species Protection

In 2010, the local government, Biscay County Council (hereafter, BCC), implemented a series of measures to address the activities that most often and seriously interfered with the Egyptian vultures' breeding, as identified in the 2000–2009 period. These included: (a) A climbing management plan for wildlife conservation (Web.bizkaia.eus, 2010)1. In this document, authorities regulated sites and periods in which climbing is allowed. Further, this plan is continuously updated and adapted to changes in nest site location of target species, mainly Egyptian vultures. (b) The BCC also implemented an inter-department management plan to enhance coordination with the forestry department and reduce the impact of forestry activities on wildlife, especially on Egyptian vultures. The main objective of this plan is to prevent forestry works and related activities around nest sites during the breeding period (from 1st March to the end of September) and to conserve local landscape around nesting sites. Finally, (c) from 2011 onward, the BCC started regulating outdoor sports, mainly outdoor races (pedestrian, bike, and motorbike). These management actions were legally regulated in 2018 (Bizkaia, 2021a;b). Every year, outdoors racings must apply for a permission and are evaluated by wildlife managers to verify that routes avoid commonly used nest sites and nesting territories of Egyptian vultures during the breeding season.

In 2015, the BCC passed the Management Plan of Vultures in the Basque Country (Bizkaia, 2021c). The main goals of that document are: (1) To assure the protection of Special Interest Areas (SIAs: areas where abundance and diversity of vulture species are fundamental for the long-term conservation of their populations) and Critical Areas (CAs: vital areas for Egyptian vulture survival and conservation); (2) to mitigate the non-natural mortality causes; and (3) to reduce human disturbances in the breeding, foraging and roosting areas. The Plan establishes critical periods for the species, from the 1st March to 15th September. The Plan also establishes general guidelines for Environmental Impact Assessments to assure the conservation of the target species through habitat retention and restoration, as well as monitoring breeding success.

Overall, BCC environmental managers assessed 5,095 files from 2010 to 2019, where the potential disturbance events on Egyptian vulture breeding territories was evaluated (Figure 4.1). Managers reported on the activities and allowed, denied or delayed them according to the potential impact on Egyptian vulture breeding performance. The potential impact of submitted activities was assessed considering (1) the number of nest sites known within that territory, (2) the frequency of use of the potentially affected nest site and when it was last used, (3) the distance and the position of the activity relative to the nest site (e.g., in front, at side, or back) of the intervention, and the presence of a buffer area (e.g., forest patch) between the nest site and the alteration area, and (4) whether other alterations were recently made within the 1 km radius and the possibility of synergistic effects with previous activities. In any case, any activity that could generate a disturbance within the 1 km radius around the 86 known nest sites must finish before the end of February, when Egyptian vultures arrive at our study area.

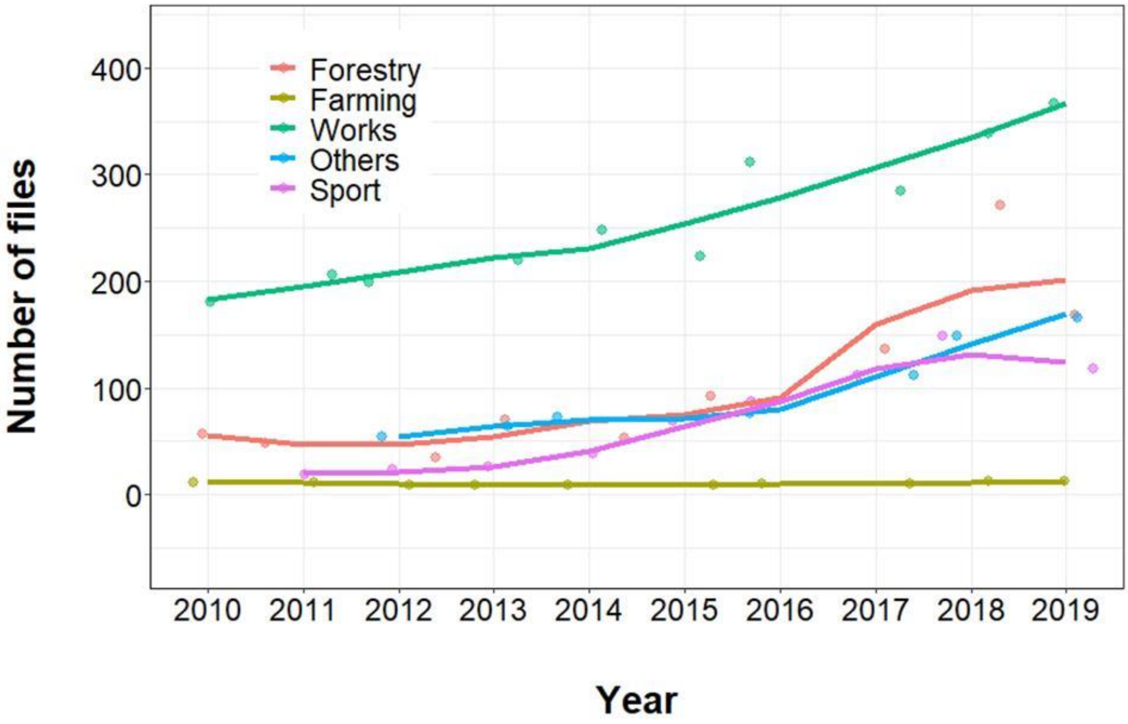

Figure 4.1. *Inter-annual variation in the number of files developed by Biscay County Council (BCC) environmental managers, where potential disturbance events on Egyptian vulture breeding areas were evaluated after the onset of the adaptative management program (2010) until 2019 (at the time of the writing, there are no available data for 2020). We considered five groups of potential disturbance events: forestry (cuts, clear-cuts, afforestation, and forest tracks; n = 1012 files); farming (activities related to habitat changes for livestock; n = 103 files); works (building or maintenance of roads, electric lines, gas pipelines, and quarries; n = 2577 files); sports (outdoor races, MTB races, and climbing; n = 639 files); and, others (new routes and tracks for climbing, walking and mountain bikes, photography projects, and game activities; n = 764 files). The lines showed the smoothed conditional means by using "loess" method in the package "ggplot2."*

Management Action Plan for the Species Conservation

In 2010, BCC environmental managers started applying management actions and a special monitoring protocol for preventing human disturbances in Egyptian vulture breeding territories. Annually, before the arrival of this migratory species from Africa to the study area, the first management measure consisted of preventing habitat alterations within

1 km of each of the 86 nest sites. Human activities that could potentially modify landscape and vegetation around nest sites (e.g., opening tracks or falling timber plots; see Morant et al., 2018 for details on such activities) must be approved by BCC environmental managers following the basis for the species protection.

After the arrival of the species to the study area, ecologists and rangers systematically monitored Egyptian vultures (Morant et al., 2020b). The first individuals usually arrive during the third week of February. The breeding cycle of Egyptian vultures starts with nest repair and nest building and courtship; both activities take place simultaneously and start 25 days before the onset of incubation (Morant et al., 2019). At this time, mates typically use a resting site close to the selected nest site. Therefore, we could reliably identify the breeding site at the end of March. In the study area, incubation starts, on average, on April 17th (Morant et al., 2019). However, the activity restrictions around all known nest sites used during the last two decades lasted until assuring incubation onset and the selected nest site. Afterward, managers authorized those activities that had been stopped in the non-selected nest sites while the activity restrictions continued around the active nest sites.

Then, from the onset of incubation until offspring fledge, ecologists and rangers monitored reproduction of all the territories. In this period, no disturbance events are expected to occur in the nesting areas. Every non-authorized disturbing activity detected within the 1 km radius of the active nest sites previously defined was immediately reported to BCC environmental managers, the potential hazard to the species analysed by managers, in conjunction with ecologists if required, and stopped immediately if deemed potentially hazardous to the species. Some disturbance events were successfully managed and quickly stopped before causing any obvious impact, but others could not be managed and stopped in time to avoid deleterious effects on the breeding territory. Low-level disturbance events were particularly difficult to manage in time to avoid negative effects. Management actions were then focused to prevent similar events (e.g., warning signs and awareness campaigns). In particular cases, if a disturbing activity had to be carried on by major force reasons, intensive monitoring of the pair was conducted, and some activities and their timing were consequently regulated. Normally, no disturbing activity was allowed during incubation and the first weeks of life of nestlings. During this time, ecologists and rangers analysed the breeding behaviour of the target pair according to the patterns described by Morant et al. (2019), and stopped any disturbance events that affected the behaviour and could cause the loss of the clutch or nestlings.

The potentially disturbing activities were only allowed once the post-fledgling dispersal began, the exact date of which varies among pairs from the first weeks of August to the end of September, or when natural failure of the reproduction event was detected (mainly due to intensive and continuous precipitations, see Zuberogoitia et al., 2014). Thus, the date on which disturbances were allowed was individually tailored to each breeding attempt.

Data Analysis

In order to assess the effectiveness of management actions over the breeding territories, we ran Generalized Linear Mixed Models (GLMMs) fitted with the Laplace approximation (Bolker et al., 2009), with productivity (number of successfully fledged offspring; 0, 1, or 2) as the response variable. We favoured a Gaussian error distribution over a Poisson one since the variance to mean ratio clearly departed from 1 (e.g., in the global model, $\bar{x}=0.647$, $\sigma2 = 0.475$) and data were right-truncated. Further, the Gaussian distribution has been shown to perform well with small count data such as clutch sizes (see McDonald and White, 2010 for more details). Territory and nest were entered as random factors (the second nested within the first), to account for the lack of independence of data due to the reuse of the same nests throughout different years. In a previous work (Zuberogoitia et al., 2014), we built a model selection using three subsets of predictor variables: nest site variables, weather variables, and disturbance variables. The disturbance model (only the disturbance variable) was the best model among the model selection procedure carried out by Zuberogoitia et al. (2014). Therefore, we considered disturbance as predictor in our model, and we also included management (0 = before, 1 = after management) and the interaction between disturbance and management as fixed factor variables. The interaction between the two factors allowed us to investigate the effect of disturbance regimes in species productivity and to assess the efficiency of the management actions. It is important to remark here that all disturbances recorded during the second decade and coded here as "after management" were real disturbances that were taking place, or about to be started (for instance, employers and machines deployed in the field, and just prepared to start working), when detected and stopped immediately or in a few hours of being detected. Therefore, we assumed they were real threats that, if unmanaged, would have provoked similar effects on breeding success as they really had in the previous decade.

In order to assess the contribution of our management approach to population dynamics, we estimated the number of fledglings that would have been lost without it. For this end, we considered the average predicted productivity for disturbances of medium (0.07 fledglings per breeding pair) and high (0.007 fledglings per breeding pair) level obtained from the model, considering data of 2000–2009. Then, we took into account cases of high and medium-level disturbances that were successfully managed in the second decade, and selected only those that raised (1 or 2) fledglings. For these nests we changed the actual, observed number of fledglings for the average expected in case we had not successfully managed the disturbances.

All statistical analyses were performed using the R software (R 4.0.2). GLMMs were run by using the "lmer" function implemented in the package "lme4" (Bates et al., 2012). We estimated the marginal and conditional variance explained by our model by using the "rsquared" function implemented in the package "piecewiseSEM" (Lefcheck, 2015). Finally, we visually inspected the normality of the residuals of our model by using the "ggresid" pannel function implemented in the package "ggresidpannel" (Goode and Rey, 2019). P-values were estimated by using the package "afex" (Singmann et al., 2021). Model performed well according to the distribution of the residuals. All the figures were done by using the package "ggplot2" (Wickham, 2016). Mean values are reported with (±) their standard deviation. Statistical significance was set at $P < 0.05$.

4.4. RESULTS

The management actions significantly reduced the impact of disturbances on Egyptian vulture breeding success. Before the implementation of management actions, we monitored 207 breeding attempts of Egyptian vultures, 136 of which started reproduction (i.e., at least one egg was laid) and produced 87 fledglings (Figure 4.2). In this period, 2000–2009, we detected a significant negative effect of medium and high-level disturbances on productivity (Tables 4.1, 4.2 and Figures 4.3A,B). After the implementation of management actions, 2010–2020, we monitored 218 breeding attempts, 185 of which started reproduction and produced 134 fledglings (Figure 4.2). In the first decade, the number of pairs that did not breed (7.1 ± 1.9 per year) was more than twice that detected in the second decade (3.0 ± 2.0 per year; t student = 6.25, $P < 0.001$). Moreover, after the implementation of the management protocol, we detected 148 events related to disturbances that could affect Egyptian vulture breeding success: 17 low-level disturbances, 59 medium-level disturbances, and 72 high-level disturbances (Table 4.1). From them, 11.7% of the low-level, 47.5% of the medium-level, and 65.3% of the high-level disturbances were managed and stopped.

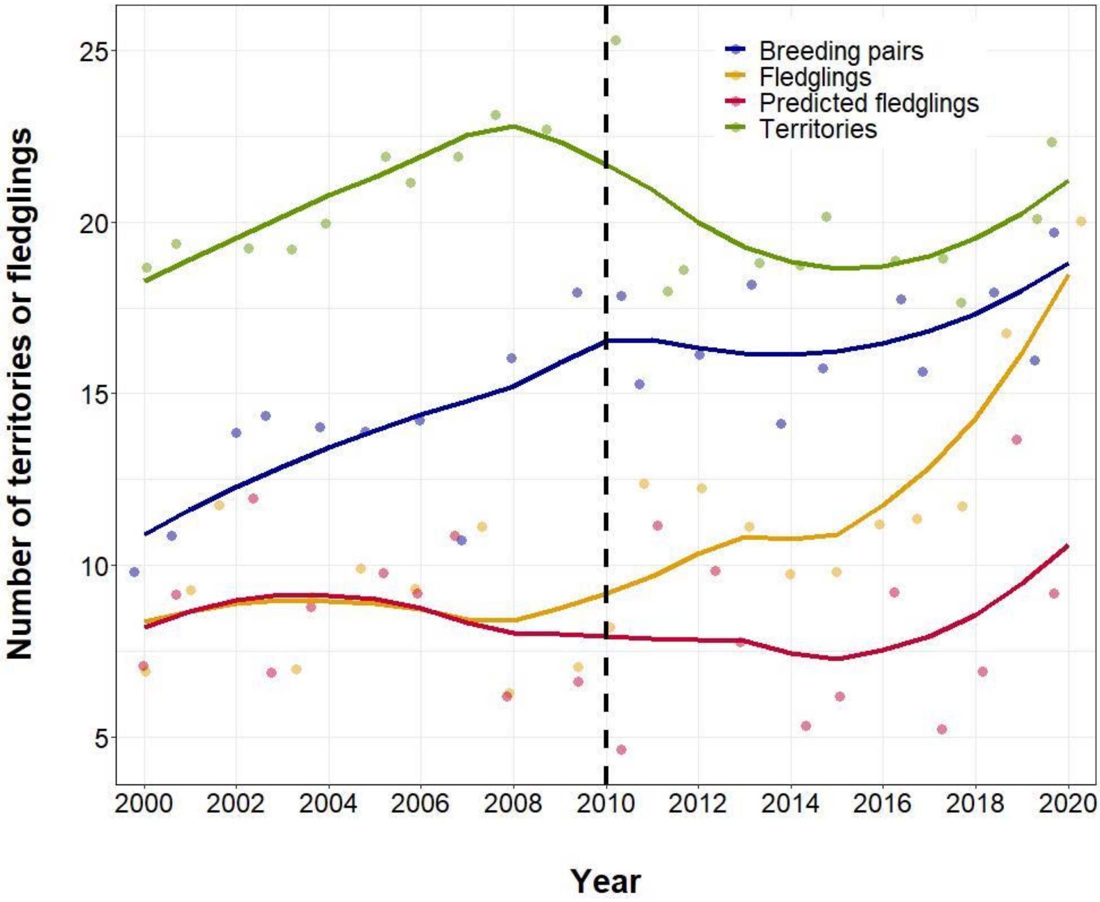

Figure 4.2. *Inter-annual variation in the number of territories (i.e., territorial pairs showing breeding behaviour), breeding pairs (i.e., pairs that lay at least one egg), number of fledglings successfully raised and the predicted number of fledglings that would have been produced without adaptative management. The vertical line shows the beginning of the management actions (2010). Coloured dots represent raw data points. The lines showed the smoothed conditional means by using "loess" method in the package "ggplot2."*

Table 4.1. *Disturbance events detected within the 1 km radius of the nest site of Egyptian vultures from 2010 to 2020. Three types of disturbance were considered according to their magnitude and persistence (low, medium and high) and whether they were successfully managed to avoid their impact on species reproduction. The number of cases for each disturbance type and the number of breeding attempts that affected are considered, as well as the final productivity (number of fledglings/pairs that start reproduction).*

	Low		**Medium**		**High**	
	Managed	Non-managed	Managed	Non-managed	Managed	Non-managed
Cases	2	15	28	31	47	25
Breeding attempts	2	14	24	28	41	17
Fledglings	3	15	22	9	47	3
Productivity	1.5	1.07	0.92	0.32	1.15	0.18

Table 4.2. *Results of GLMM considering productivity (number of fledglings) of Egyptian vultures as the response variable and disturbance types (null, low, medium and high), management (0 = before management, 1 = after management) as predictive variables (fixed factors) and the interaction between the two. The reference level for the fixed factor is the disturbance type null. The values of the estimator, standard error, the t-value, its corresponding P-value and the marginal (R^2 m) and conditional (R^2 c) variances are shown. Significant values are highlighted in bold.*

	Estimate	**St.error**	***t*-value**	***p***	**R^2 m (%)**	**R^2c (%)**
Intercept	0.900	0.104	8.644	**<0.001**	14.96	52.94
Disturbance: Low	-0.067	0.165	-0.407	0.684		
Disturbance: Medium	-1.092	0.169	-6.441	**<0.001**		
Disturbance: High	-0.737	0.179	-4.104	**<0.001**		
Management	-0.337	0.117	-2.878	**0.004**		
Disturbance: Low*management	0.431	0.220	1.958	0.051		
Disturbance: Medium*management	1.108	0.194	5.694	**<0.001**		
Disturbance: High*management	0.662	0.203	3.254	**0.001**		

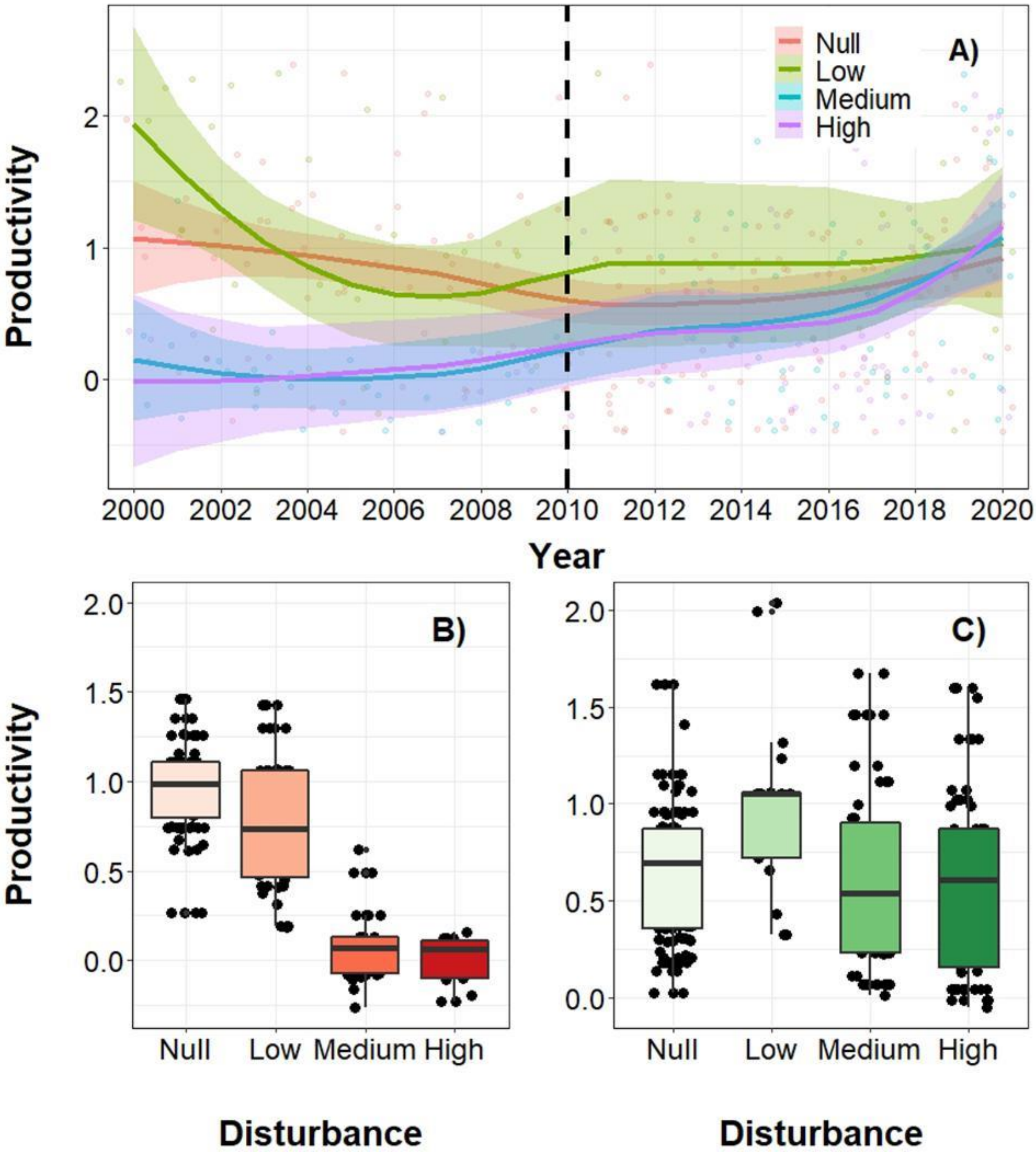

Figure 4.3. *The figure A) Temporal trends in the number of fledglings per breeding pair (pairs that lay at least one egg) during the whole study period (2000-2020) considering the disturbance regime (null, low, medium and high) that affected the breeding territories before and after the management action plan. Shaded areas represent 95% confidence intervals. The dashed vertical line shows the beginning of the management actions (2010). The B) and C) graphs showed the predicted values for productivity (ie number of fledglings successfully raised per pair that started reproduction) depending on the disturbance regime before (2000-2010) and after (2010-2020) adaptative management, respectively. Boxplots show the median, the upper and lower quartiles and whiskers indicate variability outside them. Coloured and black dots represent the raw data points in each case.*

In the managed period, almost half of the disturbance events detected after the management actions were implemented were related to forestry practices of which 58.9% of the detected cases were managed and stopped (Table 4.3). The breeding success (percentage of pairs that successfully breed per the number of pairs that start reproduction) in the managed cases (66.7%) was ca. 4 times higher than those that could not be managed and stopped in time (17.4%). Moreover, we detected the shifts in nest sites in two managed cases and five in non-managed cases. Activities related to works and quarries were previously analysed and protocolized, and most of them were correctly managed, showing a high rate of breeding success (Table 4.3). Outdoor sports, mainly individual or small group activities, people walking in the field or other activities (e.g., illegal hunting or fires, photographers, and maintenance works in buildings), were difficult to detect and to manage in time to avoid deleterious effects on reproduction (Table 4.3).

During the implementation of management actions, we detected a statistically significant reduction in the effect of medium and high-level disturbances on productivity (Table 4.2). Still, there were differences in the productivity of those territories affected by these medium and high-level disturbances and those affected by low-level disturbances (Figures 4.3A,C). In this case, the marginal variance was only 2.4%. In the managed period, we did not avoid 31 medium-level disturbances of 28 breeding attempts that finally produced nine fledglings (0.32 fledglings per breeding pair) and 25 high-level disturbances of 17 breeding attempts that finally produced three fledglings (0.18 fledglings per breeding pair).

Table 4.3. *Main disturbance events detected within of nest sites of Egyptian vultures during the study period (2000-2020): Forestry activities; quarry derived activities; public works; manned aerial vehicles and paragliding; outdoor sports (climbers, pedestrian and MTB racers); recreation activities (hikers, mountain bikers, photographers, birdwatchers); and others (illegal hunting, motorcycles, music festivals). The table shows the number of disturbance events and how many of them were managed or not, and in each case the number of pairs that switched to other nest, the number of fledglings raised and the breeding success (percentage of the number of successfully pairs/number of pairs that started reproduction).*

Disturbance events	N	Managed	N	Nest switching	Fledglings	Breeding success
Forestry activities	56	yes	33	3	28	66.7%
		no	23	5	6	17.4%
Outdoor sports	18	yes	5	1	4	60%
		no	13	3	6	38.5%
Quarry derived activities	14	yes	14	0	16	85.7%
		no	0	0	0	0%
Public works	14	yes	12	1	13	75%
		no	2	0	0	0%
Recreation activities	13	yes	1	0	1	100%
		no	12	3	8	50%
Manned aerial vehicles and paragliding	6	yes	2	0	1	50%
		no	4	0	3	50%
Others	17	yes	7	0	4	57.1%
		no	10	1	5	40%

Taking into account the results of the 21 monitoring years (global period), we found significant differences considering the interactions between the four disturbance types and managed actions (Table 4.2 and Figure 4.3).

Considering the average predicted productivity, 44 nestlings (32.1% of the chicks raised in the 2010–2020 period) would have died if management actions had not been implemented (Figure 4.2).

Overall, 72% of breeding attempts that suffered disturbances failed to breed prior to the implementation of management (2000–2009), whereas, under management (2010–2020) the number of failures due to disturbances affected 49% of the breeding attempts.

4.5. DISCUSSION

The long-term monitoring of the Egyptian vulture population in the study area allowed us to identify the effects of one particular threat: the effects of disturbance on breeding success and productivity (Zuberogoitia et al., 2008; Morant et al., 2018). We also studied the effectiveness of conservation measures taken to revert these effects (Zuberogoitia et al., 2014). The number of studies identifying threats and assessing the effectiveness of management measures on species, populations, and ecosystems has notably increased during the last decades (Richardson et al., 2020). Recently, Bolam et al. (2020) showed that conservation actions prevented 21–32 bird and 7–16 mammal extinctions since 1993, and 9–18 bird and two to seven mammal extinctions since 2010, thus showing the effectiveness of such actions in reversing negative trends and stimulating further actions. Such studies usually require a long-term effort to evaluate their effectiveness, particularly in long-lived territorial species like vultures, whose intrinsic life-history traits (e.g., delayed maturity, long-migration, and low productivity) makes them especially vulnerable (Sergio et al., 2011; Sanz-Aguilar et al., 2017; Badia-Boher et al., 2019). Notwithstanding, these studies should account for and enhance stakeholder and manager participation to promote long-term success of management actions (Durant et al., 2019). This is particularly relevant in anthropised landscapes where conservation conflicts emerge from competing interests (Redpath et al., 2013). The management framework implemented in our study area helped to reduce uncertainty about the effects of human activities on breeding Egyptian vultures, and demonstrated how coordination between all actors (i.e., ecologists, policy makers or managers, conservation practitioners, socio-economic entities, and the general public) can alleviate conservation conflicts and ensure the persistence of threatened species.

Despite the high cost that long-term monitoring entails (Morant et al., 2020b), the evidence-based information we obtained allowed us to make critical decisions on when to monitor and when to act (Bennett et al., 2018). Our measures have been adapted through time as both human practices and species responses changed. We had previously found that even though most of the forest logging activities were conducted in winter, they still had an impact on species re-occupancy and productivity, where those territories affected by habitat changes exhibited lower re-occupancy rates and breeding success (Morant et al., 2018). Therefore, to reduce the impact in the buffer areas, we extended conservation measures in both space [from the 600 m first proposed by Zuberogoitia et al. (2008) to 1 km radius] and time (including non-breeding periods, when this migrant species is not present in our study area, Phipps et al., 2019; Morant et al., 2020a).

Conservation approaches in general have traditionally focused on large, pristine, and remote areas where sources of disturbance like those described here are rare or absent. However, in highly anthropised landscapes it is not feasible to spare large areas devoted only to conservation and there is an increasing demand of natural and semi-natural areas for recreational activities (Larson et al., 2016). Yet, these areas close to human population centres can harbour endangered species or other elements of high natural value, as in our case study. Most timber related activities and outdoor sports had never been restrained due to conservation issues before 2010 when we started applying the protocol and regulating those activities around nest sites. During the first years of management, we made a communicative effort and tried to convince stakeholders and the general public about conservation issues and management measures to reduce or avoid disturbance on nesting vultures. As a consequence, most stakeholders, mainly those related to forestry, quarries and road-works, successfully adapted to conditions and limitations of conservation protocol. However, some stakeholders disagreed with our measures and regularly complained against them. What is more, there are still some outlawyers who did not agree to follow the management measures and required monitoring to prevent disturbance events. In fact, even protected areas with strict biodiversity conservation objectives suffer increasing levels of intense human pressure worldwide (Jones et al., 2018). Most of the disturbance events described in this article were detected while occurring, mainly forestry activities and outdoor sports, and BCC managers developed the managing protocol to stop them immediately. Regrettably, in some cases, we detected the activity too late. This explains why the percentage of breeding success of managed activities was not higher than we would expect.

Our results show that management measures greatly improved vital life-history values of Egyptian vultures; in fact, our study suggests that 44 fledglings may not have survived without conservation measures during the second decade of our study. However, we also must consider that those measures previously adopted by BCC, the basis of the management protocol, had a positive effect on the species conservation. During the first decade, we detected several pairs that occupied the territory, tried to breed but never achieved to lay eggs or failed during the first days. However, as we identified these problems and management measures were adapted, the number of breeding pairs increased and arrived close to the number of actual pairs (Figure 17). This is a critical outcome given the delayed maturation, low-productivity and strong fidelity to the breeding site of the species (Sanz-Aguilar et al., 2017). For instance, Serrano et al., (2021) showed that natal dispersal distances of Egyptian vultures were negatively related to natal breeding population density and population trends (social cues). Hence, increasing the breeding success with low adult mortality rate, as our case (Zuberogoitia et al., 2009), would help to increase the viability of Egyptian vulture populations, not only in the target area but also in the neighboring regions since they play an essential role in demographic processes such as source-sink dynamics (e.g., Hernández-Matias et al., 2013; Lieury et al., 2016; Weegman et al., 2016; Sanz-Aguilar et al., 2017; Soriano-Redondo et al., 2019).

Conservation programs that succeed in reducing and palliating the main threats to target species and identify and engage with all stakeholders to implement solutions, particularly in areas of conflict with high human density, should be regarded effective. Management measures accompanied by effective participation among stakeholders improve relationships, increase trust, and reduce conflict (e.g., Reed, 2008). Recognizing the important role of each and every actor is crucial toward constructing transparent and trustful relationship among interested parties (Redpath et al., 2013). For example, a key way for conservation managers to access relevant and updated scientific knowledge is through direct contact with ecologists, who conduct field research within the sites they manage (Durant et al., 2019). Similarly, ecologists should realize that decision-makers have to deal with multiple competing and often conflicting interests (e.g., species conservation in areas of high-value resource extraction), and sometimes decisions on species conservation are dictated by higher political interests rather than a lack of knowledge about the system in question (Cook et al., 2013; Redpath et al., 2015). In our case, we were able to construct a collaborative network by targeting all social dimensions of the conflict, and promoting the mutual-understanding of each party’s needs. Encouraging the involvement in species conservation of all relevant actors alleviated conflicts and paved the road toward measures that could be objectively considered balanced and successful in terms of conservation and socio-economic interests. We are far from a final solution that fully satisfies all stakeholders (Redpath et al., 2013; 2017), but our study showed that human-wildlife coexistence is still possible in an increasingly crowded and human-modified world, while considering and maintaining the livelihoods and well-being of all actors involved.

Concluding Remarks

World human population is quickly increasing, and it is expected to reach ca. 11 billion in 2100 (Roser, 2019). This means that virtually all the areas considered pristine or unaltered will be occupied in one way or another as human requirements (e.g., resources, space) increase and those already occupied may be more intensively exploited (Bowler et al., 2020). It is expected that, in a few decades, traditional grazing activities will be abandoned in large areas of the European continent and, while some regions evolve toward rewilding processes affecting the scavenger guild structure and function (García-Barón et al., 2018; Martín-Díaz et al., 2020), others will continue the intensive occupation and use of land, which may impose potentially greater impacts on natural systems (e.g., agricultural intensification, growth of urban areas; Deinet et al., 2013; Navarro and Pereira, 2015). Under these new scenarios, conservation conflicts in anthropised areas are expected to increase. In this paper, we show that management actions are essential for the coexistence between humans and threatened species in anthropised areas. Approaches like ours could be complemented with other measures such as campaigns to increase social awareness and behavioural change amongst overall population. Such measures could help to prevent some of the human pressures addressed in this paper (e.g., recreational activities in breeding areas of Egyptian vultures; Badia-Boher et al., 2019; Salazar et al., 2019) that are generally difficult to detect and manage. Taken together, accounting for all these factors can promote the persistence of Egyptian vultures and other raptors in human-dominated lands and, eventually, favour long-term conservation success.

CHAPTER 5

Winter movement patterns of a globally endangered avian scavenger in south-western Europe

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5.1. ABSTRACT

Partial migration, whereby some individuals migrate and some do not, is relatively common and widespread among animals. Switching between migration tactics (from migratory to resident or vice versa) occurs at individual and population levels. Here, we describe for the first time the movement ecology of the largest wintering population of Egyptian vultures (*Neophron percnopterus*) in south-west Europe. We combined field surveys and GPS tracking data from December to February during four wintering seasons (2014–2018). The wintering population consisted on average of 85 individuals (range 58–121; 76% adults and 24% subadults). Individuals were counted at five different roosting sites located near farms, unauthorized carcass deposition sites and authorized carcass deposition sites. Our results show that vultures tend to remain close to the roosting site. Moreover, we observed that females exhibited smaller home range sizes than males, which suggests a possible differential use of food sources. Overall, birds relied more on farms than other available food resources, particularly subadult individuals which exploited more intensively these sites. Our results showed that Egyptian vultures congregate in significant numbers at specific sites throughout the winter period in south-west Spain and that these roosting and feeding sites should be given some level of legal protection and regular monitoring. Furthermore, predictable food sources might be driving the apparent increase in the non-migratory population of Egyptian vultures, as observed in other avian species which are also changing their migratory behaviour.

5.2. INTRODUCTION

Movement is essential for most organisms in at least one stage of their life cycle, and extends across multiple spatiotemporal scales (Hansson and Akesson, 2014). Animal movements are highly variable, from daily short-distance foraging movements to long-distance movements during some stages of their life, such as juvenile dispersal. Among them, migration is an integral part of the annual cycle of many species and is one of the most studied movement patterns from invertebrates to mammals (Dingle and Drake, 2007). Migration is typically thought of as a life history strategy shared by entire populations or species. Partial migration, the most common form of migration, is found across a wide variety of taxa and is more widespread in birds (Chapman et al., 2011). That is, some individuals overwinter within their breeding region (resident individuals) while others display migratory behaviour (migrant individuals) to reach distant wintering quarters (Newton, 2010). Frequently, the coexistence of these migration behaviours appears to be driven by individual asymmetries in variables such as sex, age, body size, as well as by environmental conditions (Cadahía et al., 2017). Furthermore, switching between these two strategies could occur at population and individual level, depending on season (Ogonowski and Conway, 2009), migration direction (Berthold et al., 1992), route, timing (Studds et al., 2008), and distance to wintering grounds (Dale and Leonard, 2011).

Understanding the causes and consequences of changes in migratory behaviour is necessary to better predict population structure and dynamics (e.g., influence on survival, extent of migratory connectivity, or response to changes in breeding and non-breeding environments) (Gilroy et al., 2016). The causes that lead to these changes in migratory behaviour are well known including environmental changes via phenotypic flexibility (Teitelbaum et al., 2016); shifts in phenology through changes in inherited genetic or epigenetic pathways (Rubolini et al., 2007); habitat redistribution (Greig et al., 2017); developmental plasticity (Gill et al., 2013) and changes in abundance/availability of food resources (Oro et al., 2013). Among them, anthropogenic changes are known to affect the movement ecology and behaviour of long-lived species through the provision of abundant and spatially stable food subsidies (Gilbert et al., 2016). For instance, this can cause several behavioural changes at individual and population levels, including dietary shifts, changes in foraging techniques and changes in social systems to find food, and also affects individual fitness and survival (Oro et al., 2013). However, there is a lack of knowledge about the consequences of changing migratory patterns (from migratory to resident) in species with overlapping breeding and non-breeding grounds. In particular, little is known about how species behave in those environments during winter through the study of movement patterns across time and space and on the impacts of the utilization and availability of predictable food resources on daily movement patterns and migratory behaviour. Whether animals are resident or migratory has major consequences for interactions and processes in local environments (Bauer and Hoye, 2014). In fact, human-induced changes, and the effects of climate and land-use changes in animal movement patterns have been linked to population declines in migratory species worldwide (Tucker et al., 2018).

Nowadays, thanks to the emerging use and rapid improvements in telemetry techniques (Wilmers et al., 2015), we are able to determinate variations in migratory strategies (Weimerskirch et al., 2015), and disentangle interactions between animals and their abiotic and biotic environment (Kays et al., 2015). The integration of these techniques with traditional approaches (e.g., population monitoring) could help to better understand which factors underlie ecological and evolutionary processes in migration ecology and integrate them in conservation and management decisions. Basic movement parameters, BMPs hereafter, are used to describe movement paths (see Signer et al., 2019) as well as to identify common movement patterns (Edelhoff et al., 2016). Likewise, the use of analytical methods to assess space use (i.e., resource utilization functions; hereafter RUFs) are of great utility to identify which factors underlie those patterns from a mechanistic perspective (Marzluff et al., 2004). One of the most used parameters to asses space use and resource selection is the home range estimator. Home range is the direct result of movement driven by habitat selection and other external factors, biotic interactions, and intrinsic factors related to individual state (Börger et al., 2008). In addition, RUFs, which basically consist on a multiple regression analysis that accounts for spatial and temporal autocorrelation of tracking data (Marzluff et al., 2004), are a reliable method to (1) define the fidelity to a site according to space use and sites of ecological significance in the life history of animals (López-López et al., 2014); (2) check availability and distribution of resources (van Beest et al., 2010); and (3) to improve inference on the spatial factors influencing behaviour (Edwards et al., 2009).

The use of indicators (i.e., BMPs) gains significant relevance on the study of space use in populations of long-lived vertebrates with an altered migratory pattern (Cagnacci et al., 2011). Therefore, understanding how populations with altered migratory patterns spatially behave in anthropogenic environments is crucial for their conservation and management (Montsarrat et al., 2013; van Overveld et al., 2018). Vulture species have shown high behavioural plasticity with regards to local habitat structure and resource availability (López-López et al., 2013). Furthermore, they are adequate ecological indicators and the differences in movement patterns within and between populations could help to understand complex ecological associations (Montsarrat et al., 2013; van Overveld et al., 2018). In this context, the BMPs and space use estimators are an essential tool to (1) disentangle movement patterns over time and underlying factors, (2) unravel the determinants of space use, and (3) detect highly used trophic resources by vultures’. This results in benefits to wildlife managers aimed at reducing vulture-related conflicts (Devault et al., 2005) and conservation of these species.

The spatial ecology of the Egyptian vulture (Neophron percnopterus) is still poorly known (Alarcón and Lambertucci, 2018), and most of the studies have focused on pure migrant or pure resident (i.e., insular) populations (López-López et al., 2014; van Overveld et al., 2018). In this study, we describe for the first time the spatial ecology and resource use of a unique Egyptian vulture population which, contrary to the commonest migratory pattern, winters in south-west Europe (instead of migrating to the Sahel region of Africa), by means of the combination of field surveys and telemetry information. To this end, we firstly describe the overwintering population size and its variation over time. Secondly, we test if vultures' movement, extracted from BMPs, depend on both individual characteristics (i.e., age and sex) and temporal variation on environmental characteristics within the wintering season. Likewise, we test the use of different predictable food resources at fine-scale thoroughout the wintering season. Finally, we characterize the determinants of space use and identify primary drivers of vultures resource utilization through RUFs.

5.3. MATERIALS AND METHODS

Study species

The Egyptian vulture is a medium-sized, territorial scavenger distributed from Western Europe to India and South Africa, and is globally listed as Endangered by the IUCN (BirdLife International, 2016). As much as 40% of the European breeding population is found in Spain (Del Moral, 2009). The European breeding population is estimated at around 3000–4700 pairs (BirdLife International, 2015). It is a migratory bird that abandons its European breeding areas between late August and February (Phipps et al., 2019). The species exhibits high migratory connectivity at large spatial scales, but very diffuse migratory connectivity within subpopulations, with wintering ranges up to 4000 km apart for birds breeding in the same region, and each subpopulation visiting up to 28 countries (Phipps et al., 2019). European populations winter in sub-Saharan Africa and the Arabian Peninsula, with juveniles often remaining in the winter range for more than a year after their first migration (Oppel et al., 2015; García-Ripolles et al., 2010). Apart from these mainland populations, there are also sedentary populations inhabiting in Mediterranean islands (i.e., Menorca) and Macaronesian islands (Canary Islands, Cape Verde), and non-migratory breeding populations in sub-Saharan Africa (BirdLife International, 2015). Moreover, records from wintering individuals exist in southern Spain since mid-eighties (SEO/BirdLife, 2012), and more recently, one young and two adults were observed in Sicily (Italy) during the wintering season 2015–2016 (Di Vittorio et al., 2016). During the twentieth century, the population of this long-lived scavenger has steadily declined across large parts of its European and African range, mainly due to unnatural mortality caused by poisoning and electrocution (BirdLife International 2015; , Buechley and Şekercioğlu 2016). However, the survival rates are known to be higher in sedentary populations (Sánz-Aguilar et al., 2015).

Like other vulture species, the Egyptian vulture presence is usually bounded to landscapes where livestock farming practices are usual (López-López et al., 2014), as well as those regions where traditional pastoralism is still present (Mateo-Tomás and Olea, 2010). Although Egyptian vulture also feeds on wild prey (Donázar 1993), livestock is also frequently highlighted as a cornerstone in Egyptian vulture conservation, with the decline in extensively bred livestock considered a critical threat (BirdLife International 2016; Mateo-Tomás and Olea 2010). The species is listed as Vulnerable at both national and regional levels according to Spanish environmental legislation. The Egyptian vulture population remained stable in the study area between 2008 and 2016, including 143–155 breeding pairs (data provided by the regional government, Junta de

Extremadura), which represents approximately 13.6% of the Spanish population (Del Moral 2009).

Study area

The study area is located in the western Iberian Peninsula and covers 1750 km2, corresponding to the administrative region of Cáceres (Extremadura, Spain) (Figure 5.1). The climate is typically Mediterranean semi-arid to dry sub-humid with some oceanic influence with mild winter temperatures and autumn rainfall (Felicísimo, 2001). Average monthly temperatures are mild, but absolute minimum temperatures easily reach negative values in winter months when frosts are frequent (range 4–7 °C) (Felicísimo 2001). Very low human population density, a markedly rural environment, and scarce industrial activity define the region, which is also recognized as one of the major biodiversity hotspots of the Mediterranean region (López-López et al., 2011). The Natural Protected Areas network and the Natura2000 network cover 6.9% and 31% of the region, respectively (Traba et al., 2007).

Landscapes are mostly characterized by the so-called “dehesas” (sometimes referred to as the “Spanish savannah”), agrosilvopastoral systems composed by holm oak (Quercus ilex) and corn oak (Quercus suber) forests which were progressively thinned until forming wood-pasture used for animal grazing and foraging plus crop production. Most of the region’s land is used for agriculture, combining arable and extensive livestock rearing. Overall, the livestock numbers maintained over time with slight variations. In 2005, a total of 504,908 cows, 1.6 million sheep, 174,608 goats, and 206,897 pigs whilst in 2018, a total of 592,546 cows, 1.2 million sheep, 138,291 goats, and 154,585 pigs were censused in the study area (data provided by the regional government, Junta de Extremadura). The livestock carcass disposal in the study area is allowed according with the EU legislation and regulation policies (CE 142/2011; Royal Decree 1632/2011). Moreover, CE 830/2005 made the requirements to dispose carcasses for feeding vultures at authorized feeding points more flexible, and the prohibition on carcass disposal was unofficially lifted (Arrondo et al., 2018).

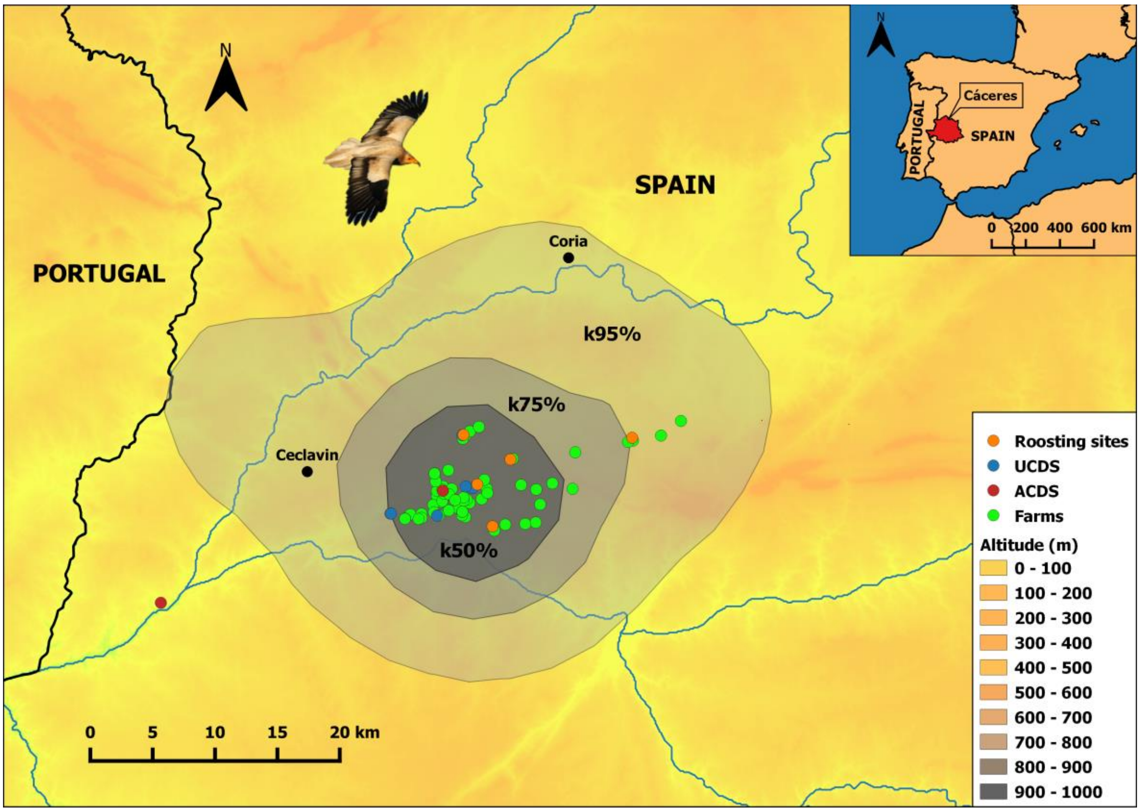

Figure 5.1. *Location of the study area (upper right) including wintering roosting sites during 2014 – 2018, unauthorized carcass deposition sites (UCDS), authorized carcass deposition sites (ACDS), and farms. The shaded areas show three different kernel density isopleths levels derived from all individuals corresponding to 50 %, 75 %, and 95 %, respectively. The black dots represent major towns for spatial context. The present map was done by using QGIS 3.8.3 desktop version (http://qgis.osgeo.org).*

Vulture capture and tagging

From September 2015 to January 2017, we trapped 12 Egyptian Vultures (2 adult males, 1 subadult male, 4 adult females, and 5 subadult females) with remotely triggered cannon nets in the surroundings of their main roosting sites in NW Cáceres. All captured individuals were ringed with yellow alphanumeric plastic and metal rings and fitted with 48 g solar-powered GPS/GSM transmitters (E-obs GmbH, Munich, Germany). Tracking devices include a GPS providing geographical coordinates, altitude, speed, bearing, and tridimensional accelerometry. Tags were programmed to record fixes (i.e., GPS positions) at 5 min intervals from 1 h before dusk to 1 h after sunset. Also, when battery levels were above a threshold of 3950 mV, GPS devices recorded locations at 1 Hz resolution (i.e., 1 location/s) during 15 min intervals called “super-bursts.” All device units were attached as backpacks using a 0.55″ (14 mm) wide Teflon ribbon harness. The weight of the transmitters and rings was 64 g, thus being below 3% of the bodyweight (mean body mass = 2176 g; range 1950–2650 g; n = 12), i.e., below the recommended limits to avoid adverse effects (i.e., 3% body mass threshold, see, e.g., Sergio et al., 2015).

Vultures were tracked throughout the annual cycle. For this study, we subset data to retain only information corresponding to the overwintering period (1st December to 28th February), according to the average dates of Egyptian vulture migration in Spain (Finlayson 1992; Panuccio et al., 2017) and our field experience. According to Onrubia (Onrubia 2015), pre-breeding median passage time at the Strait of Gibraltar is 8th March with 95% confidence interval ranging from 20th February to 9th May; and post-breeding median passage time is 8th September with 95% confidence interval ranging from 23rd August to 24th September. Given that many migratory adults have already started their northward migration in January/February (i.e., there could be a movement towards breeding sites any time from January), we first visually inspected movements to breeding areas (if any) to ensure that none of the tagged birds exhibited territorial/breeding behaviour. After this previous exploratory analysis, we considered 1st December to 28th February as a conservative approach to include only actual wintering birds in our study. In order to homogenize the resulting dataset, we resampled locations at 5 min intervals and removed high-frequency locations (i.e., super-bursts period). Data were downloaded and incorporated automatically to the online Movebank data repository (www.movebank.org) and are publicly available upon request.

Wintering roost sites identification and population monitoring

The wintering population was monitored monthly from December to January (two censuses per wintering period each year) between 2014 and 2018. Censuses were conducted at dusk using continuous focal sampling methods at a secure distance to avoid any disturbance to the birds (Zuberogoitia et al., 2008). Adults and subadults were classified according to plumage characteristics. We also identified food resource types where vultures were observed feeding during the sampling period in the surroundings of the wintering roosting sites. We classified food resources into three different categories: farms, authorized carcass deposition sites (hereafter ACDS), and unauthorized carcass deposition sites (hereafter UCDS). UCDS were those points close to farms where farmers released carcasses to the field without sanitary control.

Basic movements parameters estimation and use of predictable food resources

We calculated a set of basic movement parameters (BMPs) of the tagged individuals over three wintering seasons, namely: home range size (km2), cumulative distance (km), intensity of use, straightness and net squared displacement (km2) (further details in Appendix B Table B1). We obtained all metrics for each 15-day interval period (fortnight) of each wintering season, calculating the mean of each parameter for each individual/fortnight combination (n = 115 individual/fortnight combinations). Home range size were obtained from the 95% kernel density estimation (KDE) by using “rhrKDE” function of the “rhr” package for R (Signer and Balkenhol 2015). The other movement parameters (see above) were derived by the “amt” package (Signet et al., 2019).

We also calculated the proportion of non-roost GPS locations for each individual and fortnight that fell within a 300 m buffer distance to farms, UCDS, and ACDS. We selected this measurement because farmers could drop carcasses at variable distances. Buffers were generated by using “geoprocessing tool” function implemented in QGIS 3.8.357.

Modeling space use

In order to asses vultures’ space use, we used a modeling approach based on RUFs (Marzluff et al., 2004; Hooten et al., 2013). RUFs are often used to understand how species are related to landscape characteristics by measuring the intensity use of resources available in space, which shape the environmental niche of species (e.g., food availability, land-use, human disturbance, and topography, among others) (Hooten et al., 2013). Furthermore, one of the main advantages of the RUF method is that it accounts for spatial autocorrelation by incorporating a Matern correlation function (Marzluff et al., 2004). According to Marzluff et al.’s (2004) approach, we calculated the Utilization Distribution (UD) defined as the spatial probability distribution that gives rise to a spatial point process (i.e., the recorded telemetry locations; Hooten et al., 2013). We obtained UD values from 95% KDE. To assess resource selection, we selected a set of environmental variables illustrative of the foraging habitat and ecological requirements of the species (see electronic Appendix B Table B2). We set a spatial resolution of 200 m for environmental predictors (i.e., topography, land-use and productivity). In the case of livestock density and human disturbance, we rasterized and downscaled to 200 m spatial resolution the data from polygons at each municipality level. Additionally, given that defining the overall spatial extent for resource selection studies is often subjective (Boyce 2006), we established our maximum extent unit as the maximum home-range-scale determined by kernel contour volume of 95% (kernel 95%), which in turn represents landscape characteristics (Marzluff et al., 2004).

Space use estimators

Data were partitioned by individual and wintering season. We computed 95% kernel density contours for each individual to generate the UD using "rhrKDE" function of the "reproducible home range" (rhr) package for R (Signer and Balkenhol 2015). We estimated the reference bandwidth, which defined the extent of the UD, using the "href" function implemented in the "rhr" package. UD values ranged from 0 to 95% according to kernel density estimators, where 0 was the lowest value of habitat use and 95 represented the highest value of space use. The UD was processed and included as a raster shapefile in a Geographical Information System (GIS) and converted into points to match covariate values to each pixel of 200 m at which environmental variables were recorded (i.e., livestock density, human disturbance, land-use, topography, and primary productivity) (see Appendix B Table B2). Spatial analyses were done in QGIS 3.8.357 and R version 3.5.1 (R Development Core Team, 2018).

Statistical analysis

We used Linear Mixed Models (LMMs) to investigate variation in (1) BMPs and (2) the use of predictable food resources over time including fortnight, age, and sex as predictors. Sex, age and fortnight were entered in the models as fixed factors. Individual identity and wintering season were entered as a random intercept effects in all models. We entered the response variable (i.e., proportion of locations) by using square root arcsine transformation in the model of the use of predictable food resources. We further included resource type (i.e., farms and UCDS, excepting ACDS, given the lack of fixes within 300 m buffer of ACDS) as a two-level fixed factor, to investigate whether birds spent a different amount of time in the surrounding of different resource types. Significance of fixed effects was tested by a full model approach61. Models were fitted by maximum likelihood method using "lmer" function of "lme4" package (Bates et al., 2015) for R version 3.5.1 (R Development Core Team 2018). We visually inspected the homogeneity of variance and normality of residuals. We computed marginal and conditional R2 following using the piecewiseSEM R package (Lefcheck, 2016) to assess the overall explanatory power of the model (i.e., for fixed and random effects separately). Significance was tested by a likelihood ratio test (Anova, “car” package; Fox et al., 2014). Moreover, we estimated the marginal means for each significant factor by using “emmeans” package (Lenth et al., 2019).

Before running statistical models of RUFs, we checked for the correlation between environmental variables. When two variables showed a correlation coefficient higher than |0.5|, the one with lower biological significance was removed from the analysis. (see Appendix B Table B3). Variables were scaled and mean-centered in the full RUF models.

Resource utilization functions were fitted using “ruf.fit” function implemented in the “RUF” package (Marzluff et al., 2004).We ran full models for each individual (n = 12) including all predictor variables that could determine utilization distribution61. The importance of each resource to variations in the UD (i.e., the measure of resource use) was indicated by the magnitude of the standardised coefficients of the RUFs (Marzluff et al., 2004). To test the consistency in the resource utilizations at the population level, we averaged coefficients and standard errors for each variable using the equations (1) and (2) from Marzluff et al., (2004) (see also Donovan et al., 2011 for a similar approach). Mean values were reported with (±) standard deviation, unless stated otherwise. Statistical significance was set at $p < 0.05$.

5.4. RESULTS

Population monitoring and food resources

Five winter roosting sites were detected in the study area during four overwintering seasons (2014–2018, Figure 5.1). Not all of the five winter roosting sites were simultaneously detected. In the first overwintering season (2014–2015) three winter roosting sites were identified, whilst the rest of them were detected during 2015–2016. One of the roosting sites could not be accurately surveyed because of the risk of disturbance, although the presence of wintering individuals was confirmed. Roosting sites were separated by 7.82 ± 1.34 km on average (3.32–13.52 km). On average, we counted 85 ± 10 individuals (58–121): 65 ± 10 adults (37–99) and 20 ± 2 subadults (15–25) (Figure 5.2). We counted on average 6 ± 5 individuals (range 1–12) on the roosting site 1, 33 ± 26 individuals (range 6–61) on the site 2, 21 ± 15 individuals (range 5–42) on the site 3, and 27 ± 6 individuals (range 20–32) on the site 4 during the four overwintering seasons. We identified 50 farms, five UCDS, and one ACDS in the surroundings of the wintering roosting sites. The mean distance between roosting sites and the nearest farm or UCDS were 0.28 ± 0.6 km (0.14–0.48 km) and 4.24 ± 2.41 km (0.09–2.41 km), respectively. The distance between the unique ACDS within the study area and roosting sites was 6.85 ± 5.11 km (2.81–15.76 km).

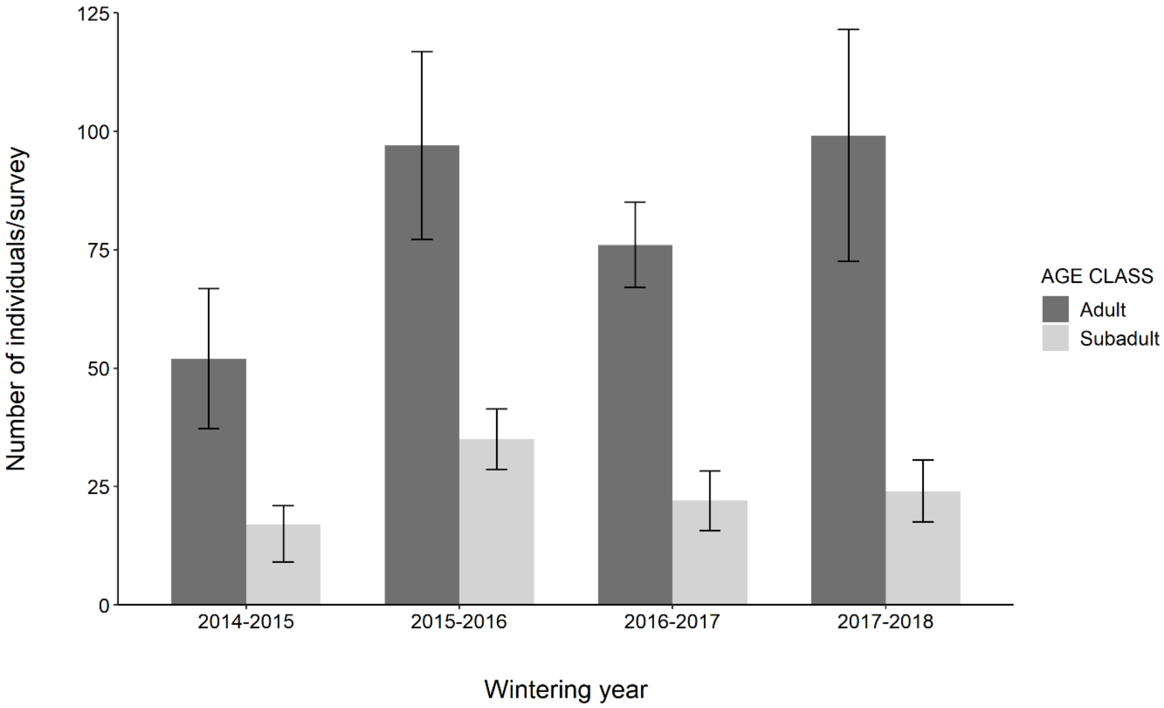

Figure 5.2. *Summary of number of individuals surveyed during four consecutive wintering seasons in Cáceres (Extremadura, western Spain). The standard deviation of each age class is shown as error bars.*

BMPs and use of predictable food resources

Our analyses were based on 123,137 GPS locations. During the study period, one of the tagged individuals lost the transmitter in the breeding area during summer 2017 (see Appendix B Table B4). Furthermore, of all tagged individuals, two of them exhibited migratory behaviour during the following wintering season after tagging, leaving the breeding grounds to migrate to Africa. Therefore, from these individuals we only retained locations in the study for the winter season they remained in the trapping area. Overall, the mean distance between breeding and wintering the five wintering roost sites was 101 ± 121 km (20 – 345 km) for 6 of the tagged individuals. The rest of the tracked individuals (n = 6) did not breed during the study period.

The mean BMPs across individual/fortnight combinations (n = 115) were 38.66 ± 36.44 km2 (7.61—117.77 km2) for home range size, 346.03 ± 192.87 km (107.27–776.75 km) for cumulative distance, 35.51 ± 20.03 km2 (15.26–80.26 km2) for net square displacement, 0.06 ± 0.08 (0.01—0.31) for straightness index, and 25.26 ± 7.30 (11.96–33.10) for intensity of use. The mean value for the use of predictable food resources was 17 ± 0.07% (3–25%). We did not observe any location within 300 m of ACDS during the study period.

LMMs for cumulative distance and net squared displacement showed a significant effect of fortnight, with increasing movement activity through the winter (Table 5.1; Figure 5.3). Moreover, females exhibited smaller home ranges than males (Table 5.1). Adult individuals showed higher values of cumulative distance than subadults. On the contrary, net squared displacement values were higher in subadults than in adults (Table 5.1). The variation captured by our three predictor variables (< 15%) compared with that captured by random terms was low (Table 5.1) for all BMPs. Only the cumulative distance model captured more than 10% of the variability in the data (18%). The results of the model for the use of predictable food resources also showed that there were differences among age groups and the type of food subsidies used by individuals (Table 5.1). Overall, individuals made more intensive use of farms than UCDS. Likewise, subadult individuals exhibited higher values of use of farms and UCDS than adults (Figure 5.3). In this case, the variability in the data was highly captured by the predictor variables (> 50%) (Table 5.1).

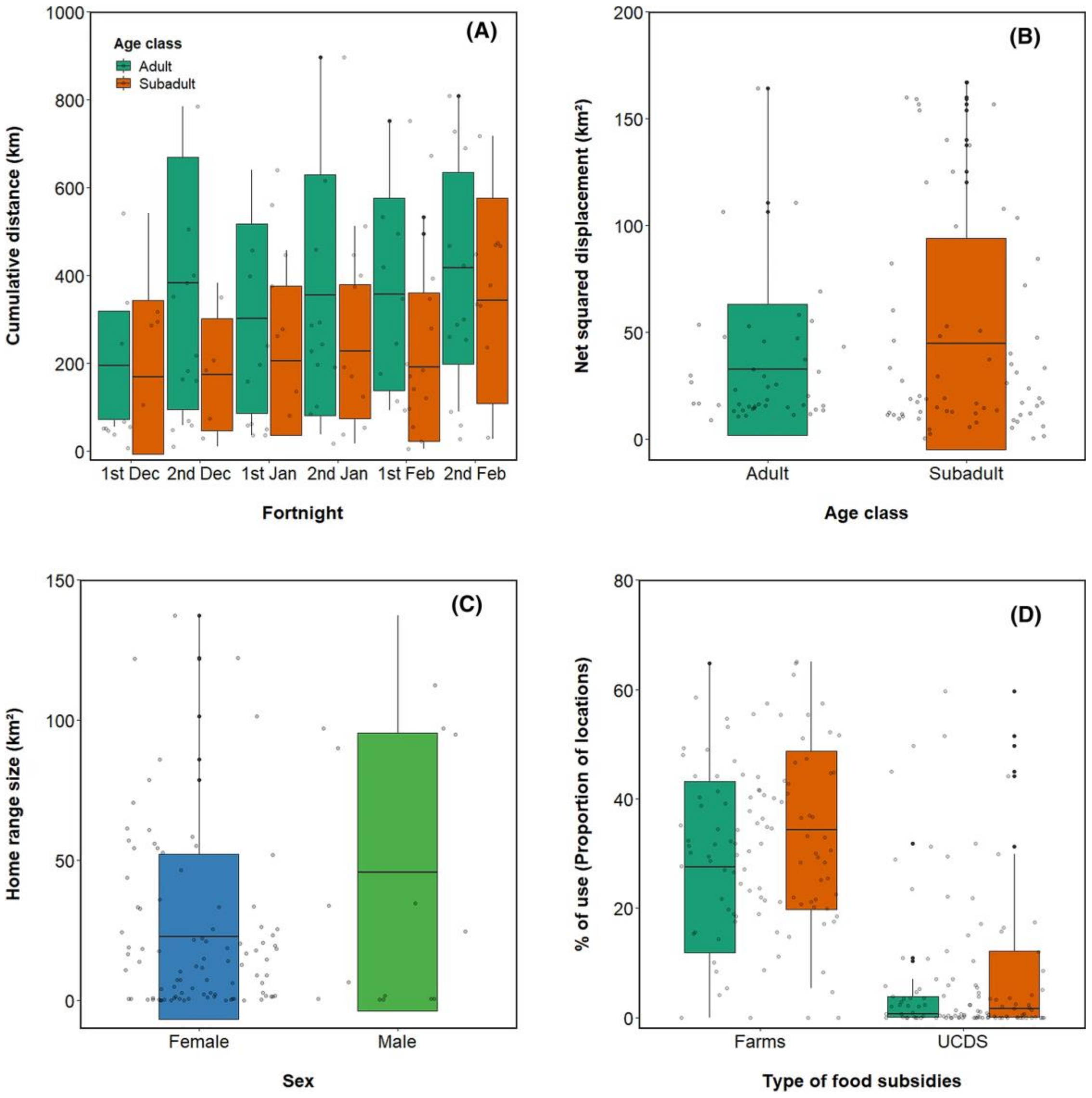

Figure 5.3. *Values of the significant variables included in the full models for cumulative distance, net squared displacement, home range size and use of the different food subsidies of the tagged individuals (n = 12) corresponding to four wintering seasons (2015–2018). White dots represent the raw data points. The standard deviation is shown as error bars.*

Table 5.1. *Estimates for fixed terms of full models for each BMPs and the use of predictable food resources.*

Variable	Predictors	Estimate ± SE	Chisq	Pr(>Chisq)	R^2 fixed	R^2 random
Home range size	Age	-10.14 ± 11.38	0.716	0.397	0.081	0.221
	Sex[a]	36.297 ± 15.834	4.984	**0.025**		
	Fortnight	1.410 ± 2.429	1.322	0.932		
	Intercept	29.176 ± 13.057				
Cumulative distance	Age[b]	-149.089 ± 50.992	8.893	**0.002**	0.183	0.546
	Sex	137.767 ± 85.389	2.637	0.104		
	Fortnight[c]	30.137 ± 7.949	19.769	**0.001**		
	Intercept	271.520 ± 71.718				
Intensity of use	Age	-5.098 ± 3.065	2.906	0.088	0.048	0.169
	Sex	4.683 ± 4.221	1.100	0.294		
	Fortnight	0.437 ± 0.709	4.285	0.509		
	Intercept	24.533 ± 3.746				
Straightness	Age	0.047 ± 0.046	0.992	0.319	0.028	0.603
	Sex	-0.042 ± 0.076	0.363	0.546		
	Fortnight	-0.008 ± 0.007	4.720	0.450		
	Intercept	0.089 ± 0.048				
Net Squared Displacement	Age[d]	23.250 ± 9.731	5.946	**0.014**	0.090	0.180
	Sex	-19.927 ± 13.498	2.388	0.122		
	Fortnight	5.769 ± 2.432	8.117	0.149		
	Intercept	3.749 ± 14.019				
Use of predictable food resources	Age[e]	4.403 ± 1.534	6.837	**0.008**	0.601	0.013
	Sex	-3.965 ± 2.064	2.157	0.141		
	Fortnight	-0.064 ± 0.384	0.329	0.997		
	Type[f]	-0.409 ± 0.025	258.900	**<0.001**		
	Intercept	-1.821 ± 2.137				

Space use

According to the population-level models for the full combination of each individual–resource category, the RUF analysis showed that the best predictors of space use at the population level were food availability, particularly goat density and cow density, to a lesser extent, as well as land use variables (forest and agriculture lands) (Table 5.2; Appendix B Table B5). On the contrary, areas with high density of sheep, pigs and variables related to human disturbance such as areas close to villages and artificial surfaces were avoided.

Table 5.2. *Results of the averaged coefficients* ($\widehat{\beta_j}$) *and standard errors from the full RUFs models of the tracked individuals (n = 12) (see Appendix B Tables S2 for details). Abbreviations: SE = standard error; var = variance; LCI = lower confidence interval; UCI = upper confidence interval.*

Variable	Estimate (β_j) ± SE	var(β_j)	LCI (95%)	UCI (95%)
Sheep	-0.407 ± 0.193	0.022	-1.017	0.203
Pigs	-0.318 ± 0.175	0.008	-0.712	0.076
Cows	0.304 ± 0.295	0.036	-0.134	0.741
Goats	2.356 ± 0.279	0.017	-0.399	5.110
Distance to roads	0.007 ± 0.132	0.006	-0.427	0.441
Distance to towns	-0.310 ± 0.137	0.007	-1.244	0.624
Forest	1.821 ± 0.504	0.128	0.513	3.129
Artificial	-1.161 ± 0.998	0.339	-2.786	0.463
Agriculture	1.127 ± 0.399	0.107	-0.151	2.405
Slope	-0.748 ± 0.161	0.018	-1.946	0.450
NDVI	-0.186 ± 0.089	0.003	-0.623	0.251

5.5. DISCUSSION

Our results provide the first insight into the movement patterns of the largest overwintering population of the Egyptian vulture in south-western Europe. Population monitoring data reveals that the number of wintering individuals was 121, which were congregated in five close roosting sites throughout four wintering seasons. We observed that most birds counted in each survey/wintering season (see Figure 5.2) were adults (75.98%). Yet, it remains unclear if the population is made up of subadults that do not migrate and then remain, or adults that opt to not migrate even after several successful migrations. The probability of switching migration tactic should increase with age particularly for residents (Eggeman et al., 2016), but what causes the differences in wintering numbers is unknown. To date, there are only two sites in western Europe where similar behaviour had been reported, with only 20–30 individuals surveyed in the mid-eighties in the south of Spain (SEO/BirdLife 2012) and, more recently, three individuals in Sicily (Italy) (Di Vittorio et al., 2016).

Communal roosting is widely distributed among animals, and some of the proposed benefits of aggregation include the exchange of information for finding food, mate acquisition, and thermoregulatory purposes (Blanco and Tella, 1999). In birds, especially soaring raptors that exhibit social behaviour, it is important to access safe places to rest, meet, exchange information, obtain refuge from predators, and avoid adverse weather conditions (Lambertucci and Ruggiero, 2013). In this context, the observed distances from roosting sites to farms and UCDS (see Figure 5.1) may suggest that predictable food sources may attract animals to the resting trees (van Overveld et al., 2018). This could explain the small home range size found in our study (< 50 km2) when compared to the home range size found during the same period in a sedentary population of the species (> 100 km2; van Overveld et al., 2018) and much smaller than that of individuals overwintering in Africa (> 9000 km2; García-Ripollés et al., 2010).

We observed that home range size was affected by intrinsic factors, particularly sex. However, the poor variability captured by our models suggests that other non-evaluated factors might also be operating, such as environmental conditions or intraspecific interactions in the wintering roosting sites (Bijleveld et al., 2010). Furthermore, the observed results could also be due to the disparities in the sample size regarding the sex of individuals (nine females and four males). We found that females exhibited smaller home range sizes than males. This pattern could decrease intraspecific competition by food resources in the study area (farms, UCDS, and ACDS) due to the unpredictable nature of food supplies (van Overveld et al., 2018).

We found differences in net squared displacement among age classes with larger values in subadults. Adults exhibited a more marked sedentary behaviour than subadults, likely due to the experience and the knowledge of the place of those predictable food sources are. The short distances between roosting sites and feeding points could be advantageous in reducing foraging distance and thus energy expenditure while increasing fuel load during winter when adverse weather conditions affect birds' flight capacity (Montsarrat et al., 2013). Non-experienced subadults, however, tend to move longer distances looking for predictable and also natural (unpredictable) food sources to meet energy requirements (van Overveld et al., 2018). Similarly, we found that individuals travelled longer distances in the course of the winter. In this case, adult birds tended to move longer distances than subadult birds. These larger movements closer to spring could be related to the onset of the breeding season (Powell et al., 2012), particularly for adults which, if they were migratory individuals, would be travelling 300 km per day north from their wintering ranges in Africa any time from January onwards (García-Ripollés et al., 2010).

Individuals can vary in their use of predictable food resources according to age, sex, cultural and personality differences (Oro et al., 2013). Here, we found that overall, subadult birds rely more on predictable food resources than adults. Likewise, both adults and subadults make more intensive use of farms than UCDS. These results suggest that the intensity of the use is driven by individual traits, particularly by social status (van Overveld et al., 2018). In this context, younger bird's preference seems to be explained by their limited environmental knowledge comparing to adult individuals (Sánz-Aguilar et al., 2015). Although some studies showed that vultures rely more on feeding stations than on the surroundings of cattle farms (López-López et al., 2014), our results reveal that farms play a more important role comparing to UCDS and ACDS, with the latter never being visited by the vultures tracked in this study. The observed high-intensity use of these sites may suggest that those places might have also become more predictable (and thus more stable) during winter compared to other available food resources like UCDS and ACDS (but see Margalida et al., 2010). Likewise, it may also drive the changes, not only regarding foraging patterns, but also the establishment of resident populations as it has been seen in other species (e.g., white storks), depending on artificial food supplies (Gilbert et al., 2016).

The RUF analysis showed that vultures preferred forest areas ("dehesas") and agricultural lands with high goat density and some cows far from towns. In these places vultures benefit from feeding on newborn cattle as well as the excrements of cows, where they obtain carotenoids which are in turn essential pigments for status signaling (Negro et al., 2002). This reflects the main landscape characteristics of the wintering area of this unique population of an endangered vulture. In fact, Extremadura's "dehesas" represent one of the hottest hotspots of vertebrate diversity across Europe (López-López et al., 2011). A combination of mild climatic conditions as well as biogeographical and refugia effects that occurred during the last glaciations (Rey Benayas and De La Montaña 2003) make this area of Europe particularly favourable for the establishment of resident populations of species that were once largely migratory such as the White Stork or the Egyptian vulture.

Evolutionary and conservation implications

Our results showed that mainland Egyptian vulture population should be reclassified from migratory (excluding insular populations that are resident) to a facultative partially migratory species. Gilroy et al. (2016) noted that species with more considerable within-population variability in migratory movements might be more resilient to environmental change and facilitate adaptive responses to climate change. The number of threats affecting Egyptian Vultures in their African winter quarters is increasing (Botha et al., 2017). Therefore, a shift from a migratory behaviour to a sedentary one could have positive effects on the conservation status of the Egyptian vulture in Europe in the long-term (Santangeli et al., 2019). However, the continuous presence of some individuals in a given area implies that they are also subject to threats that are only faced during the breeding period for migratory conspecifics (Phipps et al., 2019), such as human disturbances and habitat alterations in roosting or nesting sites, collisions with wind farms and illegal poisoning (Sánz-Aguilar et al., 2015). Besides, the strong dependence on food resources provided by humans direct or indirectly by intensive livestock farming practices could increase poisoning risk (Blanco et al., 2019). Overall, we encourage managers and conservation practitioners to take into account the emergence of these new behaviours to ensure adequate conservation of existent or new wintering roosting sites. Furthermore, we recommend the integration of movement patterns, foraging ecology and the use of protected areas to assess species susceptibility to different threats (Phipps et al., 2019), to better inform conservation planning, and to improve management decisions, ensuring population viability and reducing human-vulture conflicts (Duriez et al., 2019).

CHAPTER 6

Environmental and social correlates, and energetic consequences of fitness maximisation on different migratory behaviours in a long-lived scavenger

Submitted: Morant, J.*, Scacco,M., Safi, K., Abad-Gómez, J.M., Álvarez, T., Sánchez, Á., Phipps W.L., Carbonell, I., García J., Prieta J., Zuberogoitia, I., López-López, P. (2021). Environmental and social correlates, and energetic consequences of fitness maximisation on different migratory behaviours in a long-lived scavenger. Journal of Animal Ecology. Under review.

6.1. ABSTRACT

Partial migration, in which a proportion of the population remains resident while the other migrates to a distinct location during winter, is one of the most widespread migratory strategies among taxa. Despite the causes and consequences of each migratory behaviour being investigated, few studies offer a comprehensive assessment showing how the trade-off between environmental/social factors - fitness and energetic consequences - are interwoven to promote the coexistence of migratory and resident behaviours within a single species. Here, we compiled field monitoring data of wintering population size and telemetry data of 25 migrant and 14 resident Egyptian Vultures *Neophron percnopterus* to: 1) analyse how environmental and social factors modulate resident population size, 2) compare fitness components (i.e., survival and reproduction), and 3) energetic consequences between migratory and resident individuals across wintering and non- wintering seasons. We estimated the effects of a set of environmental predictors on wintering population size by using correlation tests. The effect of social factors was explored in terms of attraction to conspecifics by modelling the relationship between censused adult individuals and subadults. We then evaluated the effect of different migratory behaviours on fitness by comparing the breeding performance and survival between migrant and resident individuals. Finally, we used energy expenditure, flight efficiency and activity duration to measure the energetic consequences of the two migratory behaviours. We observed that livestock numbers, particularly cattle, positively correlated with the wintering population size. Subadult birds increased linearly with censused adult birds which evidenced age-specific social attraction. Resident birds exhibited higher survival probabilities and lower breeding activity. Resident birds also showed higher energy expenditure, less flight efficiency, and lower activity due to shorter day lengths in winter. On the contrary, migratory birds showed more breeding attempts but lower survival. Moreover, they spent less

energy and flew more efficiently at longer distances, benefitting from longer days in African wintering quarters. Our results offer new insights to understand why and how Egyptian Vultures benefit from one strategy or another and that the coexistence of both migratory forms is context-dependent.

6.2. INTRODUCTION

The drivers of animal movement and its consequences pose some of the most challenging questions in ecology research. Among the various forms and realisations of animal movement, migration is the most conspicuous phenomenon and has attracted scientists' attention for centuries. Animal migration is defined as a bidirectional and repeated movement between two different places, usually breeding and wintering areas, with a residency period in each location (Hansson and Akesson, 2014). One of the most widespread strategies in migratory species is partial migration, in which part of the population remains in the breeding grounds while some individuals move to a distinct place to overwinter (Chapman et al., 2011a). The life-histories of individuals, in species simultaneously exhibiting these two well-marked behaviours, are subject to (and shaped by) different environmental, social and evolutionary forces (Lunberg, 2013). Disentangling which factors determine the stability and persistence of these two strategies is crucial to understand the emergence of the migratory behaviour (Turbek et al., 2019).

Environmental (e.g., climate, resources) and social cues (e.g., location or presence of other individuals) are among the most influencing factors modulating migratory behaviour in partial migratory species (Shaw and Couzin, 2013). Therefore, changes in these factors may favour migration or residency, and ultimately affect survival and reproduction (Buchan et al., 2019). Among the environmental cues, milder winters and higher food availability during winter could favour residency at higher latitudes, which increases individual survival and enables early reproduction and higher breeding success (Meller et al., 2016; Gilroy, 2017). On the contrary, migration could be more advantageous by abandoning the resource-depleted regions during the non-breeding season which could increase both the chances of survival and reproduction (Winger et al., 2019; Winger and Pegan, 2020). In terms of social cues, in long-lived species, the decision to migrate or not may come from learning or following more experienced individuals which could enhance the survival of less-skilled individuals (e.g., juveniles; Mellone et al., 2011; Teitelbaum et al., 2016). These findings show that despite the great progress that has been made in understanding the contribution of survival and reproduction to the maintenance of these two migratory behaviours, less attention has been paid to their energetic consequences. Energy expenditure is a key link between behaviour and overall fitness (Grémillet et al., 2018), therefore addressing energetic consequences of different migratory strategies is of paramount interest.

The recent advent of high-resolution Global Positioning Systems (GPS) in combination with tri-axial acceleration data, have allowed researchers to study how much energy is spent by animals during crucial periods of their annual cycle (i.e., breeding season; Grémillet et al., 2018), estimate how expensive or efficient it is to move depending on their kinematic patterns (i.e., flapping flight; Williams et al., 2020) and even investigate which factors limit activity duration (Pokrovsky et al., 2021). Integrating this energetic perspective into the study of migratory strategies could help to understand 1) the indirect energetic consequences of changes in those environmental and social factors that modulate migration and residency, 2) the trade-offs between fitness (e.g., survival and reproduction) and energy expenditure of both strategies and, 3) whether migratory or residency affect movement efficiency and activity duration. Overall, these three aspects could help explain the relative contribution of environmental conditions, social factors, fitness and energy expenditure, to the coexistence and persistence of these two strategies in partial migratory species (Gilroy, 2017). This is of great importance to predict not only how current and future environmental changes could impact populations but also to design effective conservation measures that account for within-species behavioural migratory diversity and preserve species functionality and their role in ecosystems (Gilroy et al., 2016).

Here, we untangle from a mechanistic perspective which factors modulate and shape both migratory and residency strategies in a long-distance soaring migrant, the Egyptian vulture Neophron percnopterus, by combining field monitoring and GPS tracking data of a partially migratory population in Spain. This endangered species ranges across southern Europe, northern Africa, the Middle East and Central and South Asia (BirdLife International, 2020). While migratory individuals regularly travel >4,000 km between their northern breeding and southern wintering grounds by using several distinct migratory flyways (Phipps et al., 2019; Buechley et al., 2021), other individuals overwinter in southern and south-western Spain (García et al., 2000; Morant et al., 2020). The Egyptian vulture is an obligate scavenger that frequently consumes both carrion from livestock and wild ungulates (Donázar, 1993). The species exhibit complex social behaviour forming large individual congregations outside the breeding season at highly preferred feeding stations (e.g., farms) and nearby temporary roosting sites (García-Alfonso, 2020; van Overveld et al., 2020a). Altogether, these traits make it an ideal study species to assess how different migratory strategies coexist.

We firstly investigate the correlates underlying the partial migratory strategy observed in the Egyptian vulture population overwintering in south-west Spain. Secondly, we investigate the consequences of either residency or migration and aim to identify the factors that balance between the costs and benefits associated with both strategies. We therefore hypothesize that: 1. there should be a relationship between the number of resident individuals and environmental conditions (e.g., temperature and food) and social factors (e.g., conspecific attraction); 2. different strategies (migration and residency) should differ in terms of reproduction (e.g., number of breeding years and number of successful breeding years) and survival; and 3. that differences in reproductive output and survival should be offset by different energetic requirements. Finally, 4. We expect that both migratory strategies yield different outcomes in terms of energy expenditure, flight efficiency and activity duration during winter.

6.3. MATERIALS AND METHODS

Field monitoring data

We gathered data from two different annual censuses of the wintering Egyptian vulture population in Cáceres, Extremadura, Spain (see Appendix C. Supporting information C1 for details). We accessed to two sources of data: 1) data from the Spanish Ornithological Society, in which the wintering population was monitored on a yearly basis by censusing individuals (without differentiation of age classes) in January between 2006 and 2019; 2) our own monitoring project, where the wintering population was monitored twice monthly from December to February between 2014 and 2019 with adults and subadults classified according to plumage characteristics (more details in Morant et al., 2020a). In the first case, censuses were carried out in one roosting site until 2014. From 2014 onwards, four additional wintering roosting sites were discovered and censused taking advantage of GPS tracking of some individuals that were tagged in 2014 (n=5, see Morant et al., 2020a for details).

Movement data

We used data from 39 Egyptian Vultures belonging to three different populations in the Iberian Peninsula, namely: Extremadura, Duero/Douro and Castilla-La Mancha/Valencia (see Appendix C Figure. S1). Of the 39 birds, seven (n=6 adults and n=1 juvenile) were captured and tagged in Castellón and Guadalajara provinces (Spain) between 2007 and 2009 with a solar-powered GPS tag from Microwave Telemetry (Columbia, Maryland, USA), 19 (n=11 adults, n=5 subadults, n=3 juveniles) were captured in Cáceres (Extremadura, Spain) between 2014 and 2020, and fitted with solar-powered GSM-GPS-ACC transmitters (n=16) (E-obs GmbH, Munich, Germany) and Ornitela (n=3) devices, while 13 were equipped in

Duero/Douro (Bragança, Portugal; Zamora, Spain; Salamanca, Spain) with Ecotone-Skua (n=3 adults, n=1 subadults, n=2 juveniles) (Ecotone skua), and Ornitela (n=2 adults, and n=5 juveniles) devices (see Appendix C Table S1 for details). GPS fixes and associated data were acquired at temporal resolutions ranging from one location per 5 minutes to one location every 2 h, with dormancy periods during the night (from 22.00 p.m. to 4.00 a.m.) (see López-López et al., 2014, Phipps et al., 2019 and Morant et al., 2020 for more details on the tagged individuals; see also Appendix C Table S1.). Individual ages at deployment were estimated in calendar years based on plumage traits of different age classes. We classified juveniles as individuals in the first calendar year, immatures as individuals in the second to fifth calendar year and adults as individuals in the sixth calendar year or older (Forsman, 2016). The sex of individuals was determined by using molecular sexing techniques (Fridolfsson et al., 1999).

All captured individuals were equipped with yellow and red alphanumeric plastic rings, metal rings and a GPS transmitter. All transmitters weighed 24–63 g, <3% of body mass, which is below the recommended limits to avoid adverse effects (Bodey et al., 2018) and were attached using backpack or leg-loop harness systems. All the GPS and accelerometry data were automatically incorporated and downloaded from the online Movebank data repository (www.movebank.org; Wikelski and Kays, 2019).

Birds were divided into “migrant” (n=24) (i.e., birds that exhibited usual migratory behaviour overwintering in the African quarters; Appendix C Figure S2A; see for example García-Ripollés et al., 2010) and “resident” (n=12) (i.e., birds that did not migrate and remained in the iberian Peninsula during the study period; Appendix C Figure C3B; see Morant et al., 2020a for details). Two of the tagged birds, initially resident, exhibited migratory behaviour the following wintering season, when they left the breeding grounds to migrate to Africa. Therefore, we considered them resident during the period they remained in the study area and migrant after this period in our analyses (see also Appendix C Table C2. for details of individuals used in each analysis).

Environmental and social correlates of migratory behaviour

We analysed the relationship between the number of resident birds during winter and different environmental factors, namely; 1) early-winter temperature in the current season (i.e., mean temperature between Nov-Dec), 2) mid-winter temperature recorded in the previous year (i.e., mean temperature between Dec-Feb) (see Meller et al., 2016 for a similar approach); 3) food abundance in the study area (e.g., livestock numbers). We also added 4) breeding population size in the study area. Temperature information was recorded for 2006-2019 (AEMET, 2020). Livestock numbers, including cows, pigs (both from intensive and extensive farming systems), goats and sheep were obtained from the annual census conducted in the study area (data provided by the regional government, Junta de Extremadura). Data of breeding population size was obtained from the annual systematic surveys carried out in Cáceres between 2006-2019 by rangers during the breeding period (April-August) (data provided by the regional government, Junta de Extremadura).

We then investigated how the above-mentioned factors influenced the number of wintering vultures by computing Spearman correlation tests between the number of wintering individuals at the roosting sites recorded in the censuses between 2006 and 2019 and the environmental conditions in the respective years.

To investigate the effect of the social factors, we modeled the number of wintering subadults recorded in the census carried out between 2014 and 2019 wintering seasons (Nov-Feb) as a function of the number of adults recorded in the same censuses. We ran Generalized Linear Mixed Models (GLMMs) with Poisson distribution error and log-link function and we entered the year as a random factor in our model to account for the effects of a repeated census every year. We estimated marginal and conditional R2 by using "piecewiseSEM" R package to assess the models' overall explanatory power (i.e., for fixed and random factors).

Breeding and survival consequences of migratory behaviour

We estimated the number of breeding years of each tagged individual (i.e., number of years that an individual had bred independently of the breeding output since the tagging date) and successful breeding years (i.e., number of years an individual had bred and raised at least one chick since the tagging date).

We only selected data from adult individuals (>5 calendar years) since subadult individuals do not usually breed (Serrano et al., 2021). We used data recorded during field monitoring during the breeding season for each individual and year. Individuals' nests were identified by using GPS locations and later confirmed in the field. Breeding status (i.e., breeding/non-breeding) of each individual was confirmed during April-June, when the tagged individual and its pair were observed copulating, arranging the nest and incubating. Breeding success of tagged individuals was confirmed when at least one chick was successfully raised at the end of the breeding period (August; see Morant et al., 2019 for details). If the breeding information (i.e., breeding and breeding success) from tagged individuals could not be confirmed during the fieldwork (e.g., due to logistic or economic limitations), we used the "nestR" package (Picardi et al., 2020) to assess breeding output for each individual and breeding season (see Appendix C Supporting information C2 for details).

To construct our survival database, we gathered data on each GPS-tagged individuals' survival at the end of the study period, in our case, 28th February 2021. We estimated the number of days between the first and the last tagging date. For each individual we assigned a binary value as event indicator, being 0 if an individual was alive at the time of the last

GPS location (28th February 2021) or 1 if an individual had died. We also recorded individuals' age (namely age class) for those who were alive at the end of the study period and of the dead individuals (i.e., corresponding to the last GPS location date where casualties occurred). In case there was no clear evidence of individual death (e.g., picture of the dead individual or reliable information from collaborators or official entities), we could reliably separate deaths from cases of transmitter-failure based on three simple indicators extracted from the tags (see Appendix C Supporting information C3). Although we cannot rule out the possibility of some effect, we assume that tagging with the transmitters had a negligible impact on individuals' absolute survival (e.g., Bodey et al., 2018; Buechley et al., 2021).

We used the breeding dataset to examine whether different migratory strategies exhibited differences on reproduction. We modeled the number of cumulated breeding years and the number of successful breeding years as a function of migratory type (migrant and resident) by running Generalized Linear Models (GLMs) with Poisson error distribution and log-link function. To elucidate the effect of time on the decision of breeding and on breeding success, we also included the number of tracking years as a covariate in our models. We ran separate models for the number of cumulative breeding years and breeding success.

We evaluated the effect of migratory behaviour (migrant and resident) on daily survival by running Cox regression models with right-censored data (Pollock et al., 1989). We also entered age class (adult, subadult and juvenile) at the end of the study period to account for the effects of age-specific variation on survival. We measured the interaction between migratory behaviour and age class. The model was fitted by using "survival" package (Therneau, 2018).

In the case of the breeding model (i.e., GLM), we explored the overdispersion of selected models using the AER package (Kleiber and Zeileis, 2008) to ensure that our model did not violate the assumption of

Poisson distribution (i.e., variance and the mean are the same). We also computed the overall explanatory power of the selected model (D2) by using "modEva" package (Barbosa et al., 2015) to inspect the proportion of variation explained by our best models. In the case of the survival models, we checked the overall explanatory power by using the "Rsq.ad" function which measures the proportion of variance explained by the best models.

Energetic consequences of migratory behaviour

We investigated the energetic consequences of adopting one migratory strategy or other. In particular, we examined differences in energy expenditure, flight efficiency and activity duration among migratory and resident birds.

Energy expenditure

We estimated the energy expenditure in two different seasons (non-winter: March-Oct, and winter: Nov-Feb) using the Overall Dynamic Body Acceleration (hereafter ODBA), calculated from the tri-axial accelerometry data (hereafter ACC) (Shepard et al., 2008; Gleiss et al., 2011). We used birds from which ACC data was recorded (migrant=9, resident=13). ODBA can be considered a proxy of energy expenditure since it is positively associated with oxygen consumption and carbon dioxide production (Wilson et al., 2006, 2019) and the mechanical work produced by muscles and internal organs (Gleiss et al., 2011; Bishop et al., 2015). Furthermore, the daily, integrative summary of daily energy expenditure from ODBA is even more effective when the parts with high-energy locomotion (e.g., flapping flight) are modelled separately from other behaviours (Duriez et al., 2014; Stothart et al., 2016).

ACC data were collected in bursts on three axes (X—sway, Y—surge, Z—heave) for a duration of 2-3 s every 5-10 min at 20 Hz from Ornitela and E-Obs devices, respectively (see Appendix C Table S1). Firstly, we estimated the energy expenditure calculated as the average

ODBA value for each burst of 2-3s along the three axes (X, Y, Z). We transformed raw acceleration data into physical unit "g" (Laich et al., 2011) by using "moveACC" package (Scharf 2018). To this end, we assigned the calibration values of intercept and slope provided by manufacturers for each device type (Ornitela and E-Obs, respectively). We then estimated the average ODBA value (in gravitational units) for each burst. We finally estimated the mean daily ODBA by averaging the ODBA values per day, for each individual, year, month and day (see Wilson et al., 2019).

Secondly, we estimated the flight type (flapping or non-flapping) for each burst, by extracting wingbeat frequency from the ACC data (O'Mara et al., 2018). Finally, we classified each wing beat frequency as flapping or non-flapping. We identified and removed outliers in wingbeats (being <2 or >6 beats per second), representing about 1% of all bursts classified as flapping (see also O'Mara et al., 2018 for a similar approach).

We analysed the energy expenditure (i.e., mean daily ODBA) among the two migratory behaviours and flight types (i.e., flapping and not flapping flight). We also considered season (i.e., wintering and non-wintering periods) to account for differences among different periods in our model. We ran GLMMs with Gaussian distribution including cumulative daily ODBA as response variable, and migratory type, flight type and season as covariates. We consider the interaction between 1) migratory behaviour and flight type, and 2) between migratory behaviour and season covariates.

Flight efficiency

We calculated flight efficiency based on the percentage of time spent daily in flapping flight in relation to the daily distance travelled during non-winter and wintering seasons. We selected flapping flight since it is considered the costliest activity in soaring birds, given the disproportionate energy expenditure compared to all other behaviours (e.g., Williams et al., 2020).

We estimated the percentage of time spent flapping by counting the daily flapping events for each individual from the former energy expenditure database (see section 2.5.1). Flight types were extracted from the ODBA database, whereas the cumulated distance was estimated from the GPS data. Given that individuals tagged with different devices had different sampling schedules (5 min fix recording period for E-Obs devices and 30 min for Ornitela devices from some birds; see Appendix C Table S1), we resampled our database to 30 min period and excluded superburst periods (<5 s). We estimated the cumulative daily distance, which is the distance covered in one day (or the sum of the distance covered in each 30 min segment), by using the "amt" package (Signer et al., 2019). Flight efficiency was then calculated as the ratio between daily percentage of flapping flight and daily distance.

To analyse whether there were differences in flying efficiency among migratory and resident birds in wintering and non-wintering periods, we modelled the daily percentage of time spent flapping as a function of daily cumulative distance (km) and migratory behaviour (migrant and resident). Since we expect that the highest difference among both migratory behaviours would occur in winter, we also included season (wintering and non-wintering period) as a factor in our model. We considered the interaction between cumulative distance, migratory behaviour and season in our model. We used a beta regression model and considered the proportion of time spent flapping ranging from 0 to 0.5 (i.e., 0-50%). We ran a glmmTMB model implemented in the "glmmTMB" package with beta family and logit link (Brooks et al., 2017).

Activity and day length

To compare the activity duration between migrant and resident individuals, we followed the procedure proposed by Pokrovsky et al., (2021). We first calculated the mean ODBA values for each hour, and then we summed all the values to get daily estimates of ODBA value for each day. We also used the GPS data to estimate the day length by using "geosphere" package (Hijmans, 2016). We then joined both datasets to the most proximal timestamp. For estimating how many hours the tagged vultures remained active, we counted the number of hours that were greater than a certain threshold of activity. This threshold was estimated as mean ODBA for the non-moving bird. We considered birds as non-moving when 1) two consecutive GPS coordinates were equal, 2) there were at least six ODBA bursts between these GPS values, and 3) the movement among these two points did not exceed the mean location error of the GPS devices (this being for Ornitela of ±3.4 meters and ±1.9 meters for e-obs tagged individuals; see Fleming et al., 2020). We used 20 measurements from 7 different birds for each migratory type. The average values of the activity threshold were 0.067 and 0.051 for migrant and resident birds, respectively.

We inspected the consequences of migratory strategy across seasons and different day lengths in terms of the number of hours that Egyptian Vultures remain active. We thus modelled the activity duration (in hours) by running linear mixed-effects models (LMMs) in which migratory behaviour (migrant and resident), season (winter and non-wintering periods) and day length were entered as covariates. We considered the interaction among these three variables to ascertain which migratory behaviour is more beneficial across seasons (assuming that for instance longer days in Africa may benefit migrants in winter).

In the three analyses, individual identity and year were entered as random terms to account for the measures of the same individuals and within the same year. For the energy expenditure and activity duration model, we estimated marginal and conditional R2 by using "piecewiseSEM" R package to assess the model's overall explanatory power. In the case of the flight efficiency model (i.e., glmmTMB), the proportion of the total variance explained by the fixed and random terms was estimated by using performance package (Lüdecke et al., 2020).

Spatial and statistical analyses were done in R version 4.0.0 (R Core Team, 2020). In all analyses the models were compared by using the Akaike Information Criterion (AIC; Burnham and Anderson, 2002), corrected for small sample sizes (AICc). The best model was that with the lowest AICc value. All models with a difference of ΔAICc < 2 were compared to the best model (Burnham and Anderson, 2002). For the best model, homogeneity of variance and normality of residuals was inspected by using "ggresid" package to check the goodness-of-fit of our best models (Goode and Rey, 2019). All tests were two-tailed, statistical significance was set at $p < 0.05$, and all means were given together with standard error.

6.4. RESULTS

Environmental and social correlates

We found that the livestock numbers were the only environmental covariates significantly correlated to the number of resident individuals during winter. The number of wintering individuals was positively correlated to the number of cattle (rho= 0.63, P= 0.022) but negatively correlated to the number of goats and sheep (rho= -0.65, P= 0.017 and rho= -0.56, P= 0.045, respectively) (Figure 6.1A-C). The number of pigs intensively and extensively managed were also negatively correlated but the relationship was not significant (rho=-0.48, p=0.094 and rho=-0.42, p=0.16, respectively) (Figures 6.1D and E). We neither found significant correlation with breeding population size (rho=-0.49, p=0.088; Figure 6.1F) and early and mid-winter temperatures during winter (rho=0.44, p=0.13 and rho=0.17, p=0.58, respectively) (Figures 6.1G and H).

We observed that social factors greatly influenced the number of subadults censused at roosting sites. Our results showed a significant relationship between the number of subadults and number of adults (Appendix C Table C3; Table 6.1). The number of subadults increased linearly together with the number of adults, explaining almost 49% of the total variance of the model (Figure 6.2).

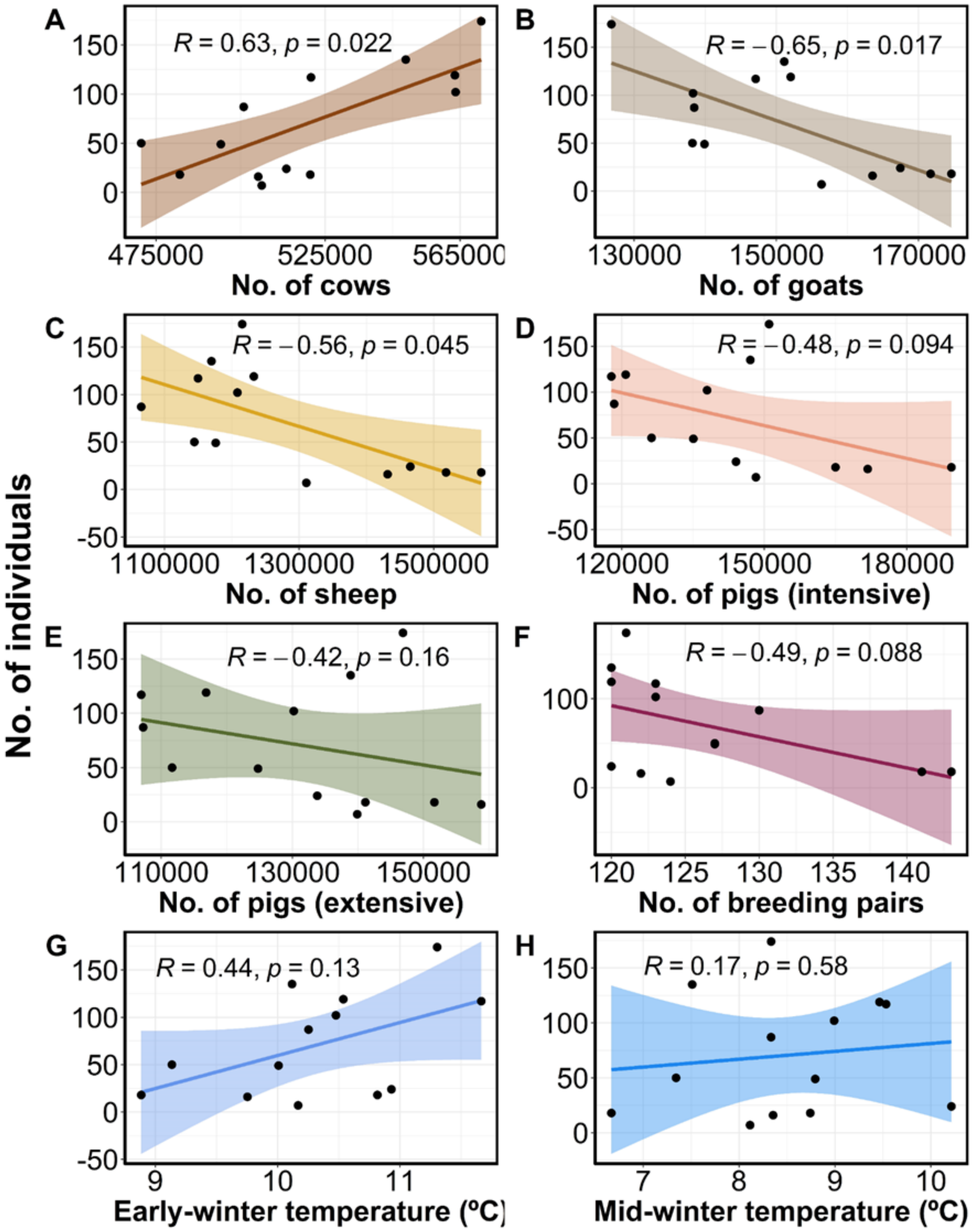

Figure 6.1. *Spearman correlations between censused Egyptian vultures on roosting sites throughout thirteen wintering seasons (2006–2019) and; (A-E) number of livestock censused; (F) breeding population size in the study area; and (G-H) early and mid-winter temperatures (ºC). Black dots represent the raw data points. The shaded areas represent 95% confidence intervals.*

Table 6.1. *Estimates for fixed terms of the best models of social correlates, breeding and survival and energetic consequences. For the breeding, survival and environmental correlates models, Migratory type and Age class were coded as a factor, being "Migrant", and "Adult" the reference values for statistical comparisons. Significant values are highlighted in bold. Abbreviations: SE= Standard error.*

Hypotheses	Predictors	Estimate ± SE	z value	P-value
Social correlates	Number of adults	0.184 ± 0.002	3.649	**<0.001**
Breeding	Migratory behaviour (resident)	-0.722 ± 0.324	-2.228	**0.025**
	Tracking years	0.310 ± 0.088	13.547	**<0.001**
	Migratory behaviour (resident)	-0.600 ± 0.359	-1.669	0.095
	Tracking years	0.323 ± 0.090	3.565	**<0.001**
Survival	Migratory behaviour (resident)	9.97e-8 ± 1.07	-15.1	**<0.001**
	Age class (Juvenile)	33.8 ± 1.13	3.12	**0.001**
	Age class (Subadult)	0.831 ± 0.805	-0.242	0.801
	Migratory behaviour (resident)*Age class (Juvenile)	-	-	-*
	Migratory behaviour (resident)*Age class (Subadult)	1.91e+4 ± 1.07	15.3	**<0.001**
Energy expenditure	Migratory behaviour (resident)	0.665 ± 0.122	5.436	**<0.001**
	Season (Winter)	-0.388 ± 0.028	-13.474	**<0.001**
	Flight behaviour (Others)	-1.677 ± 0.026	-63.208	**<0.001**
	Migratory behaviour (resident)*Season (Winter)	0.235 ± 0.034	6.879	**<0.001**
	Migratory behaviour (resident)*Flight behaviour (Others)	-0.653 ± 0.031	-20.792	**<0.001**
Flight efficiency	Cumulative daily distance	4.6e-05 ± 2.3e-04	0.203	0.839
	Migratory behaviour (resident)	-0.025 ± 0.170	-0.151	0.879
	Season (Winter)	-0.420 ± 0.034	-12.286	**<0.001**
	Cumulative daily distance*Migratory behaviour (resident)	0.003 ± 0.0003	12.732	**<0.001**
	Cumulative daily distance *Season(Winter)	0.002 ± 0.0003	6.897	**<0.001**
	Migratory behaviour (resident) *Season(Winter)	0.723 ± 0.034	21.179	**<0.001**
Activity duration	Day length	0.805 ± 0.034	23.222	**<0.001**
	Season (Winter)	12 ± 3.734	3.215	**0.001**
	Migratory behaviour (resident)	6.731 ± 0.953	7.057	**<0.001**
	Day length * Season (Winter)	-1.060 ± 0.327	-3.235	**0.001**
	Day length * Migratory behaviour (resident)	-0.380 ± 0.393	-9.677	**<0.001**
	Season (Winter)*Migratory behaviour (resident)	-2.494 ± 3.800	-6.563	**<0.001**
	Day length* Season (Winter)*Migratory behaviour (resident)	2.226 ± 0.334	6.650	**<0.001**

* No Juveniles for the class resident are found at the end of the established period in the survival analyses.

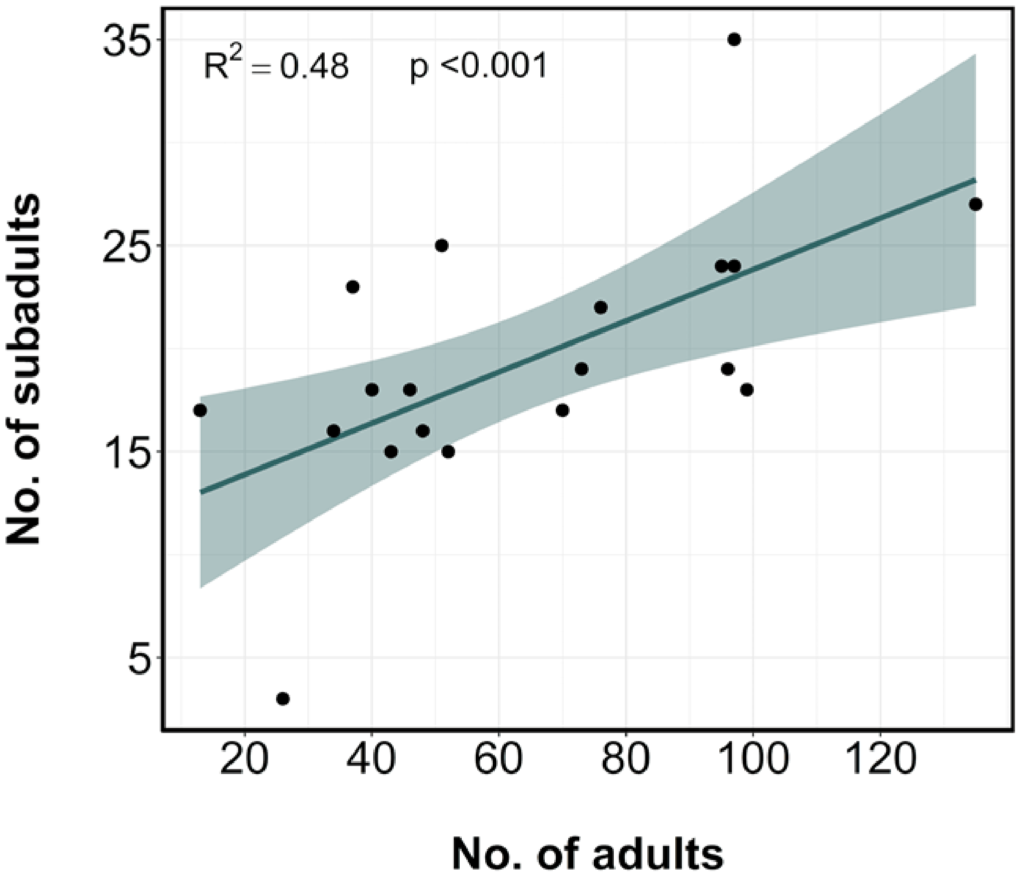

Figure 6.2. *Relationship between the number of Egyptian vulture subadults and number of adults censused in roosting sites (n=5) throughout five wintering seasons (2014–2019). Black dots represent the raw data points. The shaded area represents the 95% confidence interval. R2 showed the marginal variance explained by the model.*

Breeding and survival consequences of migratory behaviour

Overall our results showed that migrant birds bred significantly more often than resident birds (mean= 2.63 years, SD=1.92, and mean = 1.09 years, SD= 1.04, respectively) (Appendix C Table C3; Table 1; Figure 6.3A), and that the number of breeding years increased together with the tracking years for both migratory behaviours (Figure 6.3B). Migratory and resident birds experienced similar breeding success (mean= 1.95 years, SD=1.61, and mean = 0.91 years, SD= 0.83, respectively) (Appendix C Table C3; Table 6.1; Figure 6.3C). Not surprisingly, in both migratory behaviours the number of successful breeding years also increased with the number of tracking years (Figure 6.3D).

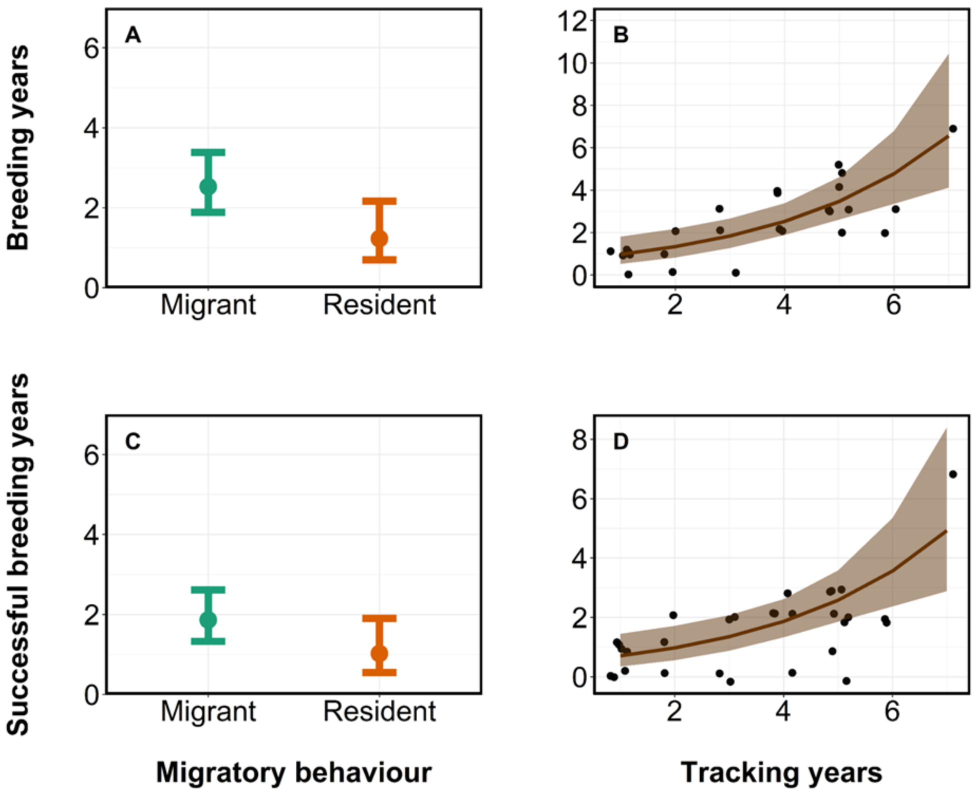

Figure 6.3. *Predicted values of the significant variables included in the best models of breeding. Figure A represents the cumulative breeding years for each migratory type throughout the study period. Figure B shows the effect of time on the cumulative and successful breeding years from the tracked birds. Differences between migrant and resident birds on successful breeding years are shown in the figure C. The figure D shows trends in successful breeding years respecting the time birds were tracked. Black dots represent the raw data points. The bars (Figure A and C) and shaded areas (Figure B and D) represent 95% confidence intervals.*

We observed a total of 13 casualties of the tagged birds (33% of all tagged birds) at the end of the study period, of which 12 were migratory birds and one was a resident bird. The casualties occurred in Spain and Portugal (n=2) and the rest of them in African quarters (n=11). Our results showed a significant difference in survival probability between migratory behaviour and between age classes (Appendix C Table S3; Table 6.1). Resident birds exhibited higher survival rates than migrants for all age classes (mean= 0.9, SD=0.09, and mean=0.71, SD=0.16, respectively; Figure 6.4A and 4B). Moreover, survival of juvenile birds was significantly lower (mean= 0.50, SE=0.19) compared to that of subadults and adults (mean=0.75, SE=0.17, and mean=0.79, SE=0.1, respectively) (Figure 6.4C).

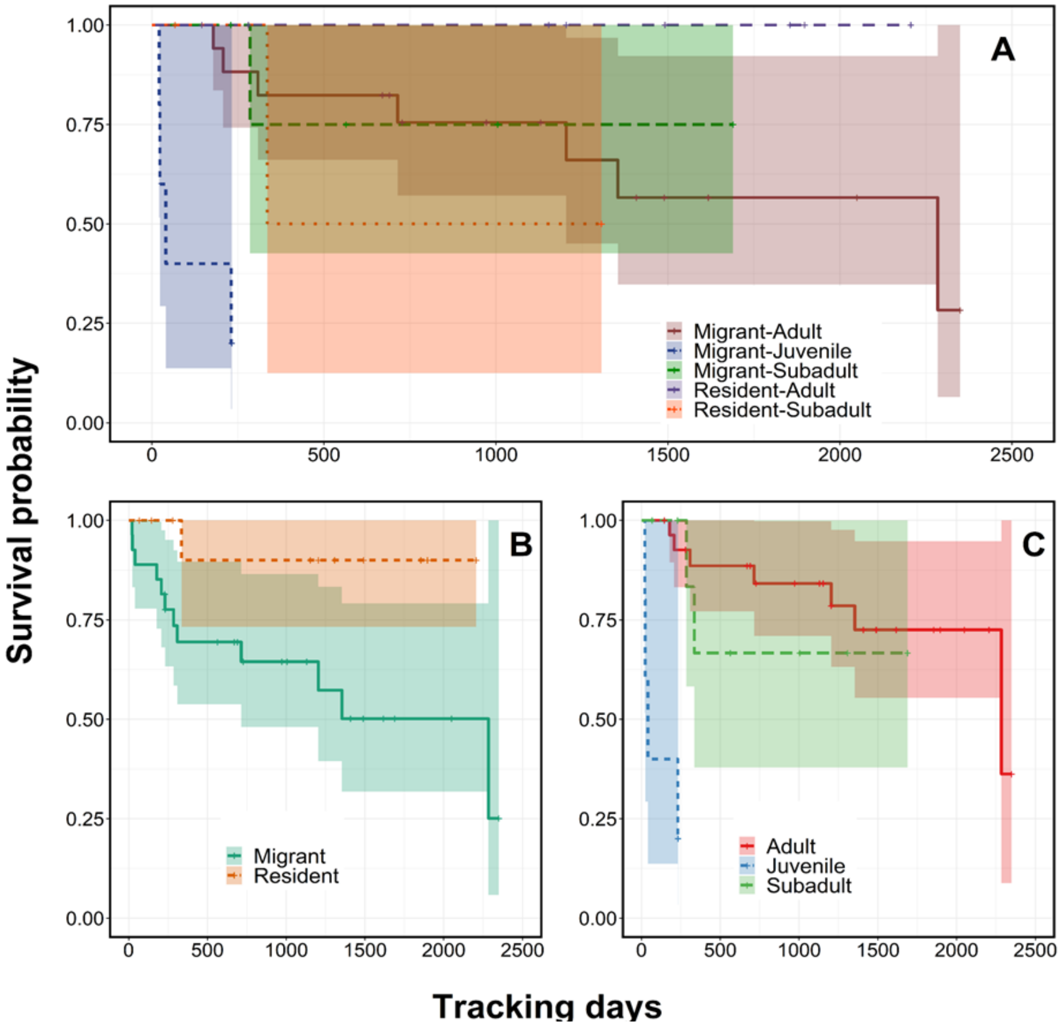

Figure 6.4. *Survival analysis results for different migratory behaviours x Age class (A), migratory behaviour (B) and Age class (C) by using cox regression method for GPS-tracked individuals (n=39) during the study period. The upper plot shows each migration strategy's survival probability throughout time (in days) since the first tracking day. Each step in the lines represents the death of an individual in each case. The shaded area represents 95% confidence interval.*

Energetic consequences of migratory behaviour

In general, Egyptian Vultures spent much less energy in winter than in the non-winter seasons. Migrant birds spent less energy compared to resident birds in costly flight types like flapping, particularly in winter (mean=3.02 g, SD=1.62 and mean=3.93 g, SD=1.66 g, respectively) (Appendix C Table C3; Table 6.1; Figure 6.5A). Migrant and resident birds spent similar energy in other flight behaviours (i.e., soaring, gliding) than resident birds in both non-wintering and wintering seasons (mean=1.65 g, SD=0.469 g, and mean=1.55 g, SD=0.518 g, respectively) (Table 6.1). Overall migrant birds spent less time flapping relative to the distance they covered compared to the resident birds during non-wintering period and further peaking in the wintering season (Appendix C Table C3; Table 6.1; Figure 2.5B). Moreover, resident birds exhibited a less efficient flight during the wintering season in Iberian Peninsula compared to migrant birds (mean=4.8 %, SD=2.73 %, and mean=2.63 %, SD=2.31 %, respectively). Finally, overall, we found that activity duration significantly increased with day length which varied along with seasons and migratory behaviour (Table 6.1). Migrant and resident birds exhibited similar activity duration in the non-wintering season when both remained in the Iberian Peninsula and thus, shared similar day length values (mean=12.6 hours, SD=2.95, and mean= 13.4, SD=2.54, respectively; Figure 6.5C and D). On the contrary, we found significant differences between migratory behaviour in winter, when migrant birds exhibited higher activity values during winter than resident birds (mean=11.4, SD=2.49, and mean=10.6, SD=2.22, respectively; Figure 6.5C and D).

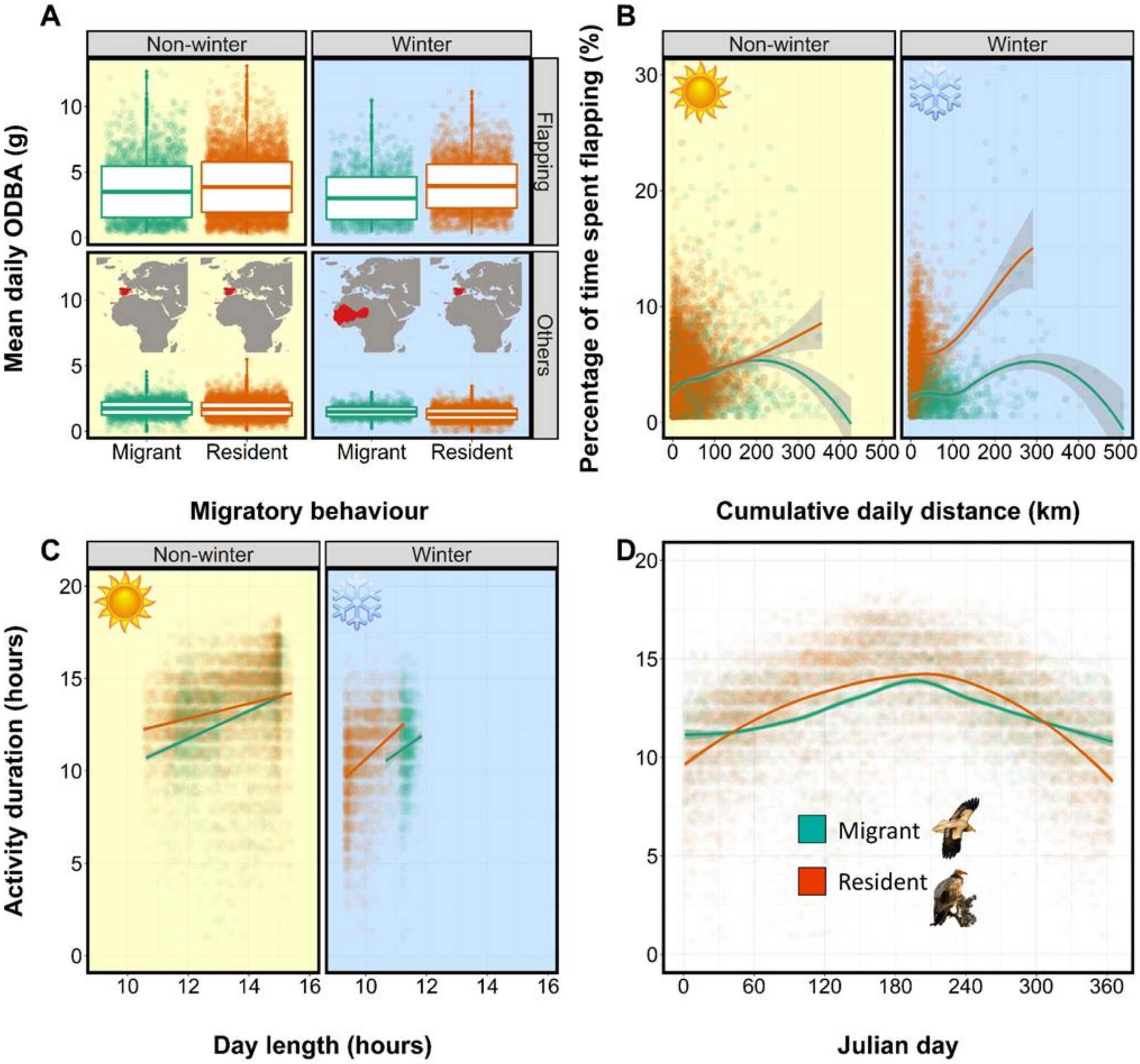

Figure 6.5. *Differences between migrant and resident birds in energy expenditure (expressed as cumulative daily ODBA in gravitational units [g]) among different flight behaviours in non-winter and wintering seasons of (A) and percentage of time spent daily in flapping flight respecting to the cumulative daily distance among migrant and resident birds during non-winter and wintering seasons (B). The figures C and D show the activity duration respecting to the day length and julian day, respectively. In figure A, the horizontal line in the box plot represents the mean, whilst the standard deviation is shown as error bars. Shaded areas represent 95% confidence intervals in figure B. Colored dots represent the raw data points. Photo Credits of Egyptian Vultures by Jon Morant and Miguel Ángel Múñoz Memole.*

6.5. DISCUSSION

In this study we disentangled the causes and consequences of migratory behaviour in a long-distance partial migratory bird, the Egyptian Vulture. We showed that environmental (food) and social (attraction to conspecifics) cues are primary correlates of variation in wintering population size across time. Interestingly, we observed that migrants exhibited higher breeding activity (i.e., number of breeding years) than resident individuals, whereas residents showed higher survival probabilities than migrant individuals. We found that overwintering in the breeding grounds seemed to be energetically more expensive than migrating. Overall, resident birds spent more energy and flew less efficiently during winter than migrants. Furthermore, daily activity duration of residents was lower due to the short days during winter in the Iberian Peninsula. In summary, our findings showed that optimal migratory strategy is context-dependent. Residency may be advantageous in terms of resource availability and survival, but it is energetically costly. On the contrary, migration is less costly and may allow individuals to invest more energy in reproduction which may explain the observed high breeding rates and lower survival probabilities. Therefore, our results suggest that the coexistence of different migratory behaviours may be balanced by a complex trade-off between fitness and optimal energy allocation shaped by environmental and social factors.

The role of environment and sociality

Global change has become one of the most influencing factors on partial migratory species in recent decades (e.g., Gill et al., 2019; Van Doren et al., 2021). Species rapidly respond to milder winters and increasingly predictable and available food pulses at higher latitudes by shortening migratory routes and even by remaining in the breeding areas during winter (Haest et al., 2019; Nuijten et al., 2020; Riotte-Lambert and Mathiopoulos, 2020 and references therein). However, our results showed that responses of birds are more influenced by proximate factors such as a significant increase in food availability and social cues rather than the climate (e.g., temperature). Indeed, it is known that anthropogenic food subsidies may greatly influence changes in migratory patterns in social species (Oro et al., 2013). The White Stork (Ciconia ciconia) is one such example that has become resident in Europe (e.g., Rotics et al., 2017; Arizaga et al., 2018), due to the increase of year-round available food sources at rubbish-dumps (Gilbert et al., 2016). Our results showed that adult Egyptian Vultures may attract subadults and less experienced individuals by remaining in a particular place where resources are abundant and predictable (see Morant et al., 2020). This pattern has also been observed in White Storks (see also Rotics et al., 2016) and other sedentary populations of Egyptian Vultures where collective foraging in areas of high food predictability and availability (e.g., farms) could benefit individuals with lower social status, such as juveniles or subadults (García Alfonso et al., 2020; van Overveld et al., 2020b). Overall, our results evidence that migratory decisions at the population level might be influenced by the environment (e.g., food availability), and modulated by sociality.

Fitness maximisation

Recent studies on fitness benefits of migration or residency strategies yield clear evidence that in terms of survival residency is more beneficial than migration (Buchan et al., 2019). Our results are in agreement with these findings and suggest that improved climate conditions and year-round resource availability could contribute to the observed higher survival rates (e.g., Satterfeld et al., 2018). In fact, we found that all age classes exhibited higher survival rates in residents as compared to migrants. Hence, residency could be particularly beneficial for immature and juvenile birds that exhibited higher mortality rates associated with migration (see Grande et al., 2009; Sanz-Aguilar et al., 2017). However, Buechley et al., (2021) found that migratory Egyptian Vultures experienced higher survival rates at African wintering grounds. The higher survival at non-breeding grounds, linked to the fact that juvenile Egyptian Vultures spend the first years of their lives in African grounds until reaching adulthood (Donázar, 1993), showed that a certain parity might exist among survival rates among migratory and non-migratory birds that could contribute to the coexistence of both behavioural strategies (Gilroy, 2017).

Our findings showed a clear breeding advantage for migrant birds. However, it could be expected that resident birds could increase breeding performance due to their earlier access to best-breeding sites and earlier reproduction (Pulido and Bethold, 2010). According to our results, it is also possible that in resident birds specific components of fitness are maximized (i.e., survival) at the expense of reproduction. Migrants, on the contrary, may allocate more resources towards reproduction while they are subjected to direct mortality costs of migration (Soriano-Redondo et al., 2020; Buechley et al., 2021). However, the observed similar breeding success between migrants and residents may indicate a clear advantage towards residents, since improved conditions during breeding season can result in better productivity for both migrants and residents, in addition to improved survival for residents (see for example Griswold et al., 2011). In this context, maximisation of certain fitness components could occur if some individual traits such as physical condition are compromised due to unfavourable conditions experienced in winter (Chapman et al., 2011b).

Overall, our results showed a complex trade-off between survival and reproduction which could lead to a selection of an optimal strategy that maximises certain fitness components for migratory behaviour (Chapman et al., 2011b). More importantly, they may indicate that migratory and resident species have different life-history strategies (e.g., migratory species live faster than resident ones) that promotes the coexistence among both forms (Soriano-Redondo et al., 2020).

Impact of migratory behaviour on energy allocation

Overall, we observed that residency is more energetically costly than migration, particularly during the wintering season. These results are contrary to previous studies showing that residency in breeding grounds in Europe could increase survival probability and decrease energy expenditure (see Flack et al., 2016; Rotics et al., 2017). We observed that resident individuals invested more effort flying in wintering ground than migrants, particularly they invested more time in costly flight types like flapping for the same travelled distance. These results suggest that migratory birds experienced better flying conditions and can travel farther by using gliding and soaring flights which minimize travel costs (see for example Rotics et al., 2016). Moreover, resident individuals exhibited lower activity duration due to shorter daylight hours in the Iberian Peninsula (Pokrovski et al., 2021). Therefore, our findings may indicate that the decision to stay may offset the higher energy spent in wintering grounds with harsher conditions (Rotics et al., 2018). However, residents may also compensate for the higher energy expenditure by reducing their wintering foraging areas and exploiting highly predictable food resources such as farms close to their roosting sites (Appendix C Figure C3 and Table C4; see also Morant et al., 2020 and Soriano-Redondo et al., 2021).

6.6. CONCLUSIONS

We showed that the resident populations of Egyptian Vultures are influenced by the increased resource availability in wintering grounds. Interestingly, our results suggest that such change in environmental conditions could be amplified by species-specific behavioural traits such as attraction to conspecifics (van Overveld et al., 2020a; b). We also observed that each migratory form may maximise a certain fitness component (i.e., survival or reproduction). Resident individuals may maximize their survival by exploiting predictable and easily available trophic resources (e.g., farms, López-López et al., 2014; Morant et al., 2020) that compensates for the higher energy cost of moving in unfavourable conditions during winter. Migrant individuals could benefit from more seasonal and unpredictable resources but better environmental conditions in African wintering quarters that improve their flight capacities (e.g., reducing flapping flight due to higher availability or thermals; Flack et al., 2016) and more daylight hours to forage (e.g., due to longer days in Africa in winter; Pokrovski et al., 2021). In summary, our results reveal a complex trade-off between fitness components between migrant and resident behaviours which could offset the energetic consequences of selecting one strategy or the other. Taken together, these insights could help better understand coexistence of both migratory forms in partial migratory species.

GENERAL DISCUSSION

Vulture conservation in the XXIst century lives one of its major challenges of all times. With more than 75 % of the Earth surface under human pressure and an ongoing rise in resources to fulfil human necessities (Venter et al., 2016; Watson et al., 2018), Old World vultures keep their strongholds in human-dominated landscapes (Donázar et al., 2016; Arrondo et al., 2020). It is thus evident that vulture conservation requires approaches that go far beyond protecting large areas for their conservation (e.g., Cruz et al., 2021) and trying to avoid counterproductive effects in areas where conservation and human interest enter into conflict (Nyhus, 2016). New conservation perspectives need to harmonise vulture conservation and human activities in human-dominated landscapes. This thesis show how long-term population monitoring and movement ecology could help to 1) understand better species ecology (e.g., breeding behaviour, space use, resource selection), 2) decipher species responses to human activities, 3) assess species status, improve management plans and monitoring protocols, and 4) effectively identify feasible targets for species preservation and foster vulture-human coexistence in anthropised landscapes.

The first step to establish functional links between behaviour and conservation is to fill gaps in basic aspects of their ecology, social life, and the ecological factors underlying species breeding systems of long-lived territorial species such as raptors (Tapia and Zuberogoitia 2018). In particular, the knowledge of mating and parental care could help decipher how human impacts could alter such behaviour and evaluate the effects of such alterations at population level on highly philopatric species such as vultures (Donázar 1993; van Overveld 2020). Vultures, particularly Egyptian vultures, are monogamous species with extended breeding periods (~6 months) in which parental tasks required the joint effort of both pair members (Chapter 1). This highlights that parents (despite potential variations) depend on each other, which could determine the breeding success. From a more applied perspective, whether a pair member dies or is disturbed and remains for a long period far from the nesting site could have fatal consequences for the nestlings/fledglings (e.g., Zuberogoitia et al., 2008) and could have effects at population level (e.g., demographic imbalance due to human-related mortality could reduce the probabilities of finding optimal mates; van Overveld et al., 2020). Furthermore, since both parents spent the same effort during reproduction (and therefore spent similar time at nest or nest surroundings), it may be exposed to similar human stressor levels. For instance, it could increase vigilance behaviour and decrease parental care due to noise from traffic or recreational activities (e.g., Strasser and Heath, 2013; Ng et al., 2019). This could also incurs survival costs for parents and even compromise future reproduction (Royle et al., 2012; Tarwater et al., 2011). Also, activities in human-dominated landscapes are increasing in duration and intensity, and usually overlap in time and space. This could potentially influence the stress levels of nestlings, increasing the likelihood of death by decreasing their growth rates (e.g., Watson et al., 2021).

The study of parental investment and data of breeding behaviour from long-term monitoring programs determine when major events such as incubation and hatching occur throughout the breeding season. This information is particularly useful for implementing conservation and management programs that consider when target species are particularly vulnerable (e.g., incubation and hatching; Chapter 1) and for designing standardised monitoring protocols (e.g., Perrig et al., 2019). Effectively assessing whether a species occupies a specific site and subsequent detection of its occurrence is crucial in ecological and population monitoring of threatened species (Lindenmayer and Lickens, 2010). The use of behavioural indicators (e.g., breeding behaviour) allows the designation of optimal strategies for the monitoring of populations by establishing when and how much economical and time effort should be invested (Chapter 2). The latter is crucial given that most studies in ecology and conservation projects are often performed in cost-constrained contexts that require prioritisation and optimal budget allocation (Possingham et al., 2001; Gerber et al., 2018). In the case of elusive species such as Egyptian vultures, which exhibited low detection rates (Mateo-Tomás and Olea, 2011; Chapter 2), it is crucial to determine under which circumstances the species is more likely to be detected. For instance, conservation practitioners may want to determine whether to manage a potentially harmful human disturbance in a nesting territory during sensitive periods such as incubation. Hence, the decision to keep monitoring or take part and manage (e.g., stopping a potentially disturbing human action) could have serious economic consequences. In these circumstances defining detection values for target species under different scenarios should be a priority (Bennett et al., 2018). Budget reallocation between and within monitoring programs is also possible depending on what the objectives are. Further, it could be adapted to fulfil species basic management requirements in cases of logistic constraints or limit financial budgets for monitoring and conservation programs (van Eeden et al., 2017). For example, allocating resources to those periods in which species is more plausible to be detected (e.g., nestling period) reduces the time and money that needs to be invested, therefore, being more cost-effective (Chapter 2; Wu et al., 2021).

Improving the knowledge of species' life cycle, such as the breeding period, also offer crucial insights on territory occupancy and nesting site selection (e.g., Sergio and Newton, 2003). These, indeed, are essential targets for conservation and management programs since both aspects determine the viability of populations and could influence the fitness of philopatric species (e.g., Refsnider and Janzen, 2010; Jiménez-Franco et al., 2018). In human-dominated landscapes, the number of available sites for nesting is substantially reduced for certain long-lived species such as cliff-nesting raptors. In these cases, species use the same nest every year (e.g., Jiménez-Franco et al., 2014; Beardsell et al., 2016). When alterations occur, individuals could be forced to abandon such sites and select lower quality sites (Stanback and Rockwell, 2003), which may negatively affect breeding outcomes (Chapter 3). Therefore, the conservation of such places should become a priority rather than protecting vast areas (e.g., Eveillard-Buchoux et al., 2019). In this sense, temporal bans may help to warrant the coexistence between economically profitable activities such as resource extraction, which entails substantial habitat changes (i.e., due to clear-cuttings in areas dedicated to monoculture plantations) and conservation of sensitive species such as the Egyptian vulture (Zuberogoitia et al., 2008; 2014). However, re-evaluating pre-existent conservation measures is necessary when the population-level responses to such measures are not evident or, worse, showed negative trends in crucial parameters such as nest re-occupancy and productivity (Chapter 3). How species respond to habitat alterations in nesting site surroundings may be used to define where and when those alterations may be allowed and properly managed (e.g., Santangeli et al., 2013). One way to do so is to design adequate spatio-temporal buffers and employ specific landscape components (e.g., forest patches) to reduce the effect of such habitat alterations and permit human actions take place (Chapter 3). This exemplifies how behavioural indicators based on species tolerance to human activities may guide the directionality of the management actions to reverse negative effects.

Although the measures above-mentioned might palliate the effects of certain human activities, multiple human alterations may overlap in anthropogenic landscapes (Wilson et al., 2020). This generates scenarios in which territories inhabited by the species are subjected to different disturbance regimes that vary over time. Furthermore, various sources of disturbance from human activities could synergistically and interactively act on crucial parameters such as breeding (Tobias and Pigot, 2019; Wilson et al., 2020). Hence, applying management measures to reduce the adverse effects of human activities is necessary in such cases to preserve population stability and viability (e.g., Mahon et al., 2019; Norris et al., 2021). This is particularly important in species healthy populations which may act as a source for other steeply declining populations (see Serrano et al., 2021). In the case of Egyptian vulture, a species highly sensitive to alterations in their territories, conservation of every single nesting site and territory is a priority, and every action carried or planned to occur beforehand or not (by administration or any stakeholder) counts (Chapter 4). The long-term success of management actions needs all actors' active participation and coordination (e.g., stakeholders, conservation practitioners, researchers and managers) (see, for instance, Salvatori et al., 2020). Only then, such actions might result in positive long-term effects for the population in anthropogenic landscapes and could improve a set of crucial population-level parameters (e.g., number of breeding territories, nest occupancy, and productivity; Chapter 4). Furthermore, adopting such an approach could effectively reduce human-wildlife conflicts in anthropogenic landscapes and promote coexistence by reconciling human actions and species preservation (Redpath et al., 2013; Chapter 4).

Detecting how and which human activities in anthropogenic landscapes may alter individuals' behaviour also pose new challenges in contemporary ecological research. While long-term monitoring (e.g., using visual counts) allows the detection of certain behavioural alterations (e.g., breeding behaviour), others require more sophisticated techniques, such as studying animal movement (Allen and Singh, 2016; Katzner and Arlettaz 2020). Information from animal movement patterns through GPS telemetry could infer behavioural changes that enable species to thrive in human-dominated landscapes. These landscapes encompassed anthropogenic activities that could directly alter animal movement patterns and space use (e.g., by decreasing or increasing home range areas; Doherty et al., 2021), or indirectly by landscape transformation or increasing resource availability. For instance, the increase in the food availability from humans and anthropogenic climate change may alter species population dynamics, physiological changes, and even provoke changes in migration patterns such as range-shortening in migration routes (e.g., Oro et al., 2013; Chen et al., 2011).

Vultures are particularly sensitive to such changes due to their link to anthropogenic food subsidies, particularly from livestock. For example, griffon and cinereous vultures may recognise high and low carrion availability areas and modulate their space use accordingly (Arrondo et al., 2018). In the case of partial migratory species such as Egyptian vultures, the year-round availability of food linked to temperate wintering conditions seems to have triggered behavioural responses to such alterations by shifting migratory behaviour towards residency (Chapter 5), or even by changing foraging search patterns throughout the annual cycle (López-López et al., 2013). Moreover, the above-mentioned favourable conditions could also foster the grouping of the species that could attract more birds to such areas during both unfavourable and favourable seasons (see also García-Alfonso et al., 2020). Such congregations, which usually occur at roosting sites surrounding the primary trophic sources like farms, are vital for information exchange and population dynamics on the species (Donázar, 1993; García-Alfonso et al., 2020; van Overveld et al., 2020a). Furthermore, in a broader context, changes in livestock numbers in human-dominated landscapes could also modulate the dynamics at roosting sites (Chapter 5-6). This is particularly relevant when coupled with species social characteristics such as the attraction of conspecifics, which may exacerbate the effects of food availability (Chapter 6). Therefore, the farm-roosting sites interlink at a fine scale and changes in food availability at a broad scale play a crucial role in maintaining social systems in species and modulates foraging, population dynamics and migratory behaviour in a social species such as Egyptian vulture (Chapter 5 and 6).

The consequences of these human-induced behavioural alterations could also have profound effects at the population level, which have implications for species conservation. For example, conserving traditionally managed farmland areas could positively affect species conservation in a changing world. In fact, those specialist species exhibiting higher migratory diversity, such as Egyptian vultures (i.e., migrant and resident individuals), could better face environmental unpredictability (Gilroy et al., 2016; Reid et al., 2018; Shaw, 2020). Also, the growing number of wintering birds and the continuous use of roosting sites make them good conservation targets. Protecting those sites may help preserve particularly relevant social dynamics (e.g., pair-bond formation and information exchange, among others; van Overveld et al., 2020) and the invaluable ecosystem services provided by the species by removing carrion in such agricultural areas (Morales-Reyes et al., 2015). Another positive aspect to consider is that the increase in resident birds due to favourable conditions could enhance species survival (Chapter 6). The latter is particularly relevant in a species such as the Egyptian vulture with delayed maturity and reproduction and high juvenile and subadult mortality (Grande et al., 2009; Oppel et al., 2015; Sánz-Aguilar et al., 2017; Buechley et al., 2021), particularly during migration (Oppel et al., 2015).

As a counterpart, since animals could use such food abundance and other individuals' presence as sound cues, these cues may no longer provide the expected positive fitness effects (Fletcher et al., 2012; Hale et al., 2015). This is reflected in the counterintuitive results of Chapter 6 where we found that resident Egyptian vultures showed lower breeding activity and higher energy expenditure than migratory individuals. In such cases, species may compensate for the higher costs of residency due to the easiness of food acquisition by reducing their home range (i.e., a roosting site are close to sites where resources are available) (Chapter 5 and 6). However, such a decrease in the space use coupled with increased spatio-temporal predictability of farm resources may favour competition. For example, highly socially ranked individuals such as adults could force juveniles/subadults to search for food far from farms (see Chapter 5; van Overveld et al., 2018). This could increase the risk of collision with human-infrastructures (e.g., power lines) close to roosting sites (García-Alfonso et al., 2021). Finally, the increase of the intensive farming practices and more intense use of intensive farms as feeding sites by vultures could also have adverse effects, such as exposing individuals to pharmaceuticals and increasing disease risk or even death (Blanco et al., 2019; Moreno-Opo et al., 2021). All those cases exemplify how human activities are now a strong selective pressure acting on certain behavioural traits at the individual (e.g., increase of energy expenditure and bad flight efficiency) and population levels (e.g., higher exposure of resident populations to human threats).

Socio-economic changes are provoking landscape polarisation in which previously human-dominated landscapes will suffer an increase in the severity and quantity of human impacts (Corlett, 2016). In contrast, others will experience the abandonment of the land and traditional activities such as extensive livestock husbandry, particularly in rural areas (Navarro and Pereira, 2015; Perino et al., 2019). In the case of vultures, landscape anthropization poses new challenges for their conservation. For instance, land intensification and more abundant but harmful anthropogenic food sources could both benefit the species and expose them to several threats such as collisions with human-made infrastructures, human disturbances at nesting sites, high poisoning risk and human-vulture conflicts, among others (Carrete et al., 2009; Zuberogoitia et al., 2008; Gangoso et al., 2013; Duriez et al., 2019; Lambertucci et al., 2021). The ability of specialist species such as vultures and, in particular, sensitive species such as the Egyptian vulture to adapt to human-dominated landscapes will depend on their behavioural plasticity to respond to rapidly changing environments. Likewise, our ability to ensure the species persistence and the ecosystem services their offer in human-dominated landscapes will depend on both 1) the selection of suitable behavioural indicators that offer cues on the directionality of species response to human activities, and 2) our effort to track and detect changes in species response to human alterations that could otherwise compromise population stability. This will, indeed, define evidence based, effective conservation management actions at local scale (e.g., Effrat et al., 2020) that could help to design and improve broader and more ambitious conservation plans for vulture conservation in the XXI century (e.g., Botha et al., 2017).

Challenges and opportunities in the use of behavioural indicators

A key point of applying behavioural-driven-conservation measures is that these approaches usually are very species-specific. Moreover, the response to human disturbance may not only depend on species but also on individuals' sensitivity to them (Blumstein et al., 2005). This means that, in some cases, species with high ecological requirements may be insensitive to human alterations (e.g., Santangeli et al., 2013), while, in other cases, they may respond negatively in habitats with similar or even lower human disturbance regimes (Chapter 3 and 4). Also, species response to human disturbances could vary across the same distribution range (Devictor et al., 2008). For instance, Oppel et al., (2017) proved that predictive models accounting for a set of variables affecting Egyptian vulture nest re-occupancy and breeding success, despite useful, were not transferable to other geographical areas where the species was present. Therefore, these measures may be considered context-dependent (i.e., vary across areas, species, populations and even individual level), hindering conservation practitioners' implementation of such behavioural-mediated conservation measures. For example, managers or policymakers may consider it economically costly to evaluate different management actions for the same species or populations across their distribution range rather than implementing standard conservation measures (Panitsa et al., 2011; Lindenmayer et al., 2014). Also, the conservation of rare species may be considered a waste of resources when resources are limited (Neeson et al., 2018).

Single-species conservation measures could be much narrowed and have been criticised during the last century (e.g., Robert and Angelstam, 2004; Sheddon and Leech, 2008). However, such an approach could be practical when applied to apex-predator species offering invaluable ecosystem services, which inhabit places shared with other species of interest. This is particularly relevant in the Egyptian vulture, a cliff-nesting species that usually shares space with other sensitive species (e.g., griffon vultures, red-billed chough, common raven and peregrine falcon, among others). For example, applying single-species management measures could help maintain species assemblages (e.g., Bichel et al., 2016; Runge et al., 2019). Furthermore, conserving rare species is crucial for healthy ecosystem maintenance (Mouillot et al., 2013), particularly in human-dominated landscapes. For instance, it has been demonstrated that in scavenger communities, both rare and common species offer invaluable ecosystem services by removing carrion (Mateo-Tomás et al., 2017). It should also be considered that adopting such approaches are sometimes necessary in human-dominated landscapes since the social acceptance of some measures habitually depend on how the target species appeals to the public based on their appearance, status and utility (Bowen and Entwistle, 2002). Finally, selecting adequate behavioural indicators that are handful and easy to obtain, analyse and understand, mainly/specially those comparable across species and areas, is a key step in reducing uncertainties associated with variability in individuals' responses to human activities (Blumstein et al., 2005). This could help explain whether individuals exhibit a plastic response to alteration (e.g., increase in food availability or landscape transformation) in human-dominated landscapes to infer better population-level responses that may influence population dynamics at a broad scale (Brass et al., 2021). Finally, the advent of new technologies has also enabled the appearance of new behavioural-derived indicators such as energy expenditure through tri-axial accelerometry. Although the use of these indicators is still on its infancy, they offer promising ways to measure the effects of humans’ activities on species behaviour and eco-physiological consequences of behavioural changes (Wilson et al., 2019).

CONCLUSIONS

Conservation in human-dominated landscapes represents a real challenge in contemporary ecology. Therefore, disentangling how species respond to human activities in such landscapes is of great importance in designing/taking adequate conservation actions to warrant the conservation and persistence of sensitive and threatened species such as, the Egyptian vulture. This thesis demonstrates the utility of using behavioural indicators such as occupancy/detectability, breeding behaviour and space use from long-term monitoring and GPS tracking data to decipher how species respond to environmental and anthropogenic alterations and design effective conservation measures.

1. In Egyptian vultures, both sexes invest similar efforts on different parental tasks. However, crucial events such as incubation and nest hatching provoke a shift in the patterns of parental investment. There is no effect of environmental factors such as ambient temperature on parental activity but in changeover, which increases the replacement rate of adults at the nest.
2. Accounting for monitoring effort, species breeding behaviour, environmental covariates (e.g., weather), and nest characteristics (e.g., nest visibility) could help to implement cost-effective monitoring and conservation programs and to reach a trade-off between financial budgets and conservation purposes.
3. Overwintering habitat alterations could reduce nest occupancy, breeding success and productivity. Temporary and spatial bans during periods in which species is not present increases nest reuse and productivity. Moreover, determinate landscape elements that provide screening, such as forest patches, increase nest re-occupancy probability and alleviate the effects of habitat alterations in nest surroundings.
4. Management actions with multifaceted crucial behavioural targets (e.g., habitat selection, breeding success, and productivity) positively affect Egyptian vultures nests subjected to different

disturbance regimes. Thus, the combined participation of policymakers, rangers, researchers, and stakeholders is key to allow human-wildlife coexistence while warrantying economic activities in human-dominated landscapes.

5. Anthropogenic food subsidies could induce behavioural changes in Egyptian vultures. In particular, changes and practices in farmland areas may alter their migratory patterns towards residency in the Iberian Peninsula. Egyptian vultures respond to food from humans by gathering and forming large congregations at roosting sites, which are vital for species social dynamics. Species exhibited small home range areas during winter and positively selected farmland areas dedicated to livestock husbandry.
6. The increase in the available food and social attraction modulates wintering populations of Egyptian vultures. Human-induced behavioural changes towards residency increase survival probability but reduce breeding attempts. Moreover, residency increases energy expenditure and reduced flight efficiency and activity duration due to shorter days in northern latitudes. On the contrary, migration reduces individual survival and increases overall breeding performance while reducing energy costs associated with flight in African wintering quarters.

Humans could potentially alter species behaviour and how these can be used in species conservation. The present thesis addresses such by interpreting behavioural indicators and uses them in different conservation scenarios. We are still far from profoundly understand the magnitude of human alterations' effects on species behaviour and how these are traduced in real consequences at ecosystem-level processes. However, disentangling how sensitive and cornerstone species respond to such changes using different methodologies such as long-term monitoring and tracking technology is a step forward to address the further question in the ecology and conservation of species and habitats in human-dominated landscapes. Far beyond, it could help understand not only the species themselves and but also their link with the human being, which is essential to predict future changes.

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APPENDICES

CHAPTER 2 – APPENDIX A

Supporting Information

Appendices

Supporting information A.1. – Details on the monitoring costs estimates.

Supplementary tables

Table A.1. Survey costs when no covariates are considered.

Table A.2. Survey costs when nest was not visible in rainy years.

Table A.3. Survey costs when nest was visible in rainy years.

Table A.4. Survey costs when nest was not visible in dry years.

Table A.5. Survey costs when nest was visible in dry years.

Supporting information A.1. – Details on the monitoring costs estimates.

Estimation of monitoring costs

We determined the minimum number of visits (n) required to assure the occupancy with 95% of confidence. The minimum number of visits (n) was multiplied by the monitoring effort necessary in each case, being from 1 to 5 hours in each breeding phase (E), obtaining the total hours necessary in each case. Then, we estimated the cost per monitored hours (€/h) of an expert technician based on current average field work salary in Spain (i.e., 45 €/hour)(w). Overall, we computed the cost of a technician who carried out monitoring as the simple product of n, E and w:

$$C_{\text{Technician}} = n \times E \times w \quad (1)$$

We also accounted for the total cost of distance. We first considered the cost to arrive at each nest using the distance (dist) to each nest from a common point and return to the point of origin (outward journey) by using Google Maps (Google, 2019), in our case, the capital of the study area (Bilbao, mean=85.1 km, SD = 31.4 km, range= 33 - 155 km). Furthermore, we assessed the total inter-nests distance in one survey day. We considered the total number of possible visits to different nests in one day, considering the effort (hours) and a hypothetical average working time of eight hours per day. Based on our calculations, the maximum number of sites to survey in a single day was five, all of them for a single hour, three nests with a two hours effort, two for three hours and only one nest investing 4-5 hours of monitoring in a single day (nmax). The mean inter-nest distance (6.49 km and 6.31 km in 2017 and 2018, respectively) was obtained from averaged nearest neighbor distance analysis in ArcGIS 10.5 (ESRI, 2016) (d). The total inter-nest distance was obtained from multiplying the possible number of the nests to monitor in one day (from one to five) by the mean inter-nest distance. We estimated travel expenses costs by multiplying a standard cost of displacement (0.19 €/km)

(CDisplacement) by the total distance (the result of the sum of the mean distance to each nest round trip and total inter-nest distance).

$$C_{\text{Travel expenses}} = C_{\text{Displacement(€/km)}} \left[(n_{\max} d) + dist \right] \tag{2}$$

We calculated the cost of technician displacement. We first estimated the total hours invested in displacement by multiplying a standard time of displacement (2mins/km) (TDisplcamenet) by total distance (the result of the sum of the mean distance to each nest round trip and total inter-nest distance),obtaining the total minutes investing in displacement. We then converted minutes into hours and multiplied this value by the cost of the technician (w, explained above) obtaining the total cost of displacement:

$$C_{\text{Displacement cost}} = (T_{\text{Displacement(mins/km)}} \left[(n_{\max} d) + dist \right]) \times w \tag{3}$$

Finally, we calculated the total cost for assuring 95% of nest detections as the sum of the total cost of technician hours plus distance and cost of technician displacement.

$$C_{Total} = C_{\text{Technician}} + C_{\text{Travel expenses}} + C_{\text{Displacement cost}} \tag{4}$$

Table A.1. *Survey costs when no covariates are considered.*

Period	Effort (h)	Days required (n)	Total hours (h)	Cost of Technician (€)	N. of nests possible to monitor	Total inter-nest distance (km)	Total. Dist. (km)	Travel expenses (€)	Technician displacement (h)	Cost of displacement (€)	Total cost (€)
COURTSHIP	1	10	10	450	5	32.45	117.55	22.33	3.92	176.33	648.66
	2	9	18	810	3	19.47	104.57	19.87	3.49	156.86	986.72
	3	6	18	810	2	12.98	98.08	18.64	3.27	147.12	975.76
	4	5	20	900	1	0	85.1	16.17	2.84	127.65	1043.82
	5	4	20	900	1	0	85.1	16.17	2.84	127.65	1043.82
INCUBATION	1	2	2	90	5	32.45	117.55	22.33	3.92	176.33	288.66
	2	2	4	180	3	19.47	104.57	19.87	3.47	156.86	356.72
	3	2	6	270	2	12.98	98.08	18.64	3.27	147.12	435.76
	4	2	8	360	1	0	85.1	16.17	2.84	127.65	503.82
	5	1	5	225	1	0	85.1	16.17	2.84	127.65	368.82
NESTLINGS	1	2	2	90	5	32.45	117.55	22.33	3.912	176.33	288.66
	2	2	4	180	3	19.47	104.57	19.87	3.49	156.86	356.72
	3	1	3	135	2	12.98	98.08	18.64	3.27	147.12	300.76
	4	1	4	180	1	0	85.1	16.17	2.84	127.65	323.82
	5	1	5	225	1	0	85.1	16.17	2.84	127.65	368.82

Table A.2. *Survey costs when nest was not visible in rainy years.*

Period	Effort (h)	Days required (n)	Total hours (h)	Cost of Technician (€)	N. of nests possible to monitor	Total inter-nest distance (km)	Total. Dist. (km)	Travel expenses (€)	Technician displacement (h)	Cost of displacement (€)	Total cost (€)
COURTSHIP	1	39	39	1755	5	32.45	117.55	22.33	3.92	176.33	1953.66
	2	33	66	2970	3	19.47	104.57	19.87	3.49	156.86	3146.72
	3	21	63	2835	2	12.98	98.08	18.64	3.27	147.12	3000.76
	4	18	72	3240	1	0	85.1	16.17	2.84	127.65	3383.82
	5	13	65	2925	1	0	85.1	16.17	2.84	127.65	3068.82
INCUBATION	1	6	6	270	5	32.45	117.55	22.33	3.92	176.33	468.66
	2	5	10	450	3	19.47	104.57	19.87	3.49	156.86	626.72
	3	4	12	540	2	12.98	98.08	18.64	3.27	147.12	705.76
	4	3	12	540	1	0	85.1	16.17	2.84	127.65	683.82
	5	3	15	675	1	0	85.1	16.17	2.84	127.65	818.82
NESTLINGS	1	4	4	180	5	32.45	117.55	22.33	3.92	176.33	378.66
	2	3	6	270	3	19.47	104.57	19.87	3.49	156.86	446.72
	3	3	9	405	2	12.98	98.08	18.64	3.27	147.12	570.76
	4	2	8	360	1	0	85.1	16.17	2.84	127.65	503.82
	5	2	10	450	1	0	85.1	16.17	2.84	127.65	593.82

Table A.3. Survey costs when nest was visible in rainy years.

Period	Effort (h)	Days required (n)	Total hours (h)	Cost of Technician (€)	N. of nests possible to monitor	Total inter-nest distance (km)	Total. Dist. (km)	Travel expenses (€)	Technician displacement (h)	Cost of displacement (€)	Total cost (€)
COURTSHIP	1	16	16	720	5	32.45	117.55	22.33	3.92	176.33	918.66
	2	13	26	1170	3	19.47	104.57	19.87	3.49	156.86	1346.72
	3	9	27	1215	2	12.98	98.08	18.64	3.27	147.12	1380.76
	4	8	32	1440	1	0	85.1	16.17	2.84	127.65	1583.82
	5	6	30	1350	1	0	85.1	16.17	2.84	127.65	1493.82
INCUBATION	1	3	3	135	5	32.45	117.55	22.33	3.92	176.33	333.66
	2	3	6	270	3	19.47	104.57	19.87	3.49	156.86	446.72
	3	2	6	270	2	12.98	98.08	18.64	3.27	147.12	435.76
	4	2	8	360	1	0	85.1	16.17	2.84	127.65	503.82
	5	2	10	450	1	0	85.1	16.17	2.84	127.65	593.82
NESTLINGS	1	2	2	90	5	32.45	117.55	22.33	3.92	176.33	288.66
	2	2	4	180	3	19.47	104.57	19.87	3.49	156.86	356.72
	3	2	6	270	2	12.98	98.08	18.64	3.27	147.12	435.76
	4	1	4	180	1	0	85.1	16.17	2.84	127.65	323.82
	5	1	5	225	1	0	85.1	16.17	2.84	127.65	368.82

Table A.4. *Survey costs when nest was not visible in dry years.*

Period	Effort (h)	Days required (n)	Total hours (h)	Cost of Technician (€)	N. of nests possible to monitor	Total inter-nest distance (km)	Total. Dist. (km)	Travel expenses (€)	Technician displacement (h)	Cost of displacement (€)	Total cost (€)
COURTSHIP	1	16	16	720	5	31.55	116.65	22.16	3.89	174.98	917.14
	2	13	26	1170	3	18.93	104.03	19.77	3.47	156.04	1345.81
	3	9	27	1215	2	12.62	97.72	18.57	3.26	146.58	1380.15
	4	8	32	1440	1	0	85.1	16.17	2.84	127.65	1583.82
	5	7	35	1575	1	0	85.1	16.17	2.84	127.65	1718.82
INCUBATION	1	3	3	135	5	31.55	116.65	22.16	3.89	174.98	332.14
	2	3	6	270	3	18.93	104.03	19.77	3.48	156.04	445.81
	3	2	6	270	2	12.62	97.72	18.57	3.26	146.58	435.15
	4	2	8	360	1	0	85.1	16.17	2.84	127.65	503.82
	5	2	10	450	1	0	85.1	16.17	2.84	127.65	593.82
NESTLINGS	1	2	2	90	5	31.55	116.65	22.16	3.89	174.98	287.14
	2	2	4	180	3	18.93	104.03	19.77	3.47	156.04	355.81
	3	2	6	270	2	12.62	97.72	18.57	3.26	146.58	435.15
	4	1	4	180	1	0	85.1	16.17	2.84	127.65	323.82
	5	1	5	225	1	0	85.1	16.17	2.84	127.65	368.82

Table A.5. *Survey costs when nest was visible in dry years.*

Period	Effort (h)	Days required (n)	Total hours (h)	Cost of Technician (€)	N. of nests possible to monitor	Total inter-nest distance (km)	Total. Dist. (km)	Travel expenses (€)	Technician displacement (h)	Cost of displacement (€)	Total cost (€)
COURTSHIP	1	7	7	315	5	31.55	116.65	22.16	3.89	174.98	512.14
	2	6	12	540	3	18.93	104.03	19.77	3.47	156.04	715.81
	3	4	12	540	2	12.62	97.72	18.57	3.26	146.58	705.15
	4	4	16	720	1	0	85.1	16.17	2.84	127.65	863.82
	5	3	15	675	1	0	85.1	16.17	2.84	127.65	818.82
INCUBATION	1	2	2	90	5	31.55	116.65	22.16	3.89	174.98	287.14
	2	2	4	180	3	18.93	104.03	19.77	3.47	156.045	355.81
	3	1	3	135	2	12.62	97.72	18.57	3.26	146.58	300.15
	4	1	4	180	1	0	85.1	16.17	2.84	127.65	323.82
	5	1	5	225	1	0	85.1	16.17	2.84	127.65	368.82
NESTLINGS	1	1	1	45	5	31.55	116.65	22.16	3.89	174.98	242.14
	2	1	2	90	3	18.93	104.03	19.77	3.47	156.04	265.81
	3	1	3	135	2	12.62	97.72	18.57	3.26	146.58	300.15
	4	1	4	180	1	0	85.1	16.17	2.84	127.65	323.82
	5	1	5	225	1	0	85.1	16.17	2.84	127.65	368.82

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CHAPTER 5 – APPENDIX B

Supporting Information

Supplementary tables

Table B.1. Summary calculations of selected Basic Movement Parameters.

Table B.2. Environmental variables at 200 m spatial resolution used to model Egyptian vulture space use.

Table B.3. Correlation matrix of the variables used in RUF analysis.

Table B.4. Details of each tagged individual during study period.

Table B.5. Estimates of standardised RUF coefficients (β) and standard errors for each variable of the full RUF models.

Table B1. *Summary calculations of selected Basic Movement Parameters (BMPs) (see also* [1,2] *and* [3] *for further details).*

Parameter	Unit	Calculation	Abbreviation	References
Cumulative distance	m/ km	-	Increment of the X and Y values between two consecutive relocations, change in absolute spatial position	2,4,5,6
Net squared displacement	m^2/ km^2	$NSD - VarX - VarY$	X and Y = cartesian coordinates of each point of trajectory change along the path	2,4,5,6
Straightness	Range (0-1)	$\mathrm{ST} = \frac{dE}{L}$	dE = Euclidean distance between the beginning and end of the path L= Total path length	2,7,8
Intensity of use	Range (0-100)	$\mathrm{IU} = \frac{L}{\sqrt{A}}$	L = total path length A = area of the movement	9,10

Table B2. *Environmental variables at 200 m spatial resolution used to model Egyptian vulture space use wintering in Extremadura (western Spain) (see Methods section).*

		Variable	Code	Description	Hypothesis	Resolution	Data source
Environmental Conditions	Topography	Insolation	INSA	Insolation (from 1st December to 28th February).	Determinate insolation values may favour the foraging efficiency of the species.	200m	DEM 200m http://centrodedescargas.cnig.es/CentroDescargas/index.jsp
		Slope	SDLO	Slope of the terrain (%)	Areas with lower slope and terrain roughness values favor the detection of carcasses.		
		Rugosity	TOPV	Rugosity (%)			
	Land-use	Land-cover	LANDCO	Dominant "habitat", according to the main CORINE land cover levels in each cell corresponding to Agricultural, Artificial and Forest areas.	Some habitat types may facilitate the detection of carcasses in the field.	200m	CLC 2018 GeoTIFF 100m https://land.copernicus.eu/pan-european/corine-land-cover/clc2018?tab=download
	Productivity	NDVI	NDVI	Mean anual Normalized Difference Vegetation Index (NDVI).	NDVI is a indicator of habitat quality. Higher NDVI values are associated with more productive grazing environments[11].	200m	NDVI GeoTIFF 300m https://land.copernicus.eu/global/products/ndvi
	Human disturbance	Urban nuclei density	DENSN	The inverse of the Euclidean distance the nearest urban nucleus (0 value to the greatest distance between nuclei).	The presence of low populated nuclei in rural areas may favour the presence of the species.	200m	Data obtained at municipality level http://centrodedescargas.cnig.es/CentroDescargas/buscar.do?filtro.codFamilia=REDTR#
		Distance to towns	DISTOWN	Euclidean distance to towns and villages.	The presence of towns and villages may alter foraging behaviour.		
		Distance to roads	DISTRO	Euclidean distance to asphalted communication routes (roads and highways).	The presence of roads may alter foraging behaviour (12,13).		
Trophic Resources	Livestock	Cows	COWS	Livestock density (i.e., heads of cows, sheeps, pigs, and goats divided by the surface area of each local Municipality).	Livestock is an important food resource for the species and is an adequate proxy of food availability[14].	200m	Data obtained at municipality level from the the annual regional cattle census (2017-2018) performed by the regional government (Junta de Extremadura).
		Pigs	PIGS				
		Sheep	SHEEP				
		Goats	GOATS				

Table B3. *Correlation matrix of the variables used in RUF analysis based on the pooled sample of 123,137 GPS locations of the tagged individuals (n=12) (more details of each variable in Table S2). Correlated variables (>0.5) are highlighted in bold.*

	INSA	SDLO	TOPV	FOREST	ARTI	AGRIC	NDVI	DENSN	DISTRO	DISTOWN	COWS	PIGS	SHEEP	GOATS
INSA	**1.00**	-	-	-	-	-	-	-	-	-	-	-	-	-
SDLO	**0.62**	**1.00**	-	-	-	-	-	-	-	-	-	-	-	-
TOPV	**0.74**	**0.73**	**1.00**	-	-	-	-	-	-	-	-	-	-	-
FOREST	0.00	0.07	0.00	**1.00**	-	-	-	-	-	-	-	-	-	-
ARTI	0.04	0.00	0.02	-0.08	**1.00**	-	-	-	-	-	-	-	-	-
AGRIC	0.00	0.04	0.00	0.01	-0.09	**1.00**	-	-	-	-	-	-	-	-
NDVI	0.00	0.19	0.28	-0.19	0.00	0.21	**1.00**	-	-	-	-	-	-	-
DENSN	0.08	0.00	0.00	-0.06	0.09	0.06	0.31	**1.00**	-	-	-	-	-	-
DISTRO	-0.24	-0.21	-0.27	0.07	-0.06	-0.13	-0.33	**-0.62**	**1.00**	-	-	-	-	-
DISTOWN	-0.08	0.00	0.00	0.06	-0.09	-0.06	-0.31	**-1.00**	0.01	**1.00**	-	-	-	-
COWS	-0.07	-0.2	-0.25	0.00	-0.06	0.00	-0.18	-0.09	0.27	0.09	**1.00**	-	-	-
PIGS	-0.1	-0.2	-0.28	0.16	0.00	-0.22	-0.34	0.13	0.04	-0.13	0.02	**1.00**	-	-
SHEEP	-0.1	-0.19	-0.27	0.00	0.04	0.00	-0.15	0.03	0.19	0.03	0.19	0.2	**1.00**	-
GOATS	-0.09	-0.21	-0.26	0.16	0.00	-0.22	-0.31	0.08	0.07	-0.08	-0.06	0.27	0.27	**1.00**

Table B4. *Details of each tagged individual during study period.*

Ring	Age	Sex	Tag ID	ID	Tagging year	Tracking duration (days)*	Fate
9071267	Adult	F	5179	Arenal	2017	396	Alive
9071263	Subadult	F	4524	Espiga	2016	760	Alive
9068408	Subadult	F	4023	Fresnedosa	2015	1111	Alive
9071040	Adult	F	4245	Lluvia	2015	802	Alive
9071039	Subadult	F	4243	Macedonia	2015	802	Alive
9071262	Adult	F	4244	Niebla	2015	802	Alive
9071268	Subadult	M	5180	Pando	2017	396	Alive
9071261	Subadult	F	4025	Primavera	2015	802	Alive
9071241	Adult	M	5181	Taiga	2017	110	Alive
9071269	Adult	M	5181	Torre	2017	146	Alive
9071242	Adult	F	5182	Villa	2017	79	Alive
9071243	Subadult	F	5183	Viña	2017	79	Alive

***Table B5**. Estimates of standardised RUF coefficients (β) and standard errors for each variable of the full RUF models for 12 Egyptian vultures tracked by GPS satellite telemetry in Extremadura (Spain). Consistency at the population level is indicated by the mean and standard deviation of each coefficient and standard error (see also Donovan et al.,[15] for a similar approach). According to Marzluff et al., [16], the relative importance of resources is indicated by the magnitude (positive or negative) of β.*

	Livestock				**Human disturbances**		**Land-use**			**Topography**	**Productivity**
	Sheep	**Pigs**	**Cows**	**Goats**	**Distance to roads**	**Distance to towns**	**Forest**	**Artificial**	**Agriculture**	**Slope**	**NDVI**
ID	**β ± SE**	**β ± SE**	**β ± SE**	**β ± SE**	**β ± SE**	**β ± SE**	**β ± SE**	**β ± SE**	**β ± SE**	**β ± SE**	**β ± SE**
1	-2.571 ± 0.096	-0.579 ± 0.304	2.189 ± 0.097	8.110 ± 0.356	-0.477 ± 0.080	-0.966 ± 0.077	2.777 ± 0.131	-0.128 ± 0.048	2.993 ± 0.132	-0.316 ± 0.052	0.554 ± 0.078
2	-0.025 ± 0.010	-0.372 ± 0.068	0.049 ± 0.009	0.378 ± 0.072	-0.351 ± 0.015	0.282 ± 0.014	-0.017 ± 0.004	0.016 ± 0.001	-0.023 ± 0.004	-0.055 ± 0.004	0.059 ± 0.005
3	-0.221 ± 0.032	-0.610 ± 0.254	0.165 ± 0.030	1.615 ± 0.270	-0.148 ± 0.046	-0.470 ± 0.051	-0.012 ± 0.010	0.001 ± 0.003	-0.031 ± 0.012	-0.148 ± 0.017	0.074 ± 0.015
4	0.369 ± 0.009	0.276 ± 0.011	0.787 ± 0.820	-3.567 ± 0.091	-0.945 ± 0.066	-0.967 ± 0.022	6.135 ± 0.182	-9.437 ± 5.512	6.190 ± 0.183	0.226 ± 0.007	-0.109 ± 0.012
5	0.072 ± 0.003	0.036 ± 0.002	0.056 ± 0.003	0.046 ± 0.006	-0.162 ± 0.037	-0.700 ± 0.071	-0.011 ± 0.003	-0.006 ± 0.003	0.016 ± 0.003	0.030 ± 0.003	-0.033 ± 0.003
6	0.335 ± 0.173	-0.308 ± 0.204	0.956 ± 0.279	15.127 ± 0.233	2.190 ± 0.198	2.810 ± 0.200	3.219 ± 0.401	0.780 ± 0.158	4.589 ± 0.395	-0.899 ± 0.068	-0.077 ± 0.137
7	0.039 ± 0.069	0.315 ± 0.058	-0.061 ± 0.067	-0.084 ± 0.054	-0.455 ± 0.088	-0.732 ± 0.093	-0.402 ± 0.067	0.328 ± 0.036	-0.403 ± 0.072	-0.188 ± 0.064	-0.551 ± 0.057
8	0.374 ± 0.095	-0.186 ± 0.096	-0.539 ± 0.071	0.914 ± 0.918	0.072 ± 0.091	0.912 ± 0.112	1.331 ± 0.074	0.157 ± 0.018	1.251 ± 0.081	-0.375 ± 0.050	0.403 ± 0.056
9	0.015 ± 0.010	0.074 ± 0.111	-0.013 ± 0.018	-0.077 ± 0.121	-0.089 ± 0.018	-0.072 ± 0.020	-0.035 ± 0.004	-0.023 ± 0.002	-0.034 ± 0.001	-0.018 ± 0.007	-0.232 ± 0.010
10	-2.749 ± 1.759	-2.318 ± 0.931	-0.632 ± 2.088	3.276 ± 1.167	0.415 ± 0.900	-4.355 ± 0.938	3.658 ± 4.145	-0.881 ± 1.398	-1.125 ± 3.900	-7.404 ± 1.609	-2.467 ± 0.634
11	-0.346 ± 0.027	-0.119 ± 0.026	0.792 ± 0.027	2.368 ± 0.023	0.009 ± 0.023	0.042 ± 0.024	5.248 ± 0.996	-3.956 ± 3.968	0.020 ± 0.001	0.000 ± 0.023	-0.029 ± 0.023
12	-0.176 ± 0.029	-0.018 ± 0.038	-0.105 ± 0.028	0.165 ± 0.035	0.024 ± 0.027	0.493 ± 0.027	-0.039 ± 0.029	-0.787 ± 0.824	0.081 ± 0.004	0.173 ± 0.030	0.175 ± 0.037

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CHAPTER 6 – APPENDIX C

Supporting Information

Appendices

Supporting information C.1. – Details on the study area.

Supporting information C.2. –Details on the estimation of breeding parameters.

Supporting information C.3. – Details on the determination of the death of tagged individuals.

Supplementary tables

Table C.1. Metada of tagged individuals used in the current study..

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Supporting information C1.

Study area

The study area is located in the western Iberian Peninsula, corresponding to the administrative region of Cáceres (Extremadura, Spain). The climate is typically Mediterranean semi-arid to dry sub-humid with some oceanic influence with mild winter temperatures and autumn rainfall (Felicísimo, 2001). Trends observed in the last fifty years showed slight aridification of the climate (Figure S2A). Similarly, it has been observed an increase in the mean, maximum annual temperature of 1.2 °C, respecting the values observed in 1973 (Agencia Estatal de Meteorología, 2020; Figure S2B). In the same way, similar patterns were observed in mean winter temperatures and non-winter temperatures with 2.97 °C and 1.4 °C increase, respectively (reference value from the year 1973) (Figures S2C and D). Very low human population density, a markedly rural environment, and scarce industrial activity define the region, which is also recognized as one of the major biodiversity hotspots of the Mediterranean region (López-López et al., 2011). Landscapes are mostly characterized by the so-called "dehesas" (sometimes referred to as the "Spanish savannah"), agrosilvopastoral systems composed by holm oak (Quercus ilex) and corn oak (Quercus suber) forests which were progressively thinned until forming wood-pasture used for animal grazing and foraging plus crop production. Most of the region's land is used for agriculture, combining arable and extensive livestock rearing.

Supporting information C2.

Breeding information

In some cases, it was not possible to confirm neither the breeding status nor the breeding success of tagged birds in the field (n=14 individuals/breeding events/year). We then used the nestR package (Picardi et al., 2020) to identify 1) nest location when this data was not available for a certain individual/year, 2) breeding status and 3) breeding success. The package uses recursive movement patterns to locate breeding attempts and estimate their fate from GPS-tracking data of central place foragers, such as Egyptian Vultures (e.g., Morant et al., 2020; van Overveld et al., 2018). In case the nest location is known but not the breeding output for a given year, we inspected if individuals used the previous year nest/s by using trajectories with known breeding attempts, by using "find_nest" function to find nests among revisited locations. If no prior information exist, we used "find_nests" function, visualize the data to find trusted nests, select nests/non-nests to compare (e.g., to tell apart roosting sites from nests) and find trustful revisitation patterns by using "get_explodata" and "discriminate_nest" functions, respectively. When a potential nest was identified we visually inspected the area, distance to previous year/s nest/s (if any), the number of visits that it received, the days between the first and the last visit and percentage of the day of maximum attendance to confident that the location represents a true nest. Given that species breeding cycle and duration is well known (see Donázar et al., 1994; Morant et al., 2019), we estimated if an attempt was successful or not according to whether it lasted as long as the duration of a complete nesting cycle for the species. We set 153 days (from 1st April to 31th August) and a minimum of 10 visits into function parameters to differentiate the potential nests. The number of days was estimated so that it covered all species breeding cycle (see Morant et al., 2019). In either, when prior existence or previous nests or not, revisitations histories were formatted to infer whether a nesting attempt was completed or not by using "format_attempts" function. To estimate the breeding output we used “estimate_outcomes” function. This function fits a Bayesian hierarchical model to the histories of nest revisitation and estimates the probability that each nest is still active (i.e., "alive") on the last day of the attempt. The model specification includes two processes: the survival process, which is not directly observable, and the observation process, which is the signal we get in the revisitation data. The reproductive outcome is defined as the probability that the value of znest_cycle=1, i.e., the probability that the nest was still surviving after nest_cycle days (more details in Picardi et al., 2020). We used the model with p (detection) since the species attendance decreases as the chick energetic demands grow, thus decreasing during the last month (see Picardi et al., 2020 for details on modelling approach). We visually inspected by plotting the survival and detection probability through time at the population level and daily survival estimated individually for each nest. For instance, a nest whose survival remained constant or abruptly decreased before the last month, noting that the pair has bred but failed during the last breeding stages (i.e., when chick demand is higher). We then assigned 0/1 (i.e., breeding failure or success) for each individual/year/breeding season based on the probability assigned by Markov-Chain-Monte-Carlo algorithm implemented in the nestR package, being 1 the probability of success and 0 of failure. We then summed up each breeding year and successful breeding year for each individual, thus obtaining these two parameters for further analysis.

Supporting information C3.

Death of tagged individuals

We followed three indicators to separate deaths from cases of transmitter failure: (1) stationarity of GPS locations and accelerometry data (when equipped with this sensor type); (2) confirmation or disproof of stationarity by background Doppler data from the E-obs/Ornitrack/Ecotone Systems; and (3) indication of transmitter malfunctioning by low frequencies of GPS-locations preceding signal loss (see details in Rotics et al., 2017 and Sergio et al., 2018). In some individuals, the tags lost signal (e.g., in their African wintering quarters) for long time periods to then started sending data again (e.g., after six months without GPS signalling); we, therefore, set a minimum of six months as time-buffer to be confident that the lack of signal was linked to a plausible death event (see also Rotics et al., 2017).

Using the steps mentioned above we were able to successfully classify 100% of all cases of actual deaths (individuals physically recovered as dead) and 100% of actual transmitter failures (see also Sergio et al., 2019). Additionally, some individuals whose transmitter failed were later resighted during breeding season thanks to the alphanumeric ring and therefore confirmed to be alive (n=2).

Table C1. *Metada of tagged individuals used in the current study. Age is determined by using EURING ageing system (e.g. age 3 is equivalent to a one calendar year bird). Age class¹ and ² show the age of the id when tagged and at the end of the study period, respectively.*

ID	SEX	AGE	AGE CLASS¹	AGE CLASS²	GPS DATA	ACCELERATION DATA	LOCATIONS	START DATE	FINAL DATE	FATE	STATUS	TAG MODEL
ARENAL	F	>7	ADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	2343716	2017-01-29	2021-02-28	ALIVE	RESIDENT	E-obs
ESPIGA	F	9	ADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	1550829	2016-01-31	2021-02-28	ALIVE	RESIDENT	E-obs
FRESNEDOSA	F	5	SUBADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	250125	2015-02-14	2021-02-28	ALIVE	RESIDENT	E-obs
MACEDONIA	F	7	ADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	3042354	2015-12-20	2021-02-28	ALIVE	RESIDENT	E-obs
PANDO	M	7	ADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	3846878	2017-01-29	2021-02-28	ALIVE	RESIDENT	E-obs
PRIMAVERA	F	3	SUBADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	240816	2015-12-20	2021-02-28	ALIVE	RESIDENT	E-obs
TAIGA	M	>7	ADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	2369631	2017-11-12	2021-02-28	DEAD	RESIDENT	E-obs
TORRE	M	>7	ADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	468258	2017-01-31	2017-06-25	ALIVE	RESIDENT	E-obs
VIÑA	F	5	SUBADULT	SUBADULT	5 min	3 sec burst (20hz) / 5 min	772174	2017-12-02	2018-11-02	DEAD	RESIDENT	E-obs
VILLA	F	>7	ADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	2117164	2017-12-02	2021-02-28	ALIVE	RESIDENT	E-obs
JARA	F	>7	ADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	6219	2015-02-14	2015-09-09	DEAD	MIGRANT	E-obs
LLUVIA	F	>7	ADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	302895	2015-12-20	2018-09-09	DEAD	RESIDENT/MIGR	E-obs
NIEBLA	F	>7	ADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	2474508	2015-12-20	2021-02-28	ALIVE	RESIDENT/MIGR	E-obs
TEJO	M	1	JUVENILE	ADULT	5 min	3 sec burst (20hz) / 5 min	1713695	2015-07-21	2021-02-28	ALIVE	MIGRANT	E-obs
TIZON	M	5	SUBADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	35893	2014-09-24	2021-02-28	ALIVE	MIGRANT	E-obs
BERTO	-	1	JUVENILE	JUVENILE	5 min	3 sec burst (20hz) / 5 min	8197	2020-07-13	2020-09-23	DEAD	MIGRANT	Ornitela
CALDILLA	-	1	JUVENILE	JUVENILE	5 min	3 sec burst (20hz) / 5 min	35416	2020-07-11	2021-02-28	ALIVE	MIGRANT	Ornitela
SERRADILLA	M	-	ADULT	ADULT	5 min	3 sec burst (20hz) / 5 min	6533	2020-09-03	2020-09-23	DEAD	MIGRANT	Ornitela
TINOCO	-	3	JUVENILE	SUBADULT	5 min	3 sec burst (20hz) / 5 min	102238	2020-12-23	2021-01-22	ALIVE	RESIDENT	E-obs
BATUECAS	M	-	ADULT	ADULT	10 min	-	75865	2017-07-20	2018-05-01	DEAD	MIGRANT	Ornitela
HUEBRA	M	-	ADULT	ADULT	10 min	-	31450	2017-06-13	2019-05-04	ALIVE	MIGRANT	Ornitela
CAMACES	F	3	JUVENILE	SUBADULT	10 min	-	1225	2017-06-13	2020-08-26	DEAD	MIGRANT	Ornitela
BATUECASP	F	3	JUVENILE	SUBADULT	10 min	-	86755	2017-06-01	2018-04-05	ALIVE	RESIDENT	Ornitela
BRUCO	M	-	SUBADULT	SUBADULT	120 min	-	1505	2019-08-10	2019-09-02	DEAD	MIGRANT	Ecotone
DOURO	M	-	ADULT	ADULT	120 min	-	6543	2017-06-13	2019-05-04	ALIVE	MIGRANT	Ecotone
FAIA	F	-	ADULT	ADULT	120 min	-	11353	2016-07-15	2020-09-16	ALIVE	MIGRANT	Ecotone
POIARES1	F	-	ADULT	ADULT	120 min	-	1387	2017-06-15	2020-09-29	DEAD	MIGRANT	Ecotone
SENDIM	M	3	JUVENILE	SUBADULT	120 min	-	509	2017-06-15	2019-04-16	DEAD	MIGRANT	Ecotone
ARRIBAS	-	3	JUVENILE	SUBADULT	10 min	3 sec burst (20hz) / 5 min	249242	2017-07-31	2017-09-09	ALIVE	MIGRANT	Ornitela
RUPIS	-	7	SUBADULT	SUBADULT	120 min	-	10950	2017-08-01	2021-02-28	ALIVE	MIGRANT	Ecotone
IBERIA	-	3	JUVENILE	JUVENILE	10 min	-	2001	2019-10-31	2019-11-21	DEAD	MIGRANT	Ornitela
FANGUEIRO	-	3	JUVENILE	JUVENILE	10 min	3 sec burst (20hz) / 5 min	201001	2020-07-14	2021-02-28	ALIVE	MIGRANT	Ornitela
AZAHAR	F	-	ADULT	ADULT	120 min	-	14325	2007-08-09	2013-11-09	DEAD	MIGRANT	Microwave
MOLINA	F	-	ADULT	ADULT	120 min	-	6532	2008-08-14	2011-04-13	UNKNOWN	MIGRANT	Microwave
UGE	F	-	JUVENILE	JUVENILE	120 min	-	6900	2009-07-28	2012-04-28	UNKNOWN	MIGRANT	Microwave
ZAGAL	M	-	ADULT	ADULT	120 min	-	9334	2009-07-29	2013-08-26	UNKNOWN	MIGRANT	Microwave
CALIMERA	F	-	ADULT	ADULT	120 min	-	4518	2009-07-30	2011-07-27	UNKNOWN	MIGRANT	Microwave
CALIMERO	M	-	ADULT	ADULT	120 min	-	864	2009-07-30	2012-09-02	UNKNOWN	MIGRANT	Microwave
CIRILA	F	-	ADULT	ADULT	120 min	-	902	2009-07-09	2013-05-17	UNKNOWN	MIGRANT	Microwave

Table C2. *Summary of tagged individuals used in each analysis filled in Blue (see methods section).*

ID	SEX	AGE	AGE CLASS	STATUS	GPS	BREEDING	SURVIVAL	ENERGY EXPENDITURE	FLIGHT EFFICIENCY	ACTIVITY DURATION
ARENAL	F	>7	ADULT	RESIDENT	E-obs	■	■	■	■	■
ESPIGA	F	9	ADULT	RESIDENT	E-obs	■	■	■	■	■
FRESNEDOSA	F	5	SUBADULT	RESIDENT	E-obs	■	■	■	■	■
MACEDONIA	F	7	ADULT	RESIDENT	E-obs	■	■	■	■	■
PANDO	M	7	ADULT	RESIDENT	E-obs	■	■	■	■	■
PRIMAVERA	F	3	SUBADULT	RESIDENT	E-obs	■	■	■	■	■
TAIGA	M	>7	ADULT	RESIDENT	E-obs	■	■	■	■	■
TORRE	M	>7	ADULT	NON MIGR	E-obs	■	■	■	■	■
VIÑA	F	5	SUBADULT	RESIDENT	E-obs	■	■	■	■	■
VILLA	F	>7	ADULT	RESIDENT	E-obs	■	■	■	■	■
JARA	F	>7	ADULT	MIGRANT	E-obs	■	■			
LLUVIA	F	>7	ADULT	RESIDENT/MIGR	E-obs	■	■	■	■	■
NIEBLA	F	>7	ADULT	RESIDENT/MIGR	E-obs	■	■	■	■	■
TEJO	M	1	JUVENILE	MIGRANT	E-obs	■	■	■	■	■
TIZON	M	5	SUBADULT	MIGRANT	E-obs	■	■	■	■	■
BERTO	-	1	JUVENILE	MIGRANT	ORNITELA	■	■	■	■	■
CALDILLA	-	1	JUVENILE	MIGRANT	ORNITELA	■	■	■	■	■
SERRADILLA	M		ADULT	MIGRANT	ORNITELA	■	■	■	■	■
TINOCO	-	3	SUBADULT	RESIDENT	E-obs	■	■	■	■	■
BATUECAS	M	-	ADULT	MIGRANT	ORNITELA	■	■			
HUEBRA	M	-	ADULT	MIGRANT	ORNITELA	■	■			
CAMACES	F	1	JUVENILE	MIGRANT	ORNITELA	■	■			
BATUECASP	F	1	JUVENILE	RESIDENT	ORNITELA	■	■			
BRUCO	M	-	SUBADULT	MIGRANT	ECOTONE	■	■			
DOURO	M	-	ADULT	MIGRANT	ECOTONE	■	■			
FAIA	F	-	ADULT	MIGRANT	ECOTONE	■	■			
POIARES1	F	-	ADULT	MIGRANT	ECOTONE	■	■			
SENDIM	M	1	JUVENILE	MIGRANT	ECOTONE	■	■			
ARRIBAS	-	1	JUVENILE	MIGRANT	ORNITELA	■	■	■	■	■
RUPIS	-	7	SUBADULT	MIGRANT	ECOTONE	■	■			
IBERIA	-	1	JUVENILE	MIGRANT	ORNITELA	■	■			
FANGUEIRO	-	1	JUVENILE	MIGRANT	ORNITELA	■	■	■	■	■
AZAHAR	F	-	ADULT	MIGRANT	MICROWAVE	■	■			
MOLINA	F	-	ADULT	MIGRANT	MICROWAVE	■	■			
UGE	F	-	JUVENILE	MIGRANT	MICROWAVE	■	■			
ZAGAL	M	-	ADULT	MIGRANT	MICROWAVE	■	■			
CALIMERA	F	-	ADULT	MIGRANT	MICROWAVE	■	■			
CALIMERO	M	-	ADULT	MIGRANT	MICROWAVE	■	■			
CIRILA	F	-	ADULT	MIGRANT	MICROWAVE	■	■			

Table C3. *AIC-based model selection of each of the computed analyses. AICc values, AICc differences (ΔAICc) with the highest-ranked model (i.e., the one with the lowest AICc), Akaike weights (AICcw), and variability of the models explained by the predictors (deviance, D^2 for GLMs, and R^2 for random and fixed for GLMMs, respectively) are shown. Selected models are highlighted in bold.*

Hypothesis	Model	k	AIC_c	ΔAIC_c	AIC_{cw}	R^2 fixed	R^2 random
Social correlates	Number of adults	**3**	**127.7**	**0.00**	**0.968**	**48.45 %**	**16.63 %**
	Null	2	134.5	6.85	0.032		
Hypothesis	**Model**	**k**	**AIC_c**	**ΔAIC_c**	**AIC_{cw}**	**D^2**	
Breeding years	**Migratory behaviour + Tracking years**	**3**	**95.7**	**0.00**	**0.831**	**51.03 %**	
	Tracking years	2	98.9	3.18	0.169		
	Migratory behaviour	2	111.1	15.37	0.000		
Successful breeding years	**Migratory behaviour + Tracking years**	**3**	**86.2**	**0.00**	**0.574**	**45.81 %**	
	Tracking years	**2**	**86.8**	**0.61**	**0.424**	**38.45 %**	
	Migratory behaviour	2	97.7	11.51	0.002		
Survival	**Migratory behaviour * Age class**	3	69.7	**0.00**	**0.521**	**99.16 %**	
	Age class	2	69.9	**0.20**	**0.475**	**79.53 %**	
	Migratory behaviour	2	78.5	8.73	0.006		
	Null	1	81.7	11.98	0.001		
Hypothesis	**Model**	**k**	**AIC_c**	**ΔAIC_c**	**AIC_{cw}**	**R^2 fixed**	**R^2 random**
Energy expenditure	**Migratory behaviour *Flight type + Migratory behaviour *Season**	**5**	**116168.9**	**0.00**	**0.995**	**40.09 %**	**3.22 %**
	Migratory behaviour + Flight type + Migratory behaviour *Season	5	116209.2	40.31	0.005		
	Migratory behaviour + Season + Migratory behaviour *Flight type	5	116404.0	235.15	0.000		
	Null	3	134017.7	17848.82	0.000		
Flight efficiency	**Cumulative daily distance*Migratory behaviour + Cumulative daily distance*Season + Migratory behaviour *Season**	**5**	**25100.5**	**0.00**	**0.999**	**7.71 %**	**23.54 %**
	Cumulative daily distance*Migratory behaviour + Migratory behaviour *Season	5	25131.8	31.30	0.001		
	Cumulative daily distance + Migratory behaviour *Season	4	25240.7	140.17	0.000		
	Null	2	25865.3	764.77	0.000		
Acitivity duration	**Day length*Migratory behaviour*Season**	**5**	**72846.6**	**0.00**	**0.999**	**21.51 %**	**32.28 %**
	Day length*Migratory behaviour+ Day length*Season+ Migratory behaviour*Season	5	72888.4	41.80	0.001		
	Day length*Migratory behaviour+ Day length*Season	5	72889.1	42.54	0.000		
	Day length*Season+ Migratory behaviour*Season	5	72961.5	114.94	0.000		

Table C4. *Home range areas (km²) based on the monthly 95% Kernell Density Estimation of migrant (n=13) and non-migrant (n=14) tagged birds between non-winter (March-October) and winter (November-February). Average values are provided together with SE.*

	Non-winter	Winter
Migrant	1251 ± 2418	4101 ± 3031
Resident	1417 ± 2349	211 ± 564

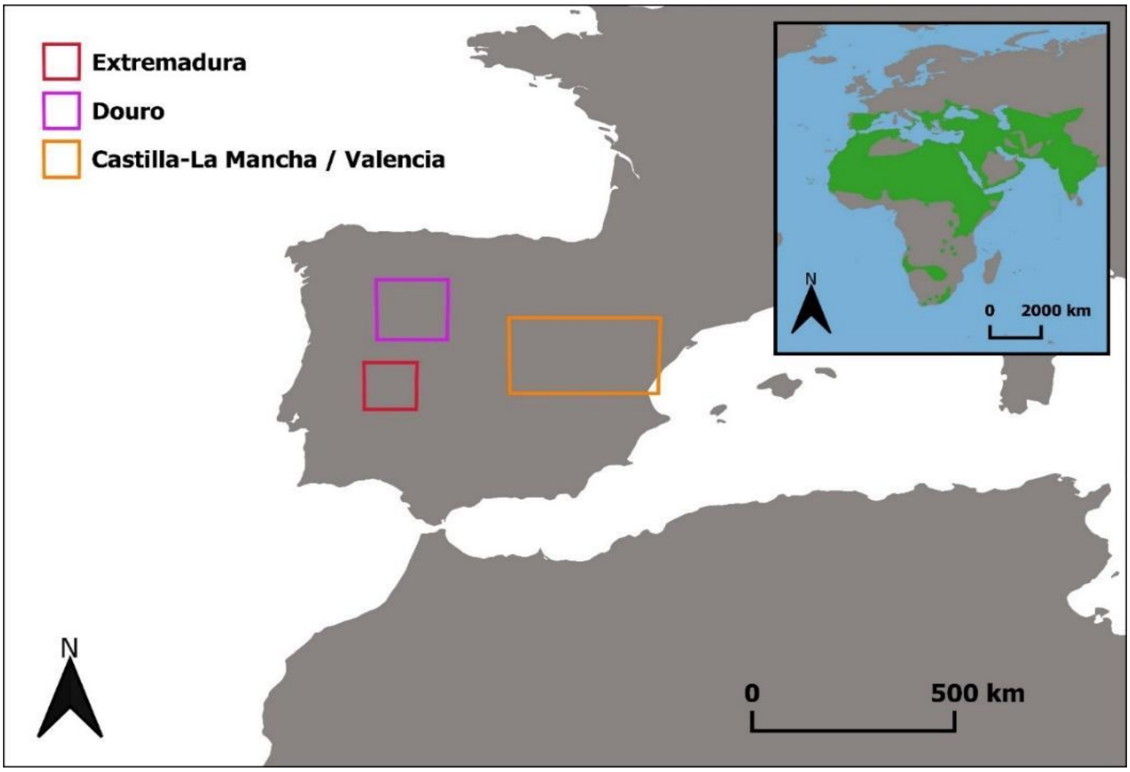

Figure C1. *Worldwide distribution of the Egyptian Vulture (Upper right) and the location of the populations from which birds were tagged, including, Extremadura (red), Duero/Douro (pink) and Castilla-La Mancha/ Valencia (yellow).*

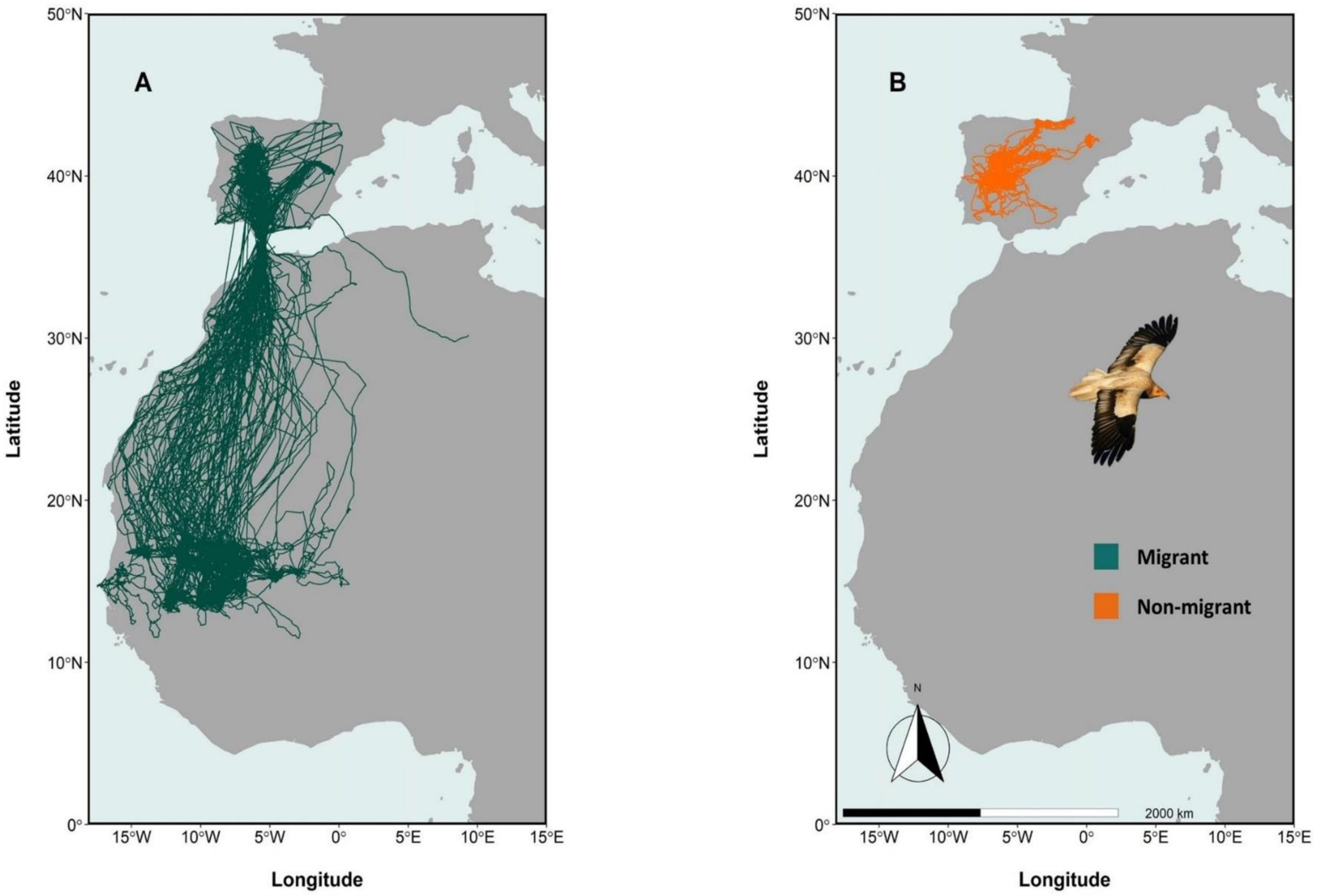

Figure C2. *Movement tracks of the tagged (A) migrant (n=25) and (B) resident birds (n=14) between 2009 and 2021.*

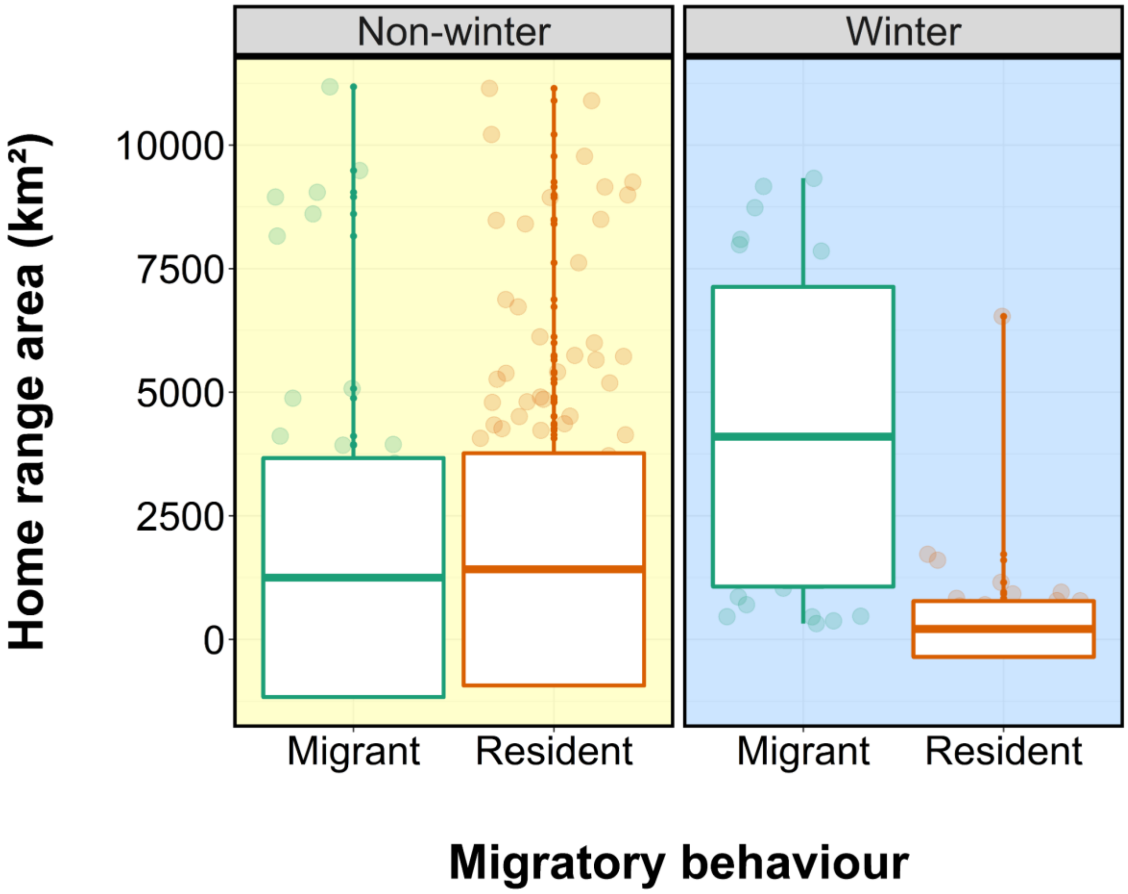

Figure C3. *Differences in the home range area (km²) based on the monthly 95% Kernell Density Estimate of migrant (n=13)* and resident (n=14) individuals during non-winter and wintering seasons. Estimates were calculated by using "rhrKDE" and "rhrArea" functions implemented in the "rhr" package (Signer and Bakenhol, 2015). The horizontal line in the box plot represents the mean, whilst the standard deviation is shown as error bars.*

**Note that only individuals tagged with E-obs and Ornitela are used for this analysis due to the timeframe differences in location recordings of Ecotone and Microwave tags.*

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Human activities transformed virtually all landscapes worldwide to fulfil their basic needs (e.g., resource extraction, agriculture or leisure activities). By doing so, they also affect species inhabiting these human-dominated landscapes. Due to their historical link to human activities, apex predators, especially vultures, are especially vulnerable to human-induced behavioural alterations and have undergone population declines worldwide. Therefore, finding a solution that reconciles vulture conservation and human activities in such landscapes is necessary. By using a set of behavioural indicators (e.g., breeding, occupancy/detectability and space use) from long-term monitoring and movement ecology, this thesis aims to build links between behaviour and conservation of Egyptian vulture Neophron percnopterus in human-dominated landscapes. The current dissertation shows that the species invests similar effort in parental care and that incubation and hatching are important tipping points during the breeding season (Chapter 1). This information could be, in turn, used to design cost-effective monitoring while accounting for imperfect detection and breeding phenology and other environmental variables that could help to adapt monitoring programs to different available budgets (Chapter 2). Similarly, the knowledge of breeding behaviour of the species could be used to infer the impact of habitat alterations on species nest occupancy and reproduction patterns and to improve conservation programs (Chapter 3), and test whether management programs and collaboration networks resulted effective in reducing the synergistic effect of various human disturbances (Chapter 4). Finally, it poses an advance in the understanding of how certain human activities that provide continuous and predictable food pulses, such as farming, could alter species space use and favour residency in partial migratory species (Chapter 5), and that human-driven changes in migratory behaviour could even have consequences on fitness and energy use of different migratory phenotypes (Chapter 6). Overall, this work demonstrates the utility of increasing vulture behaviour knowledge to ascertain the effects of human activities on the species and find coherent conservation solutions that favour its persistence and promote vulture-human coexistence in anthropogenic landscapes.

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