From Local to Regional: Demographic and Population Dynamics of a Long-lived Scavenger Species in a Changing Environment

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Doctoral Thesis 2024

Universitat de Barcelona

Cover, illustration and back cover designs: Deborah Joyce

Photographs: Arnau Soler Costa

Universitat de Barcelona

Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals

Programa de Doctorat en Biodiversitat

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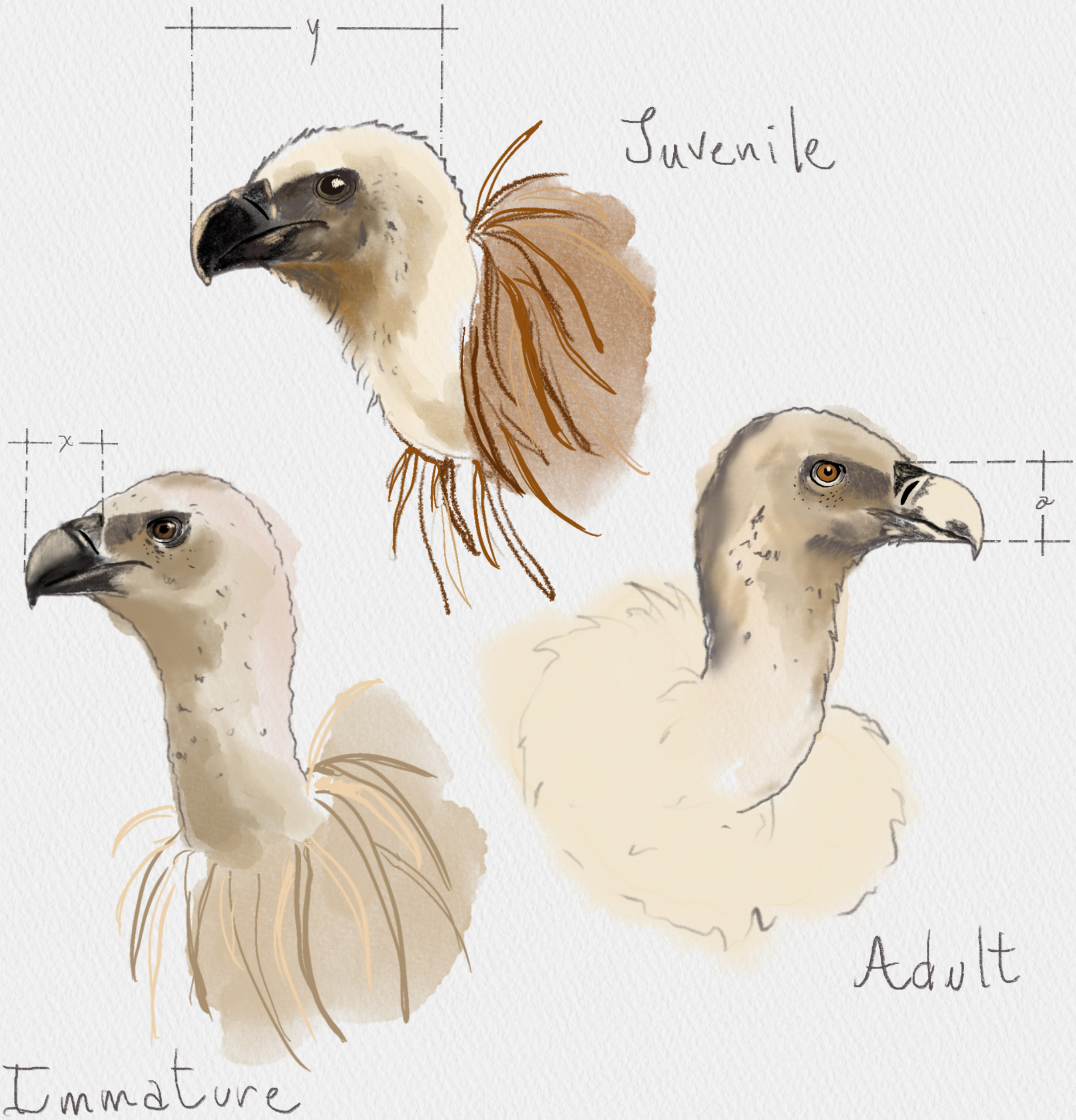
Memoria presentada por Diego José Arévalo-Ayala para optar al grado de Doctor por la Universitat de Barcelona

Barcelona 25 de septiembre de 2024

Diego José Arévalo-Ayala
El doctorando

Visto bueno de los directores y tutor de la tesis:

Dr. Antonio Hernández Matías	**Dr. Joan Real Ortí**
Codirector y tutor de la tesis	Codirector de la tesis


y
Juvenile
x
a
Adult
Immature

Quién elige el camino del corazón, no se equivoca nunca.

Popol Vuh

ACKNOWLEDGEMENTS (AGRADECIMIENTOS)

No ha sido fácil llegar al momento de escribir estas palabras. Estos cuatro años de tesis han sido de tantos altibajos que a veces fue muy duro sobrellevarlo. En este trayecto incluyo mi complicado proceso migratorio, la inestabilidad laboral y la creciente añoranza por mi tierra natal, mi familia y amigos/as que están tan lejos, que han hecho que la tesis repicara más de lo que hubiera querido. Sin embargo, también estoy lleno de agradecimiento por el crecimiento personal y profesional que la tesis me ha dejado, el maravilloso nacimiento de mi hijo, esta tierra catalana que ahora llamo hogar, y por todas las personas cercanas con quienes he conectado y que ahora considero mi familia elegida. A mi esposa, familia, amigos y amigas: ¡gracias por estar y apoyarme de alguna manera en todo este recorrido!

Mis primeros agradecimientos van a quienes más se lo merecen: mi hijo, Tawil y mi compañera de vida, Elisabeth. Hijo mío, tu nacimiento ha sido mi más grande motivación para llegar hasta este punto: no perderme más momentos sin estar a tu lado y poder verte crecer con presencia plena. Gracias, porque sin pedírtelo, me has enseñado a relativizar la tesis y otros procesos, poniéndolas en el lugar que corresponden y priorizando lo más importante: vos, tu mamá y yo. Eli, mi amor, mi compañera, las palabras se quedan cortas para agradecerte TODO el esfuerzo que has invertido en sostener esta tesis conmigo. Vos te mereces también este título por haber estado aquí a mi lado, apoyándome con mucha paciencia, pero sobre todo por escucharme en los momentos más difíciles y por celebrar mis éxitos personales y profesionales. El meu amor infinit per a tu, sempre.

En segundo lugar, quiero agradecer a mis directores, Toni y Joan, quienes me han introducido al apasionante mundo de la investigación y enseñarme los retos que conlleva dedicarse a la ciencia y conservación. Gracias, Joan, por creer en mí y en mis capacidades. Mi primer trabajo en la ciencia en este país fue gracias a los que desarrollamos con el búho real. Fueron unos aprendizajes tremendos, sobre todo a nivel profesional. Gracias por compartir tus conocimientos en el monitoreo de especies, la biodiversidad mediterránea, la gestión y comunicación con la Administración, y tu dedicación por la conservación. A Toni, quien ha sido un pilar fundamental en el desarrollo de esta tesis, te agradezco la confianza y calidez que me has brindado, así como tus amplios conocimientos en análisis demográfico. Las discusiones enriquecedoras que hemos tenido sobre estos análisis no solo han permitido que esta tesis se concretara, sino que también me han proporcionado grandes aprendizajes. Os agradezco a ambos por vuestra paciencia y respeto que me habéis dado y la dedicación que habéis puesto en este trabajo, que también es vuestro.

Una mención muy especial a mis compis, Catu y Jaume. Ha sido una enorme suerte encontrarnos aquí y poder apoyarnos en los momentos más difíciles y celebrar los buenos. Gracias por seguir estando. A Kiku Parés, gracias por todo el aprendizaje técnico en cuanto a monitoreo y extracción de muestras biológicas de búhos, pero también por tu calidad como persona. A Nico, que hemos coincidido con mi final y tu inicio de doctorado, muchas gracias y suerte en tu camino con los buitres. También quiero agradecer a todas las demás personas que me han dado en algún momento su apoyo moral, en especial a Andreia Dias, Jaume Ramot, Albert Compaña y a todos los agentes del Grup de Suport de Muntanya dels Agents Rurals con quienes compartí tantas jornadas de campo y muchas risas.

En este bloque quiero agradecer a todas esas personas que han apoyado en la realización de esta tesis de una manera u otra, tanto con la concesión de información, trabajo de campo y apoyo en los análisis de algunos capítulos. Estoy profundamente agradecido con todos los naturalistas del Grup d’Anellament de Calldetenes-Osona (GACO) que han llevado a cabo durante tantos años el marcaje de buitres en el vertedero de Orís, el cual ha sido información crucial para realizar los tres capítulos

de esta tesis. A Jordi Baucells del Institut Català d'Ornitologia (ICO) por proporcionar la base de datos de buitres anillados y de recuperaciones en Cataluña. También quiero expresar mi gratitud a Anna Riera del Consorci per a la Gestió dels Residus Urbans d'Osona, a Mar Segret del Consell Comarcal d'Osona y Verònica Tomàs de Ferrovial por proporcionar datos sobre residuos del vertedero de Orís. Un enorme agradecimiento a Sara del Centre de Recuperació de Fauna Forn del Vidre en Castellón (Comunidad Valenciana), Juan Jiménez de la Generalitat Valenciana; Manuel Alcántara, Francisco Hernández y José María Martínez del Servicio de Biodiversidad del Gobierno de Aragón; y Diego García, Joan Mestre, Rafael Molina, Joan Mayné de la Generalitat de Catalunya (GenCat) por proporcionar información crucial sobre parámetros reproductivos, censos de parejas reproductoras y buitres marcados y avistados en cada una de las tres comunidades autónomas, además de proveer datos de las causas de ingreso de buitres a centros de recuperación. A Helena Tauler del Servei de Fauna i Flora de la (GenCat) por proporcionar datos de muladares en Catalunya. A Typhaine Rousteau y Charlotte Lorand por amablemente compartir sus estimas de pérdida de anilla plástica de buitre negro *Aegypius monachus* y buitre leonado *Gyps fulvus*, respectivamente. También, me siento en deuda con personas con quienes he intercambiado correos y mensajes en foros que me han ayudado a desarrollar la modelización de cada capítulo de esta tesis, en especial a Gary White, Jim Hines y Rebecca Boys por su orientación y asesoramiento en la modelización de captura-recaptura y a Michael Schaub, José Jiménez García y Thomas Riecke por su asistencia en clarificar dudas relacionadas a modelos integrados poblacionales. Finalmente, un enorme agradecimiento a todos los ornitólogos, observadores de aves, investigadores, redes de voluntarios y programas de anillamiento que han contribuido con sus observaciones a las bases de datos de captura-recaptura a lo largo de los años dentro y fuera de España.

Más a nivel personal, quiero expresar mi mayor agradecimiento a mi familia catalana, Eli y Antonio, quienes también me han mostrado un

enorme apoyo para que pudiera terminar esta tesis. Todos esos días de cuidar y acompañar a Tawil o de hacer algún recado por nosotros para que pudiera dedicarle todo el tiempo posible a la tesis. Os lo agradezco infinitamente de todo corazón. A mi madre y mi padre, Ana Silvia y Miguel Francisco, mis hermanos Foncho y Paco, mi cuñada Claudia y mis dos sobrinos, Inti y Citlali, tan lejos físicamente, pero siempre en mi corazón. A mis tíos, tías, primos y primas, que son tantos por mencionar, pero que sé están muy pendientes de mí y mi familia. Llevo también en mi corazón a mis abuelas, mama Tila y mama Carmen, y a mis abuelos papa Chepe y papa Cande, que en paz descansen. Gracias a todos/as porque de cierta manera, me han impulsado a llegar hasta este logro académico. Esta tesis se las dedico a ustedes también.

Finalmente, quiero agradecer a todas aquellas personas que tengo el privilegio de llamar amigos/as, sea de este lado del mundo como del otro. A mis hermanos/as danzantes, que los llevo en mi mente y corazón. A mis amigos/as y colegas que en su momento tuve que decirles adiós, pero que aún seguimos conectados: a Arnoldo, Manuel, Guille, Caro, Pecci, Xiomara, Chi Min, Choco (Kawahé), y demás. A mis amigos/as catalanes, salvadoreños y de otros orígenes, con quienes me he sentido siempre apoyado y cuidado en este país, en especial a Sergi, Marina, Joan, Mireia, Edu (desde el otro lado del río), Fiorella, Jonas, Marta (y el peque Aya), Didac, Judith, Héctor, Miriam, Manu, Noe, y la familia extensa de acroyoga. A Tunantal (nuestra madre tierra), que donde quiera que esté, me sustenta.

Gracias de todo corazón.

ABSTRACT

In a rapidly changing world, the loss of global biodiversity presents a significant challenge. While sustainability has become a guiding principle for balancing the protection of the environment along with economic development and human well-being, its implementation can often be disjointed across various sectors. The incoherence in the integration of environmental policies can lead to unintended negative impacts on biodiversity, particularly for vulnerable species like vultures and the environmental services they provide. Vultures, as a highly threatened group of birds, are especially vulnerable to poisoning, but also to new circular economy and renewable energy policies such as the closure of landfills and wind energy. Thus, it is imperative to evaluate the mechanisms and demographic responses of vulture species to these new paradigms. My thesis examines the demography of the griffon vulture *Gyps fulvus* in northeast Iberian Peninsula, using long-term data to provide a comprehensive understanding of the population dynamics in response to a changing environment. In Chapter 1, we studied how the local griffon vulture population in Central Catalonia responded to reduced organic matter in an open landfill due to European sanitary measures aimed at closing landfills. Using the robust Schwarz and Arnason Jolly-Seber model, we estimated the vultures' apparent survival probability and annual abundance. We found that the available organic matter in the landfill significantly declined after a waste treatment centre was established, negatively impacting apparent survival. However, local abundance remained stable, with an increase attributed to the growth of the Catalonian breeding population. This suggests that local waste management measures had limited impact on vultures, as their high dispersal capacity allows them to find alternative food sources. In Chapter 2, we used a Bayesian hierarchical Cormack-Jolly-Seber model to analyze the age-specific demographic response of the local vulture population at the landfill, estimating apparent survival and permanent emigration probabilities under three scenarios of organic matter availability: no reduction, substantial decrease, and drastic decrease. We found a notable increase in transients among newly captured immatures and adults. Apparent survival in juveniles declined, while in immature residents increased and adult residents decreased. The results suggested that intensified intraspecific competition due to reduced food increased permanent emigration. However, resident immatures showed resilience, indicating that high-quality individuals persisted despite food scarcity. In Chapter 3, we used a multi-site Integrated Population Model (ms-IPM) to examine the dynamics of griffon vulture populations in Catalonia, Aragon, and the Valencian Community. We aimed to understand demographic processes and inform site-specific conservation strategies. We observed different trends: steady growth in Catalonia, stabilization in the Valencian Community after an initial increase, and a decline with a slight recovery in Aragon. Key growth factors varied by region: adult survival in Aragon, floater-to-breeder ratio and immigration in the Valencian Community, and all three factors in Catalonia. Density dependence affected the floater-to-breeder ratio and immigration in Catalonia and the Valencian Community, with higher emigration to the other two sites in the vultures of Valencian Community, likely due to nearing carrying capacity. Populations in Aragon and the Valencian Community are stable, while Catalonia is growing. Maintaining adult survival in Aragon is crucial, given its lower rate and potential non-natural mortality sources. This study highlights the value of ms-IPMs for understanding complex population dynamics and the need for targeted conservation strategies. In conclusion, by applying demographic models, including the ms-IPM, and addressing data heterogeneity and uncertainty, in this thesis we gained a deeper understanding of griffon vulture population dynamics. This approach helped identify key demographic drivers, identify possible environmental impacts, and inform conservation strategies, highlighting the need for cohesive policies across regions to effectively conserve vulnerable species like vultures.

RESUMEN

En un mundo en constante cambio, la pérdida de biodiversidad global supone un gran desafío para la humanidad. Aunque la sostenibilidad busca equilibrar la protección ambiental con el desarrollo económico y el bienestar humano, su implementación a menudo es incoherente entre sectores. Esto puede generar impactos negativos sobre la biodiversidad, especialmente en especies vulnerables como los buitres y los servicios ambientales que brindan. Los buitres, un grupo de aves altamente amenazado, son particularmente vulnerables al envenenamiento y a nuevas políticas de economía circular y energías renovables, como el cierre de vertederos y la energía eólica. Por lo tanto, es crucial evaluar cómo estas especies responden demográficamente a estos nuevos paradigmas. Mi tesis investiga la demografía del buitre leonado (*Gyps fulvus*) en el noreste de la Península Ibérica, utilizando datos a largo plazo para comprender la dinámica poblacional en un entorno cambiante. En el Capítulo 1, se analizó cómo la población de buitres en la Cataluña Central respondió a la reducción de materia orgánica en un vertedero, debido a medidas europeas destinadas a su cierre. A través del modelo Schwarz y Arnason Jolly-Seber, estimamos la probabilidad de supervivencia aparente y la abundancia anual. Encontramos que la disponibilidad de materia orgánica disminuyó significativamente tras la apertura de un centro de tratamiento de residuos, lo que afectó negativamente la supervivencia aparente. Sin embargo, la abundancia local permaneció estable, gracias al crecimiento de la población reproductora en Cataluña. Esto sugiere que la capacidad de dispersión de los buitres les permitió encontrar otras fuentes de alimento, mitigando el impacto de las medidas locales de gestión de residuos. En el Capítulo 2, utilizamos un modelo jerárquico bayesiano Cormack-Jolly-Seber para analizar la respuesta demográfica por edad bajo tres escenarios de disponibilidad de materia orgánica: sin reducción, disminución sustancial y disminución drástica.

Encontramos un aumento de individuos transeúntes entre los inmaduros y adultos recién capturados. La supervivencia aparente en juveniles disminuyó, mientras que en inmaduros residentes aumentó y en adultos residentes disminuyó. Estos resultados sugieren que la competencia por alimento impulsó la emigración permanente. Curiosamente, los inmaduros residentes mostraron una tendencia opuesta, sugiriendo la persistencia de individuos de alta calidad a pesar de la escasez de alimento. En el Capítulo 3, utilizamos un Modelo Integrado de Población de múltiples sitios (ms-IPM) para estudiar las dinámicas de buitres leonados en Cataluña, Aragón y la Comunidad Valenciana, con el fin de desarrollar estrategias de conservación específicas para cada región. Observamos diferentes tendencias: crecimiento en Cataluña, estabilización en la Comunidad Valenciana tras un incremento inicial y un declive con ligera recuperación en Aragón. Los factores de crecimiento variaron: la supervivencia adulta fue clave en Aragón, mientras que en la Comunidad Valenciana lo fue la relación entre individuos flotantes y reproductores, además de la inmigración. En Cataluña, los tres factores fueron importantes. La dependencia de la densidad afectó la relación flotante-reproductor y la inmigración en Cataluña y la Comunidad Valenciana, con mayor emigración desde la Comunidad Valenciana hacia las otras dos regiones, probablemente por proximidad a su capacidad de carga. Las poblaciones en Aragón y la Comunidad Valenciana están estables, mientras que Cataluña está en crecimiento. Mantener la supervivencia adulta en Aragón es fundamental, debido a su baja tasa y las posibles fuentes de mortalidad no natural. Este estudio subraya el valor de los ms-IPM para entender las dinámicas poblacionales complejas y la necesidad de estrategias de conservación global adaptadas a cada región. En conclusión, la aplicación de modelos demográficos ha permitido identificar los factores clave que impulsan la dinámica poblacional del buitre leonado, ofreciendo información para diseñar estrategias de conservación y destacando la importancia de políticas coherentes entre regiones para proteger a estas especies vulnerables.

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GENERAL INTRODUCTION

Photography courtesy of Arnau Soler Costa

DEMOGRAPHY OF LONG-LIVED SPECIES IN THE ERA OF SUSTAINABLE DEVELOPMENT

In this rapidly changing world, the ongoing loss of global biodiversity poses a profound challenge, emphasizing the critical need for sustainability (Rockström et al., 2009; Steffen et al., 2015). This guiding principle seeks to balance environmental protection with economic development and human well-being, recognizing that biodiversity conservation is essential for both ecological stability and human prosperity (Niesenbaum 2019). In this sense, understanding the demography and population dynamics of long-lived species is not only vital for advancing ecological research but also plays a crucial role in global conservation strategies to maintain biodiversity and ecosystem services they provide (Lande 1988, Paniw et al. 2023).

Long-lived species, defined by traits such as extended life cycles, delayed maturity, and low reproductive rates, are particularly susceptible to environmental changes. The population dynamics of these species are particularly vulnerable to fluctuations in vital rates, mainly survival, which is a key driver for their population stability (Sæther and Bakke 2000, Caswell 2001, Paniw et al. 2023). Even slight variations in these parameters can have significant consequences for their population dynamics, particularly in an era where anthropogenic pressures are intensifying (Selwood et al. 2015). Consequently, ensuring their conservation is not only vital for maintaining biodiversity and their ecosystem services, but also for achieving broader sustainability goals.

Sustainable development, as outlined in the United Nations' 2030 Agenda for Sustainable Development, seeks to ensure that current developmental needs are met without compromising the ability of future generations to meet their own needs (United Nations, 2015). Among its 17 Sustainable Development Goals (SDGs), several directly and indirectly influence biodiversity conservation, such as SDG 15, which focuses on "Life on Land," aiming to protect, restore, and promote the sustainable use of terrestrial ecosystems.

Progress toward sustainable development has been notable in several areas, including poverty reduction, improved access to clean water, and the expansion of renewable energy (e.g., Rao and Pachauri 2017). However, the pursuit of these goals can sometimes lead to unintended consequences. For instance, while the global shift towards renewable energy is a crucial step towards mitigating climate change (SDG 7 and 13), it can also present unintended consequences for biodiversity (Rehbein et al. 2020). While reducing carbon emissions is imperative, the proliferation of renewable energy infrastructure, such as wind farms, can inadvertently impact wildlife. Wind turbines have been linked to increased mortality in certain bird species, particularly soaring birds like vultures, due to collisions (Carrete et al. 2012, De Lucas et al. 2012, Santangeli et al. 2016). This highlights a potential conflict between the goals of renewable energy expansion and biodiversity conservation (Allison et al., 2014). Similarly, while the enforcement of sanitary regulations is essential for public health and environmental safety, it can have unintended negative effects on the demography of certain species. Specifically, the reduction of organic matter or the closure of landfills—key food sources for species accustomed to feeding in these environments—can significantly impact their survival and dispersal (Delgado et al. 2021, 2023, Arévalo-Ayala et al., 2023a, 2023b). Although the closure of landfills is important to prevent species from ingesting toxins and other harmful substances, these sites also provide an artificial and abundant food source (Plaza and Lambertucci 2017). While this might appear positive for superabundant species that exploit these resources, it is particularly concerning for vulnerable and endangered species, as food availability is a crucial factor that influences their population dynamics (see the *Food availability as a regulatory factor of demographic and population dynamics* section below).

These examples underscore the need for a nuanced approach to sustainability—one that balances human development with the preservation of biodiversity. As we work towards the 2030 Agenda, understanding the interplay between species demography, environmental pressures, and sustainable development goals will be key to formulating conservation strategies that support both ecological and human well-being.

CONSERVATION CHALLENGES FACED BY SCAVENGERS: VULTURES IN A CHANGING WORLD

Vultures are keystone scavengers for ecosystem balance, as they efficiently dispose of large quantities of decomposing organic matter (Whelan et al. 2008), therefore providing essential services to ecosystems and human well-being (Moleón et al. 2014). In some ecosystems, vultures consume very large percentages of carrion of up to 90% of carcasses (Houston 1986). Their role supports the preservation of healthy soil microbial communities (Ganz et al. 2012), regulate food chains (Kane and Kendall 2017), reduce greenhouse gas emissions (Morales-Reyes et al. 2015), and other services such as cultural inspiration and recreational value (Moleón et al. 2014). An important service for human health is preventing the spread of pathogens that could otherwise lead to disease outbreaks among humans and other animals (Houston and Cooper 1975, Berlinguer et al. 2021). For example, the loss of vultures in India due to the population collapse caused by indirect poisoning for consuming cattle carcasses treated with diclofenac at the beginning of the 21st century (Green et al. 2004), led to approximately 100,000 additional human deaths annually due to the spread of disease and bacteria that vultures would have otherwise removed from the environment (Frank and Sudarshan 2024).

Over the past few decades, the number of threats afflicting vulture populations has increased dramatically as a result of rapid environmental changes driven by human activities (Buechley and Şekercioğlu 2016, Santangeli et al. 2019). Vultures, as obligate scavengers, are the most threatened group of bird species, with a staggering 87% of the species listed as ‘Threatened’ or ‘Near Threatened’ according to the IUCN Red List (Botha et al. 2017, Margalida and Ogada, 2018; Safford et al. 2019). Several of these species’ populations are declining (particularly in Africa and Asia), and primarily as a result of indirect intoxications by veterinary drugs, intended and unintended poisoning, landscape transformation and the application of sanitary policies (Ogada et al. 2012, 2016, Margalida and Ogada, 2018). Among the 15 vulture species in the Old World, seven are now classified as "Critically Endangered" (white-rumped vulture *Gyps bengalensis,* Rüppell's vulture *Gyps rueppelli,* long-billed vulture *Gyps indicus,* slender-billed vulture *Gyps tenuirostris,* white-backed vulture *Gyps africanus,* hooded vulture *Necrosyrtes monachus,* red-headed vulture *Sarcogyps calvus*) globally, with three listed as "Endangered" (Egyptian vulture *Neophron percnopterus*, lappet-faced vulture *Torgos tracheliotos,* and white-headed vulture *Trigonoceps occipitalis*), and one “Vulnerable” (Cape vulture *Gyps coprotheres*). The only species considered as “Least Concern” for the IUCN is the griffon vulture *Gyps fulvus* (BirdLife International 2021), and three as "Near Threatened" (Bearded vulture *Gypaetus barbatus*, cinereous vulture *Aegypius monachus,* Himalayan vulture *Gyps himalayensis*).

In Asia, indirect poisoning from veterinary drugs like diclofenac has had devastating effects on *Gyps* species populations (Green et al. 2004). This nonsteroidal anti-inflammatory drug (NSAID), used in livestock, is lethal to vultures that consume the carcasses of cattle treated with it (Shultz et al. 2004). The widespread use of diclofenac in India led to the collapse of vulture populations in the 1990s and 2000s, reducing their numbers by more than 95% in some species (Green et al. 2004). Nowadays, despite the ban of diclofenac in some parts of Asia, its use remains authorized in other regions, including Spain, where it was approved for use in livestock in 2013 (Margalida et al. 2021, Cook et al. 2024). This is particularly concerning given that Spain is home to more than 90% of European vulture’s populations and there have already been cases of vultures being poisoned by this drug and another NSAID (Flunixin) in the country, highlighting the ongoing threat it poses to these avian scavenger species (Zorrilla et al. 2015, Herrero-Villar et al. 2020, 2021, Moreno-Opo et al. 2021).

Furthermore, illegal poisoning in the context of poaching and predator control, has led to an average decline of 62% in vulture populations in Africa (Ogada et al. 2016, 2022, Shaw et al. 2024). These poisonings are often aimed at large carnivores (e.g., lions and hyenas) and lead to mass vulture deaths from eating the poisoned carcasses (Ogada et al. 2015, Santangeli et al. 2017). In Africa, this problem has been exacerbated by the increasing practice of sentinel poisoning of large game animals. This is done to kill any scavenging vultures that could potentially alert conservation authorities to the poachers' illegal activities (Ogada et al. 2015, 2016). Moreover, in Europe, vultures also suffer high rates of direct and indirect illegal poisonings from human-wildlife conflicts, as well as exposure to lead, pesticides and other toxins (Margalida et al. 2008, Margalido 2012, Ogada 2014, Carneiro et al. 2015, Plaza et al. 2019). This exposure to toxins at sublethal levels might make vultures more susceptible to other causes of death, such as collisions with infrastructure like wind turbines and power lines (Espín et al. 2014, Carneiro et al. 2015).

Windfarms, power lines, and vehicles pose significant risks, and electrocution from power lines is a frequent cause of mortality (Santangeli et al. 2019, García-Alfonso et al. 2021). Vultures’ large wingspans and soaring flight patterns make them highly vulnerable to collisions with these structures, which are a common cause of injury and death (Sanz-Aguilar et al. 2015). As the demand for renewable energy and infrastructure development continues to grow, the threat to vulture populations from these hazards is likely to increase, potentially exacerbating the conservation challenges faced by these species in the future (Carrete et al. 2009, 2012).

In addition, vultures are particularly vulnerable to sanitary and sustainability measures, such as those under the circular economy model, that affects the availability of food sources and ultimately population dynamics. For example, European Regulation EC 1774/2002, implemented in response to the appearance of Bovine Spongiform Encephalopathy (BSE) in the late 1990s ('mad cow disease'), prohibited leaving livestock carcasses in the field (Margalida et al. 2010, Margalida and Colomer 2012). Although later regulations were enacted to maintain authorized supplementary feeding sites and the implementation of Protected Areas for Feeding of Scavengers to assist the conservation of scavengers, the initial loss in food supplies forced vultures to exploit other resources such as landfills, but also provoked negative effects on local demographic and population dynamics (Almaraz et al. 2022). Additionally, recent European directives aimed at closing landfills (Directive 2008/98/EC and Directive (EU) 183 2018/850) as part of circular economy model is becoming a new threat for vulture populations and other obligate and facultative scavenger species, as some populations relies heavily on these food sources (Delgado et al. 2021, 2023, Arrondo et al. 2023, Arévalo-Ayala et al. 2023a, 2023b). Although landfills provide a consistent food source for several species, including vultures, the quality of this food is often compromised by pollution and contamination (Plaza and Lambertucci 2017, Tauller-Ametller et al. 2019). Feeding at landfills carries significant risks, such as the ingestion of hazardous materials like plastics, rubber, glass, and metals, as well as exposure to pathogens, toxics and rodenticides (Matejczyk et al. 2011, de la Casa-Resino et al. 2014, Ortiz-Santaliestra et al. 2019, Oliva-Vidal et al. 2022b). However, for long-lived scavengers like vultures, the benefits of accessing such a reliable food supply, often of low-quality, may outweigh these risks (Garrido et al. 2002, Fernandez-Gómez et al. 2022, Arrondo et al. 2023, Tauller-Ametller et al. 2017, 2018, Cerecedo-Iglesias et al. 2023). In fact, landfill-sourced food can constitute up to 50% of the diet for some rare and endangered vulture species, despite its associated dangers (Tauller-Ametller et al. 2018, 2019, Ortiz-Santaliestra et al. 2019). Overall, the recent and imminent closure of landfills presents a new conservation challenge, making it crucial to analyse the demographic responses of species that rely on these facilities. Understanding how these species adapt to the loss of such a significant food source is essential for implementing effective conservation measures.

FOOD AVAILABILITY AS A REGULATORY MECHANISM OF DEMOGRAPHIC AND POPULATION DYNAMICS

Food availability is a fundamental determinant that influences demographic parameters, which ultimately drive population dynamics on vertebrate species (Oro et al. 2004). In general, research suggest that animals exhibit improved survival and reproduction outcome when food is abundant (McNamara and Houston 1987, Krebs et al. 1995, Prevedello et al. 2013, Oro et al. 2014). Conversely, when food availability is reduced, can lead to increased mortality rates, higher emigration (dispersal) rates, and lower survival, and more particularly among younger individuals who are less capable of competing for diminished resources against older conspecifics (McNamara and Houston 1987, Krebs et al. 1995, Tavecchia et al. 2007, Payo-Payo et al. 2015, Briga et al. 2017). However, the abundance of food can also interact with other ecological factors, such as predation risk (McNamara and Houston 1987, Krebs et al. 1995, Prevedello et al. 2013). For instance, greater food abundance can increase conspecific density, thereby resulting in an increase in the number of predators and predation rate (Gilroy and Sutherland 2007). In addition, recent research suggest that food availability may not affect all individuals equally in a population, as low food availability by itself can shorten lifespan and reduce survival probability in individuals from harsh developmental conditions (Briga et al. 2017, Azpillaga et al. 2018).

In an increasingly anthropized world, management measures can have a significant impact on food availability, whether in terms of prey for top predators or predictable food sources for scavenging species. For instance, during the European regulations in response to the mad cow disease outbreak, which prohibited leaving livestock carcasses in the field, Martínez-Abraín et al. (2012) found that food scarcity, driven by these regulations, led to changes in griffon vulture foraging behaviour, increasing collision risks and mortality with wind turbines as their new foraging routes to supplementary feeding sites coincided with windfarms. Similarly, Margalida et al. (2014) observed shifts in reproductive timing and breeding success, along with increased subadult mortality due to increased exposure to illegal poisoning prompted by human-wildlife conflicts in Pyrenean Bearded Vulture, linked to reduced food availability due to these regulatory changes. These behavioural adaptations to food shortages can expose vultures and other highly mobile species to novel threats, such as collisions with wind turbines or consuming dangerous food sources, further exacerbating the challenges they face for their long-term conservation.

Ecosystems around the world have been significantly altered by human-provided food sources, particularly in areas with high levels of food waste such as the industrialized countries (Oro et al. 2013). These food sources, such as fisheries discards, supplementary feeding stations (e.g., vulture restaurants, bird feeders), and landfills, are examples of predictable anthropogenic food subsidies (PAFS). PAFS are highly predictable in space and time, which attracts numerous species to feed on these resources (Oro et al. 2013, Bicknell et al. 2013, Plaza and Lambertucci 2017, Cerecedo-Iglesias et al. 2023). Research has demonstrated that PAFS can improve the survival rates of local wildlife populations, especially among younger and inexperienced individuals and during harsh conditions of diminished natural food availability (Oro et al. 2008, 2013, 2014, Seward et al. 2013, Rotics et al. 2017, Fernández-Gómez et al. 2022). However, when local or regional regulations lead to a reduction or removal of these food sources, it can result in adverse demographic effects on the species that have come to rely on them. This reduction can happen gradually or abruptly, disrupting the survival, reproduction outcome and ultimately population dynamics of affected populations (Payo-Payo et al. 2015, Delgado et al. 2021, 2023, Pinto et al. 2021, Margalida et al. 2010, 2012, 2014, Almaraz et al. 2022).

Predictable anthropogenic food subsidies can often lead to increases in population density and size among various species when food provided increases or maintains a constant supply (Oro et al. 2013). For instance, studies have shown that the population growth rates of yellow-legged gulls (*Larus michahellis*) and rooks (*Corvus frugilegus*) are positively correlated with the total annual tonnage of waste at nearby dumps (Duhem et al. 2008, Olea and Baglione 2008). Similarly, experimental feeding of pheasants (*Phasianus colchicus*) released for hunting also resulted in a significant increase in their population densities (Draycott et al. 2005). Higher densities of wild canids, such as coyotes (*Canis latrans*) and jackals (*Canis aureus*), have been observed in areas populated by humans where dumps provide an accessible food source (Fedriani et al. 2001). The availability of anthropogenic food sources in populated cities led to a high increase of house crow (*Corvus splendens*) populations over a 16-year period (Lim et al. 2003). Landfills have determined the distribution of nesting sites of white storks (*Ciconia ciconia*) and have induced high nest densities close to these facilities in the last four decades (López-García and Aguirre 2023).

The demographic response to reduced food availability can often manifests as behavioural plasticity in various species, but the impact level may depend of the species' mobility capacity and the scale of the food reduction effect. In the context of landfill closures, reduction of food availability can be very localised, yet it can have negative impacts for local populations. For instance, studies on yellow-legged gulls revealed increased dispersal and the exploitation of alternative food resources following the closure of landfills (Payo-Payo et al. 2015, Zorrozua et al. 2020). Another study on the same species indicated that juveniles, especially first-year individuals, were the most affected, showing a decrease in apparent survival (Delgado et al. 2021). Similarly, spotted hyenas (*Crocuta crocuta*) in Kenya, after the closure of an open-air landfill, expanded their home ranges and decreased the size of their core groups near the former food source, increasing their daily dispersion in search of sustenance (Kolowski and Holekamp 2007). Red foxes (*Vulpes vulpes*) exhibited an increase in home range size following a reduction in anthropogenic food supplies (Bino et al. 2010). As observed in this thesis, griffon vultures responded to the decrease in food availability at landfills primarily by visiting these sites less frequently (Arévalo-Ayala et al. 2023a, 2023b). These behavioural shifts in foraging underscore the adaptability of species in response to environmental changes, particularly when faced with reduced access to predictable food supplies locally. However, if multiple landfills close across a broader region, key vital rates such as survival and population growth rates could be negatively impacted in populations used to feed in these facilities (Pinto et al. 2021, Delgado et al. 2023).

In summary, understanding the demographic responses of species to changes in food availability is crucial for developing effective conservation measures. This knowledge is especially important as European regulations under the circular economy framework, such as those prompting the closure of landfills, are currently being implemented (Delgado et al. 2021, 2023, Arévalo-Ayala et al. 2023a, 2023b). These changes have the potential to significantly impact various species that have adapted to rely on anthropogenic food sources such as landfills. Despite the importance of these changes, there is still limited research on how such regulations influence the population dynamics of obligate and facultative scavengers. Given that food availability is a key factor driving survival rates, reproductive success, and overall population dynamics (Sæther and Bakke 2000, Caswell 2001), it is imperative that future studies prioritize understanding species' responses to landfill closures.

THE GRIFFON VULTURE AS A STUDY SPECIES

The griffon vulture (*Gyps fulvus*) is a long-lived scavenger species that can live up to 35 years in the wild (Chantepie et al. 2015). This species is widely distributed through southern Europe, North Africa, the Middle East, and some parts of Asia, including the Indian subcontinent and Central Asia (del Hoyo et al. 1992) (**Figure 1**). As is typical in long-lived species, griffon vultures have a slow life cycle, characterized by delayed maturity, with most individuals beginning to reproduce at 5 to 6 years of age (Blanco et al. 1997), although individuals as young as 2 years old have been known to start breeding in some cases (Sarrazin et al. 1996, Demerdzhiev et al. 2014). Furthermore, griffon vultures have low reproductive rates, typically laying only one egg per breeding season which extends for 130 days until the chick fledges (del Hoyo et al. 1992).

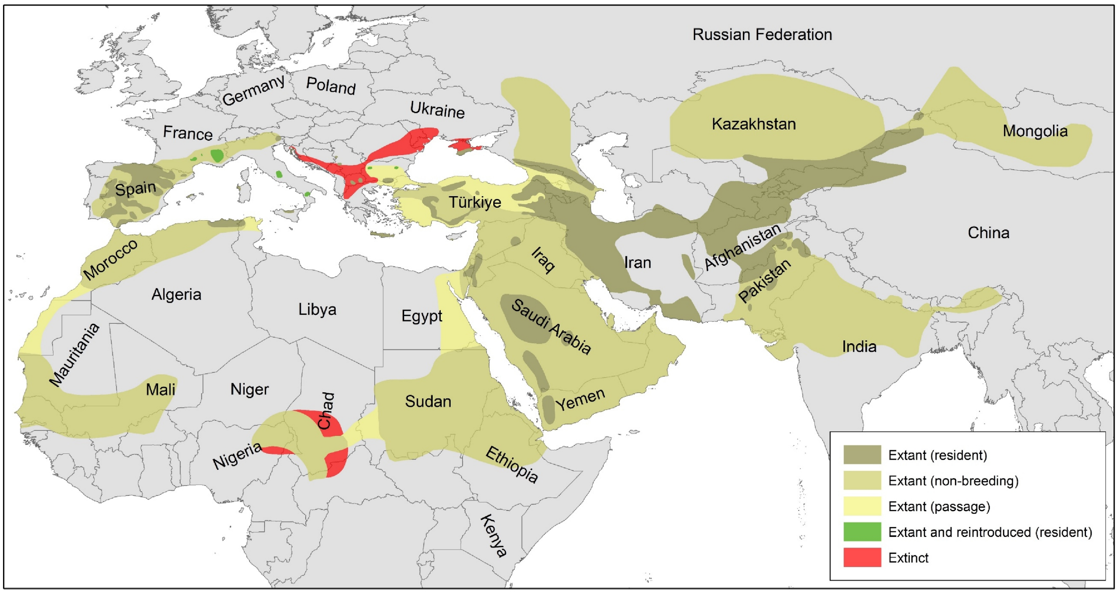

Figure 1. Global distribution of the griffon vulture *Gyps fulvus*. Species' distribution data is available from NatureServe and IUCN (2022).

Adult individuals are characterized by a white, short-feathered head and neck, with a light-coloured iris and a white collar of short feathers (**Figure 2**). Their dorsal, scapular, upper tail, and wing coverts are light brown, while their primary wing and tail feathers are black. Secondary and tertiary feathers are brown, with the tips of the tertiaries being gray. Their beaks are pale, and their legs vary from grey-brown to bluish-green, with black talons. Both sexes display similar coloration (Duriez et al. 2011, Zuberogoitia et al. 2013). Juveniles, in contrast, have a white downy head and neck, with a brown, lanceolate feathered collar and reddish-brown body plumage (**Figure 2**). As they age, their body feathers become rounded, the reddish hue fades, and their head and neck turn greyish. By three years, the collar is shorter and brown, and by five years, it resembles the adult form, though it has yet to turn white (Cramp and Simmons 1980, Duriez et al. 2011, Zuberogoitia et al. 2013).

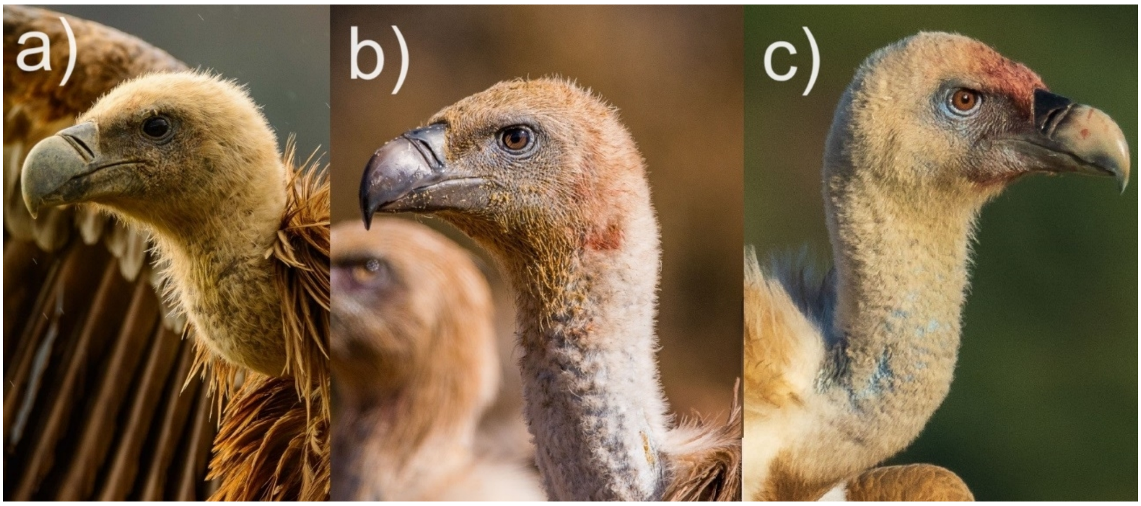

Figure 2. Griffon vultures *Gyps fulvus* of different age classes: a) juvenile (1-year-old), b) immature (between 2- and 4-year-old) and c) adult (more than 4-year-old). Photos by Arnau Soler Costa.

Griffon vultures are highly social birds, often forming large colonies and relying on communal roosts and breeding sites, usually on large cliffs, from where they soar over open lands in search for carcasses, generally avoiding woodlands (García-Ripollés et al. 2005, Dobrev and Popgeorgiev 2021). The species is typically found from sea level up to an elevation of 1,500 meters, and as high as 2,500 meters (del Hoyo et al. 1992).

Their diet varies across regions and in proportions, and consist of carrion from medium-sized and large domestic and wild animals, but also of organic matter in landfills (Margalida et al. 2007, Arévalo-Ayala et al.

2023a, 2023b, Arrondo et al. 2023). Vultures can gather in large numbers at carrion sites, sometimes exceeding 300 individuals and occasionally approaching a thousand at supplementary feeding sites (Donázar, 1993; Acha et al., 1998). In general, the number of vultures at a carcass correlates with the available food, increasing quickly before declining slowly. Larger groups may face decreased feeding rates due to high competition (Bosè and Sarrazin, 2007). Interestingly, though, access to carrion is primarily determined by age, with older adults feeding first, thereby gaining higher-quality food (Bosè et al., 2012). Indeed, juveniles are more prevalent at carrion sites in autumn since they fledge between July-August and prefer supplementary feeding stations far from breeding colonies (Bosè et al., 2012; Duriez et al., 2012).

THE GRIFFON VULTURE STRONGHOLD IN EUROPE: TRENDS AND MONITORING OF THE SPANISH POPULATION

Griffon vulture populations in southwestern Europe have experimented a substantial growth with a remarkable 200% increase in the last 15 years (Safford et al. 2019). The European population is estimated at 34,800-44,700 pairs (BirdLife International 2021), where Spain is home to approximately 90% of Europe’s griffon vulture population, with an estimated 30,946 to 37,134 breeding pairs. However, this has not always been the case. During the 1950s and 1960s, the griffon vulture population suffered significant declines due to human persecution in Spain, primarily through the widespread use of poisoned baits aimed at controlling foxes, crows, and other species considered pests (Donázar and Fernández 1990), and also due to agricultural mechanization and the decline of sheep farming (SEO 1981). Although birds of prey were granted official protection in 1966, hunting remained a significant problem for years, and the use of the pesticide strychnine was not banned until 1984 (Del Moral and Molina 2018). Conservation concerns led the Spanish Ornithological Society to undertake the first nationwide census of griffon vulture colonies in 1978, revealing a minimum of 3,240 breeding pairs in 1979 (SEO 1981).

This number doubled by 1989 and continued to rise, reaching 17,337 pairs by 1999 (Arroyo et al. 1990, Del Moral and Martí 2001). The increase in the number of griffon vulture breeding pairs between this period was primarily linked to changes in the abundance of livestock (cow, sheep, pig and goat), which served as a key food source for these scavengers (Parra and Tellería 2004). While population growth has slowed in the 21st century, with 24,609 pairs recorded in 2008 and 30,946 pairs in the most recent census in 2018 (17.5-26% of increase) (Del Moral 2009, Del Moral and Molina 2018), the trend suggests that the population may be nearing the carrying capacity of its environment (**Figure 3**). In fact, reproductive rates such as productivity and reproductive success assessed during the national censuses have shown a gradual decline, suggesting a demographic compensatory regulation in response to the population increase (Carrete et al. 2006, Fernández et al. 2008) (**Figure 4**). Based on these indirect evidences, it is suggested that the griffon vulture population is likely approaching a state of equilibrium within the constraints of its available resources and habitat, as the species has likely reached a point where further population expansion may be limited by factors such as food availability, nesting site competition, and other environmental factors (Carrete et al. 2006, Fernández et al. 2008). Nevertheless, the 2018 census marked the first-time breeding populations recorded in the Balearic Islands and the province of Valencia (**Figure 5**), though Galicia, the Canary Islands, Huelva, Ceuta and Melilla still lack breeding populations.

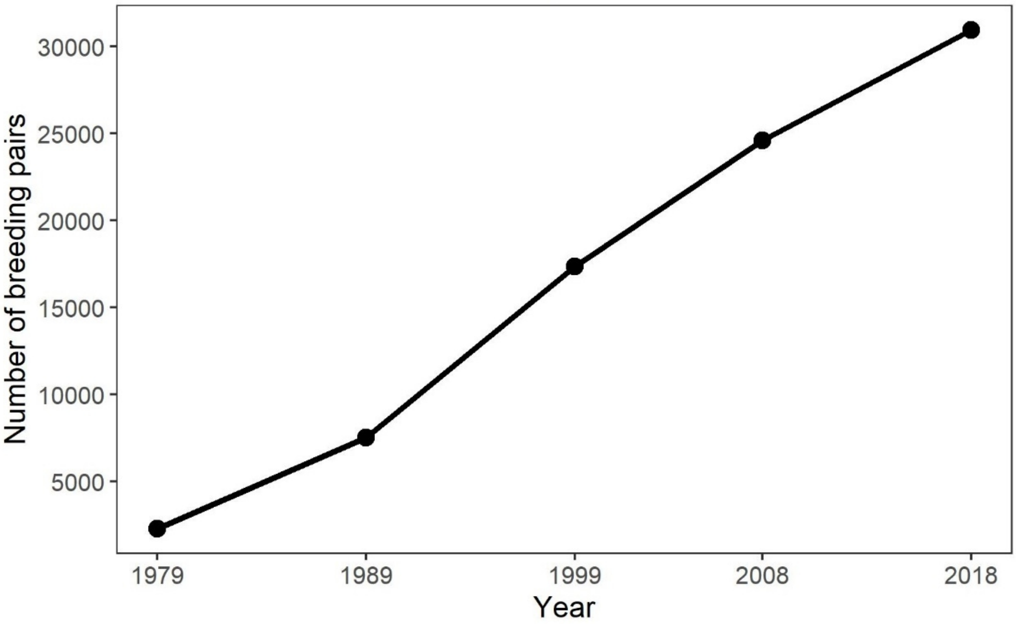

Figure 3. Population trend of griffon vulture breeding pairs in Spain. Census data were obtained from the species' censuses performed nationally every decade since 1979 (SEO 1981, Arroyo et al. 1990, Del Moral and Martí 2001, Del Moral 2009, Del Moral and Molina 2018).

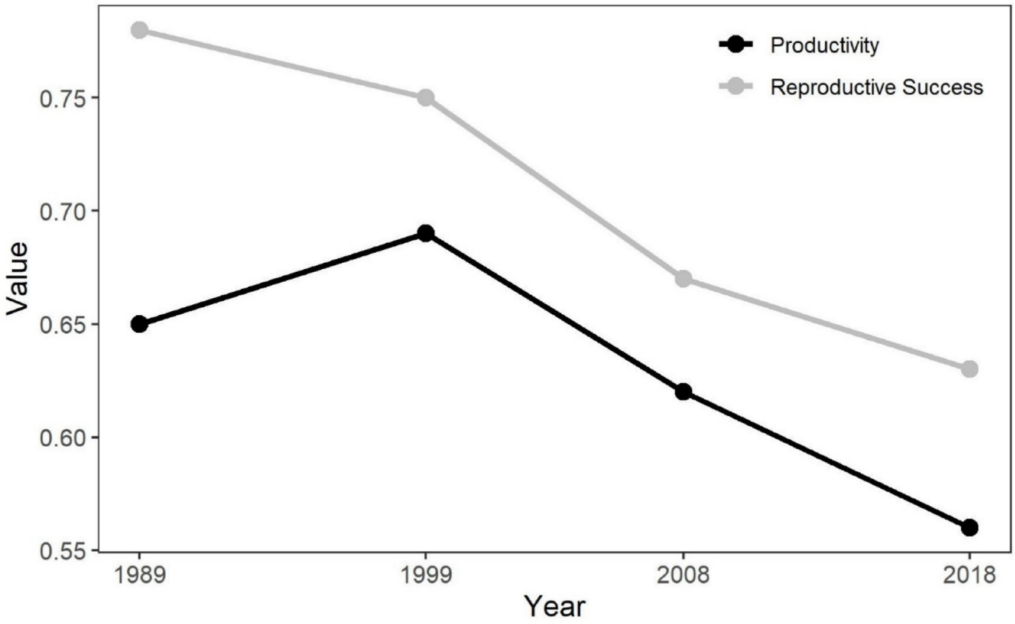

Figure 4. Reproductive rates of griffon vulture breeding population in Spain. Data was obtained from the species' censuses performed nationally every decade from 1989 to 2018 (Arroyo et al. 1990, Del Moral and Martí 2001, Del Moral 2009, Del Moral and Molina 2018).

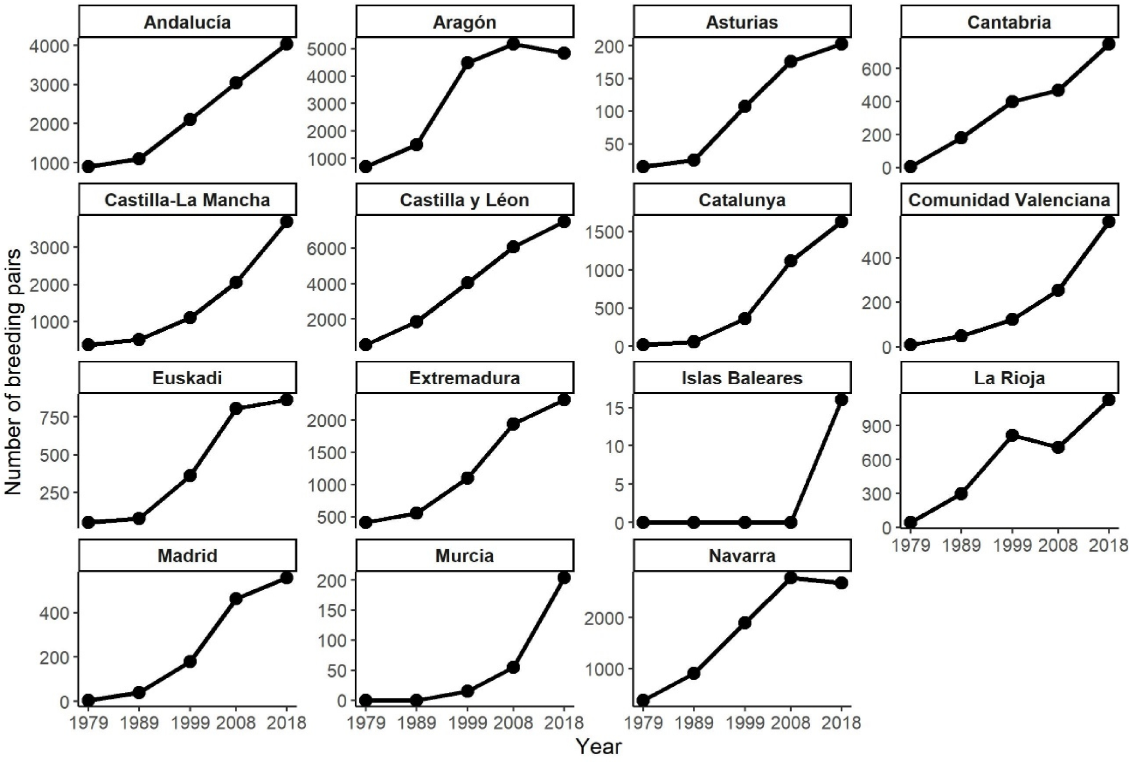

Figure 5. Population trends of griffon vulture breeding pairs in each of the autonomous communities in Spain. Census data were obtained from the species' censuses performed nationally every decade since 1979 (SEO 1981, Arroyo et al. 1990, Del Moral and Martí 2001, Del Moral 2009, Del Moral and Molina 2018).

UNDERSTANDING POPULATION INTERCONNECTIVITY TO ENHANCE LOCAL CONSERVATION STRATEGIES: THE USE OF DEMOGRAPHIC AND POPULATION MODELS

The overall trend of the griffon vulture population in Spain has been positive (Del Moral and Molina 2018), however, local population dynamics may be relevant to understand the overall dynamics of large spatially structured populations and, therefore, local conservation needs may differ across regions. For example, a population decline has been observed in Aragon and Navarra in 2018 census compared to 2008 census (Del Moral and Molina 2018), with a 7% decrease in Aragon, particularly in Teruel province, where the reduction approached 24%, and a near 4% decrease in Navarra. Although the population decline observed in Aragon can be attributed in part to limited census coverage in some areas (Del Moral and Molina 2018), factors such as high levels of landscape anthropization (Arrondo et al. 2020) (see Figure 5) but also differing conservation strategies may also play a role (García-Macía et al. 2021).

Spain serves as a notable example of a political decentralization, where authority is transferred to subnational governments (i.e., autonomous communities). Within this framework, each autonomous government assumes responsibility for executing and enforcing conservation policies, implementing biodiversity measures, and monitoring species within its range. The importance of decentralized governance in Spain relies on balancing local autonomy with inter-regional coordination to achieve cohesive and effective conservation efforts at a broader scale (e.g., Morales-Reyes et al. 2017). However, this decentralized administration often results in considerable variation of conservation policies with regional biases and in some cases, with potential coordination challenges due to distinct regional idiosyncrasies and differing environmental priorities (Jordan and Liefferink 2004, Agranoff 2007, García-Macía et al. 2021). This is particularly concerning for highly mobile species like vultures, as they move across administrative and political boundaries, often transcending these non-natural divisions (Arrondo et al. 2018). Different conservation policies and actions across regions can affect movement of individuals and ultimately influence local population dynamics, as the exchange of individuals in the form of emigrants or immigrants can alter the demography and distribution of vulture populations within a given range (Péron et al. 2010, Lambertucci et al. 2014, Arrondo et al. 2018, Seward et al. 2019). An illustrative case was the response to the BSE outbreak which led to a prohibition on leaving dead livestock in extensive farming areas and the subsequent reversion of sanitary policies by the establishment of protected feeding zones for scavenger birds under European regulation (EC) No 1069/2009. In compliance with European directives, Spain enacted national Royal Decree 1632/2011, establishing feeding areas for necrophagous species. However, the implementation of these measures was late, and varied widely across regions in terms of area establishment criteria and coordination (Morales-Reyes et al. 2017, López-Bao and Margalida 2018, Mateo-Tomás et al. 2018), which ultimately affected significantly food availability for scavengers, making them opt for other dangerous trophic sources that negatively impacted populations (Martínez-Abraín et al. 2012, Margalida et al. 2014). For instance, and encompassed within this thesis, Aragon adopted them in 2013, Catalonia in 2012, and the Valencian Community in 2014. Furthermore, each region designed its Protected Areas for Feeding of Scavengers zones differently—Aragon selected specific municipalities covering 50% of the region, Catalonia focused on public forests above 1400 meters and specific municipalities, ultimately covering only 13% of its area, while the Valencian Community targeted Special Protection Areas (SPAs) within the Natura 2000 network, encompassing 20% of its territory.

Dispersal and connectivity among populations are essential for the conservation of long-lived and highly mobile species such as vultures. These processes promote gene flow, help prevent inbreeding, and enhance the resilience of populations, all of which are crucial for the long-term survival of the species (Baguette et al. 2013, Margalida et al. 2013, Serrano et al. 2021). Given that vultures cover vast home ranges and frequently cross multiple administrative borders, maintaining connectivity and conservation strategies coherence is particularly critical for their populations (Doxa et al. 2013, Lambertucci et al. 2014, Arrondo et al. 2018, López-Bao and Margalida 2018). However, this requires not only the preservation of habitat corridors but also addressing barriers to movement (e.g., different sanitary measures that modulates food availability between regions, Arrondo et al. 2018), a task that becomes more challenging as human activities increasingly alter landscapes (Doxa et al., 2013). To achieve this, it is crucial to understand the overall population dynamics and which demographic rates are key drivers, both at the local and the overall population level, especially in the context of individual exchange between populations (Oro and Ruxton 2001, Fernández-Chacón et al. 2013, Drake et al. 2021, Schaub and Kéry 2022).

Accurate and comprehensive data collection is crucial in population ecology for obtaining reliable demographic and population estimates for enhancing conservation management of species (Doak et al. 2005). Traditional single-state capture-recapture methods—which are based on capturing, marking or tagging and recapturing/resighting animals in several occasions and in systematized way (marks can also be DNA, radio-transmitter or GPS devices; e.g., Petit et al. 2016, Foster et al. 2018), are valuable for informing of key demographic parameters, and a wide range of model formulations exists nowadays to obtain estimates of survival, growth, recruitment and even abundances, while accounting for imperfect detection (Lebreton et al. 1992, Cooch and White 2019). However, as the study area reduces in scale, capture-recapture methods often fall short in capturing important parameters such as migration processes (i.e., emigration and immigration) (Pollock et al., 2002; Sandercock, 2016). For instance, overlooking emigration can significantly impact survival estimates, as capture-recapture methods often cannot differentiate between mortality and permanent emigration. Therefore, the survival probability estimated is ‘apparent’, as individuals not recaptured in subsequent occasions could either be dead or alive somewhere else out of the study area (Marshall et al. 2004, Horton and Letcher 2008). Furthermore, flexible multistate models, which account for multiple observed states of recaptured individuals, offer valuable insights into survival, especially when mark-recoveries from dead individuals are available from within and outside the study area (Lebreton et al. 1999, Lebreton and Pradel 2002, Lebreton et al. 2009). This formulation permit to effectively disentangle apparent survival in true survival and site fidelity (Lebreton et al. 1999). Additionally, as initially formulated, these models allow researchers to estimate movement probabilities between different sites where capture-recapture efforts occur, providing estimates of dispersal, site fidelity, and movement between locations (Lebreton et al. 2009). However, they do not directly infer how these movements influence population fractions or quantify their contributions to population dynamics, such as growth (Schaub and Kéry 2022).

Similarly, population counts are useful for covering large areas and estimating overall abundance and population growth rate, but they often suffer from issues such as double counting or missing individuals (Kéry and Schaub 2012, Kellner and Swihart 2014, Schaub and Kéry 2022). Additionally, these counts typically lack associated uncertainties (when survey repetitions are not done) and do not directly provide estimates of key demographic parameters like survival, reproduction, and dispersal that are essential for understanding population dynamics and guiding effective conservation efforts (Kellner and Swihart 2014, Nichols, 2014, Ficetola et al., 2018). This limitation hampers a thorough understanding of the role of vital rates, including the impact of immigration and emigration on population growth (Hovestadt and Poethke 2006, Poethke et al. 2011, Millon et al., 2019; Wu et al., 2020). Without comprehensive analyses that identifies all key demographic processes, conservation measures may be ineffective, as they do not address the complexities of populations and spatial processes (Schaub et al., 2010; Tavecchia et al., 2016; Millon et al., 2019; Wu et al., 2020). To overcome these challenges, it is crucial to integrate multiple data sources and utilize specialized and advanced statistical methods to accurately assess these demographic processes to provide a more holistic view of population dynamics (Kéry and Schaub 2012, Schaub and Kéry 2022). In this sense, Integrated Population Models (IPMs) have emerged as a powerful tool to address these limitations, enabling the joint estimation of key vital parameters such as survival, productivity and population sizes by combining data from multiple sources (i.e, capture-recapture, counts, and surveys on reproductive parameters) to provide a more comprehensive understanding of population dynamics (Besbeas et al. 2002, Schaub and Abadi et al. 2010, Kéry and Schaub, 2012, Plard et al. 2019). These models are particularly useful for studying species with complex life histories and high mobility, as they can incorporate spatial heterogeneity and dispersal processes, offering crucial insights of key vital drivers and their role on local population dynamics for the conservation of the species (Péron et al. 2010, Seward et al. 2019).

In this thesis, robust capture-recapture data from thousands of griffon vultures were applied to evaluate, on a local scale, the demographic response in terms of apparent survival, local abundance, and the probability of permanent emigration after the first capture and marking across different age classes, to the reduction of food availability resulting from the enforcement of European regulations aimed at reducing and closing landfills, using both frequentist and Bayesian frameworks. On a regional scale, data from national censuses, productivity, and capture-recapture campaigns from three griffon vulture populations were merged into a multisite IPM within the flexible Bayesian framework. This approach explicitly modelled the movement probabilities of individuals between populations to estimate true survival, different population fractions, and demographic rate contributions to population dynamics while accounting for permanent emigration from the study area, demographic stochasticity and uncertainties around estimates. By directly informing of migration processes with data, this approach provided a more comprehensive understanding of the underlying interpopulation dynamics, offering critical insights for effective conservation strategies for highly mobile species like vultures.

AIMS AND SCOPE

In this thesis, we examine the demographic response and population dynamics of a long-lived scavenger species, the griffon vulture *Gyps fulvus*, in response to a changing environment at both local and regional spatial scales. The research generates important knowledge for understanding how vultures respond to new circular economy policies aiming to achieved sustainability at the local level, as well as for accounting for interconnectivity across populations when modelling population dynamics, which is crucial for developing effective conservation strategies for highly mobile species. We addressed the following specific objectives:

- To assess the demographic response in terms of apparent survival and local abundance of griffon vultures to the reduction of organic matter in an open landfill.
- To determine the age-specific demographic response in terms of apparent survival and the probability of permanent emigration after the first capture in response to the reduction of organic matter in a landfill.
- To identify the key demographic drivers that influence population dynamics in three neighbouring vulture populations under decentralized conservation practices.

In **Chapter 1**, we investigated the impact of the reduction of organic matter in an open landfill following the installation of a waste treatment centre (WTC) on the local population of griffon vultures in Central Catalonia (NE Iberian Peninsula) over a seven-year monitoring period (2012 to 2018, inclusive). To achieve this, we used the Schwarz and Arnason formulation of the Jolly-Seber model, a robust capture-recapture method that allows for the estimation of apparent survival and local abundance while accounting for heterogeneity in the data due to the presence of transients and immediate trap-response. This model enabled us to quantify the demographic response of the vulture population to changes in food availability at the landfill, providing a detailed understanding of how these scavengers response to food shifts driven by the application of circular economy policies.

In **Chapter 2**, we assessed the age-specific demographic response of griffon vultures to the reduction of organic matter in the open landfill of Central Catalonia. We employed a hierarchical Bayesian formulation of the Cormack-Jolly-Seber model to estimate apparent survival and the probability of permanent emigration after the first capture across different age classes (juveniles, immatures, and adults) over an 11-year monitoring period (2012 to 2022, inclusive). Specifically, we evaluated the demographic response across three distinct periods corresponding to different organic matter regimes at the landfill: before WTC installation ('normal' food regime), first after WTC period (substantial reduction of 84%) and a second after WTC period (extreme reduction of 96%). The Bayesian approach allowed us to simultaneously estimate age-specific apparent survival for resident and transient individuals, transience probability and its uncertainty, and recapture probabilities while accounting for common sources of heterogeneity such as immediate trap-response and individual heterogeneity among age classes. This chapter highlights the differential impacts of reduced food availability on various age groups, emphasizing the importance of including age structure into demographic and population dynamics models.

In **Chapter 3**, we extended our analysis to a regional scale by focusing on three neighbouring griffon vulture populations in the northeastern Iberian Peninsula, specifically within the administrative divisions of Catalonia, Valencian Community, and Aragon. Over a 14-year period of long-term monitoring (2008 to 2021, inclusive), we utilized a multisite Integrated Population Model (ms-IPM) to comprehensively assess the dynamics of these populations. The ms-IPM framework integrates data on breeding pair counts, survival, and reproduction, while also estimating key population fractions, including breeders and floaters, as well as immigration and emigration rates. Additionally, the model allowed us to evaluate the contribution of vital rates to the population growth rate and to analyse density-dependent effects. This approach enabled us to identify the key demographic drivers influencing population dynamics across these regions, emphasizing the importance of coordinated conservation efforts across administrative boundaries. Moreover, the IPM provided a framework for explicitly modelling immigration and emigration, two processes that are challenging to estimate but essential for understanding local population dynamics.

Overall, this thesis aims to understand the processes that shape the populations of long-lived species in human-modified environments, with a focus on improving our knowledge of vulture population dynamics—one of the most threatened groups of birds for which insufficient information exists. This information is crucial to support the management of vulture populations, particularly under decentralized governance structures. This is especially relevant for species like the griffon vulture, which are managed by different administrative bodies across their range, a scenario that is common for many other species, including other endangered species of vultures. The findings of this thesis thus offer valuable insights that can inform more effective and coordinated conservation strategies across various management jurisdictions.

SUPERVISOR'S REPORT

Antonio Hernández-Matías and Joan Real Ortí, co-directors of the doctoral thesis entitled “From Local to Regional: Demographic and Population Dynamics of a Long-lived Scavenger Species in a Changing Environment” authored by Diego José Arévalo-Ayala, hereby certify that the candidate has conducted the research described in this thesis. The thesis consists of three distinct scientific works, two of which are already published in international scientific journals listed in the Science Citation Index (SCI), while the last one is being prepared to be summited. Below, we list the two articles along with the candidate’s contributions to each and the impact factor of each journal. Additionally, we certify that no co-authors of these articles or other works presented in this doctoral thesis have used, either implicitly or explicitly, these works as part of other theses.

Chapter 1. Arévalo-Ayala, D.J., Real, J., Durà, C., Aymerich, J., & Hernández-Matías, A. (2023). Reduction of organic waste in a landfill lowers the visitation probability but not the local abundance of a long-lived scavenger species. *Bird Conservation International*, 33, e15. doi:10.1017/S0959270922000107.

- Contribution of the candidate: Data curation, design and development of analytical methods, interpretation of the results, leading of manuscript writing.
- About the journal: *Bird Conservation International* was evaluated at Journal Citation Reports (JRC) with an Impact Factor of 1.6 (2022). The Impact Factor of the journal was listed as number 9 out of 30 in the field of Ornithology (Q1), and as number 35 out of 65 in Biodiversity Conservation (Q2).

Chapter 2. Arévalo-Ayala, D. J., Real, J., Mañosa, S., Aymerich, J., Durà, C., & Hernández-Matías, A. (2023). Age-Specific Demographic Response of a Long-Lived Scavenger Species to Reduction of Organic Matter in a Landfill. *Animals*, 13(22), 3529. https://doi.org/10.3390/ani13223529.

- Contribution of the candidate: Data curation, design and development of analytical methods, interpretation of the results, leading of manuscript writing.
- About the journal: *Animals* was evaluated at Journal Citation Reports (JRC) with an Impact Factor of 3.0 (2022). The Impact Factor of the journal was listed as number 13 out of 143 in the field of Veterinary Science (Q1), and as number 12 out of 62 in Agriculture, Dairy and Animal Science (Q1).

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CHAPTER 1

Reduction of organic waste in a landfill lowers the visitation probability but not the local abundance of a long-lived scavenger species

Photography courtesy of Arnau Soler Costa

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Reduction of organic waste in a landfill lowers the visitation probability but not the local abundance of a long-lived scavenger species

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Research Article

Cite this article: Arévalo-Ayala DJ, Real J, Durà C, Aymerich J, Hernández-Matías A (2023). Reduction of organic waste in a landfill lowers the visitation probability but not the local abundance of a long-lived scavenger species. *Bird Conservation International*, **33**, e15, 1–13
https://doi.org/10.1017/S0959270922000107

Received: 04 November 2020
Revised: 07 March 2022
Accepted: 21 March 2022

Keywords:
capture-mark-recapture; Griffon Vulture; population dynamics; predictable food subsidies; landfill

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Summary

Globally, vultures are one of the most threatened of all groups of birds. European vulture populations are benefited by several anthropogenic food sources such as landfills. Current European Union directives aim to decrease the amount of organic matter dumped in landfills, reducing this important food source for some vulture species. In this context, we assessed the effect of the reduction of organic waste available and accessible for scavengers in a landfill on the visitation probability and abundance of a local Eurasian Griffon Vulture *Gyps fulvus* population in Central Catalonia (NE Iberian Peninsula), using a long-term dataset of captured-marked-recaptured individuals in the period 2012–2018. Our results indicated a decrease in the visitation probability due to a significant reduction of organic matter dumped into the landfill after a waste treatment centre was built (0.82 to 0.76) that may cause a permanent emigration of vultures in response to food reduction. However, the estimated annual abundance of vultures tended to grow over time due to the positive trend that regional vulture populations have experienced in recent decades. These results suggest that population processes occurring at regional scales are more relevant to vulture populations than local waste management measures. A reduction in locally available food can make a site less attractive, but species with high dispersal capacity such as vultures may overcome this issue by moving to other suitable sites. Although Griffon Vultures obtain most of the food from domestic and wild ungulates, a regional application of European directives could threaten an important alternative feeding source, especially in food shortage seasons where landfills could be supporting the energetic requirements of the species. Conservation strategies should be planned to counteract the possible negative effects of new European directives on scavenger populations.

Introduction

Vultures play an important role in ecosystems since they are responsible for eliminating large amounts of decomposing matter that otherwise could act as a focus of harmful diseases (Whelan *et al.* 2008, Ogada *et al.* 2012). Nonetheless, they are one of the most globally threatened scavenger groups, with at least 81% of vulture species listed as threatened or 'Near Threatened' on the IUCN Red List (Ogada *et al.* 2012, Margalida and Ogada 2018, Safford *et al.* 2019). Both the serious modifications that ecosystems have undergone, and contemporary human activities, have altered the natural supply of carrion, thereby modifying food resource selection (Oro *et al.* 2013) and affecting vulture-related ecosystem services (Moleón *et al.* 2014). In Europe, the establishment of sanitary regulations by the European Parliament and the European Council (Regulation EC 1774/2002) in response to the appearance of Transmissible Spongiform Encephalopathies (TSE) in cattle in the late 1990s, which banned the abandoning of cattle carcasses in the wild and in supplementary feeding sites, led to a significant decrease in the main food source for vultures (Martí 2003, Margalida *et al.* 2010). Although new regulations (Directive 2009/147/CE and Regulation (EU) No 142/2011) were later enacted to maintain authorised supplementary feeding sites to assist the conservation of scavengers, this important loss in food supplies obliged vultures to exploit other food resources such as landfills (Donázar *et al.* 2010), another predictable source of food commonly used by these species (Garrido *et al.* 2002, Plaza and Lambertucci 2017).

A large number of opportunistic animal species congregate in landfills due to food availability (see Plaza and Lambertucci 2017). Nowadays, for several vulture species, landfills constitute an important food resource (Tauler-Ametller *et al.* 2017). This food subsidy exists alongside other predictable feeding sites such as vulture feeding stations and helps strengthen vulture populations

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in certain regions (Oro *et al.* 2013, Plaza and Lambertucci 2017). In some areas, food from landfills represents up to 50% of the diets of rare and endangered vulture species (Tauler-Ametller *et al.* 2018), although they are also a source of low-quality and dangerously polluted food (Genovart *et al.* 2010, Tauler-Ametller *et al.* 2019, Ortiz-Santaliestra *et al.* 2019).

Despite the benefits provided by this unlimited source of food, landfills also influence the demographic parameters of several species that use them and even trigger cascade effects in ecosystems as a result of the boom in opportunistic and generalist bird and mammal species, leading to human-wildlife conflicts in consequence (see Plaza and Lambertucci 2017). In order to reduce the environmental impact of landfills, and encompassed within the framework of the circular economy, developing and developed countries are adopting new policies for reducing waste production and the amount of organic waste and other useful materials that are dumped in landfills, incinerators, and oceans (Hoornweg *et al.* 2013, Thi *et al.* 2015, Stahel 2016, Jurgilevich *et al.* 2016). In Western Europe, European directives (Directive 2008/98 /EC and Directive (EU) 2018/850) exhort member states to treat waste before its landfilling in an attempt to promote by 2035 a transition to a circular economy and reduce to less than 10% the amount of waste that reaches landfills. However, the application of this directive might imply a decrease in food availability in landfills that could have negative effects not only for opportunistic and generalist species but also species of conservation concern that exploit this resource. To date, few studies have assessed the effect of food reduction in landfills or the effect of landfills closure on local demographic parameters of certain opportunistic and generalist species (Kolowski and Holekamp 2007, Bino *et al.* 2010, Payo-Payo *et al.* 2015), and for vultures is scarce (Katzenberger *et al.* 2019).

Here, we focused on determining the visitation probability and abundance of a Eurasian Griffon Vulture *Gyps fulvus* population in Central Catalonia, where a long-term capture-mark-recapture (CMR) scheme involving thousands of individuals has been carried out in a landfill that shifted organic waste management during the study period (2012–2018). Since recyclable, non-recyclable, and organic waste is not separated effectively by households, organic matter and other recyclable material may end up in this landfill. As a mitigating measure, a waste treatment centre (WTC) was built in June 2015 to improve the separation of organic and recyclable materials from the remaining waste fraction in the municipal selective rubbish collection (hereafter WASTE) before dumping in the landfill. With the WTC, the organic fraction of municipal selective collection (hereafter ORGAN) is also received and treated before its landfilling. Our main interests are two-fold. First, from a conservation perspective, our example may help to understand how a population of an abundant vulture species responds to a local reduction of food accessibility in terms of landfill visitation probability and abundance. While the current conservation status of Griffon Vulture is 'Least Concern', increasing evidence suggest that several threats make this population vulnerable in the future (Arrondo *et al.* 2020); it is worth remembering that Asian vultures were very abundant before the unexpected crash in the 1990s that led them near to extinction (Prakash *et al.* 2003, Oaks *et al.* 2004). Second, from the perspective of the management of landfills and the conflict that vultures attending them generate (Oliva-Vidal *et al.* 2022), a reduction of organic waste is a reasonable measure to reduce the use of these infrastructures by conflicting species. Nonetheless, little information exists on whether available methods of organic waste reduction allow reducing the amount of organic waste to levels that ensure the reduction of the conflict. For example, organic waste after the implementation of measures may be still enough to sustain a large population of conflicting species (Payo-Payo *et al.* 2015). In addition, few studies have addressed the importance of regional population trends on the local dynamics of species attending these infrastructures, so that local measures may be partially ineffective. Based on these ideas, we expect that the reduction of organic matter dumped in the landfill negatively affects the visitation probability. In fact, our visitation probability is an apparent survival estimate in a capture recapture analysis. A reduction in apparent survival can result from a mixture of mortality and permanent emigration (Lebreton *et al.* 1992). Given that this species can adapt its foraging movements as a behavioural response to food availability (Donázar *et al.* 2010, Zuberogoitia *et al.* 2013), we expect a reduction of apparent survival due to a permanent emigration from the site in response of food shortage in the landfill. We interpret our apparent survival probability as a probability of vultures visiting the landfill and not as survival *per se.* For this reason, and from now on we refer to this parameter as 'landfill visitation probability'. As for abundance, we expect that it will increase due to population processes occurring at larger spatial scales irrespective of local food availability. Given that vultures can visit several feeding sites and fly enormous distances daily to forage (García-Ripollés *et al.* 2011, Monsarrat *et al.* 2013, Harel *et al.* 2016), we expect that individuals from a regional population visit the landfill at some point, irrespective of food reduction since there is still enough to attract them to the site. In this case, we considered the growing Catalonian population (Del Moral and Molina 2018) as the most representative scale of a regional population, so we would expect the abundance of vultures at the landfill to increase as well. In order to assess these predictions, we first analysed the amount of organic matter dumped in the landfill before and after the WTC was installed, then we estimated the demographic parameters of the local Griffon Vulture population, and finally, we tested if a higher population-scale such as the Catalonian reproductive pair censuses explains the abundance estimated despite the reduction of organic matter in the landfill.

Methods

Study species

The Griffon Vulture is a long-lived avian scavenger species that can live for up to 35 years (Chantepie *et al.* 2015). In Catalonia, the population increased from 1,115 pairs in the 2008 census (Del Moral 2009) to 1,628 in 2018 (Del Moral and Molina 2018). Despite declining populations in North Africa and Turkey, the overall population trend appears to be upwards and this species is now assessed as 'Least Concern' on the IUCN Red List (BirdLife International 2017). Home-range covers ~4,000 km^2 (Arrondo *et al.* 2018) and birds will fly up to 120–300 km daily to forage (García-Ripollés *et al.* 2011, Harel *et al.* 2016). Juveniles seem to be less site-dependent (i.e. they disperse longer distances and have less site fidelity) than adults and are often attracted by congregations of feeders at predictable feeding sites (García-Ripollés *et al.* 2004, Duriez *et al.* 2012, Peshev *et al.* 2018). In Europe and other Old-World regions, Griffon Vultures specialize in consuming medium-to-large vertebrate carcasses, mainly ungulates (cattle and wild deer) (Fernández 1975, Donázar 1993, del Hoyo *et al.* 1994, Xirouchakis 2005). However, some vultures frequent landfills and individual survival rates may increase since feeding at these sites is easier than searching for carcasses and competing with others for food (Garrido *et al.* 2002).

Study area and data collection

In 2012–2018, a Griffon Vulture banding scheme was carried out by the Grup d'Anellament de Calldetenes-Osona at the landfill of Orís municipality (42.07°N, 2.20°E, Central Catalonia, Spain; Figure 1), which receives waste from up to 68,868 households of Osona and El Ripollès counties (https://www.idescat.cat). The CMR sessions were performed once or twice a month on ~17 occasions a year (minimum = 9, maximum = 23) (Table S1; Appendix S1 in the online supplementary material). Captures were made using a permanent walk-in trap (see Bloom *et al.* 2007) placed ~200 m from the landfill and with a capacity for up to 300 vultures. Pig lungs, and decomposing sheep and cattle parts were supplied regularly (30–50 kg weekly) to attract the vultures. Once captured, each vulture was ringed with a metal band and a plastic distance-reading band (Garrido and Pinilla 2000). For this study, data from recaptured vultures only was used, since re-sightings were few and come from opportunistic records by naturalists with some discrepancies in the areas and periods covered.

Landfill waste management effect on food availability

In compliance with European directives (Directive 2008/98/EC and Directive (EU) 2018/850), a waste treatment centre (WTC) was built at Orís landfill, in May 2015, whose aim was to reduce the accessibility of scavengers to organic waste dumped into the open landfill. Before the WTC was opened, untreated WASTE (i.e. waste fraction of the municipal selective rubbish collection) was dumped in the landfill, which would suggest that up to that date more organic matter was available and accessible as food. After the WTC became operational, both ORGAN (organic fraction of the municipal selective rubbish collection) and WASTE pass through two different treatment lines to separate the content (recyclable, non-recyclable, and organic matter from both sources). Thus, two main sources of organic matter are deposited into the landfill and are available and accessible as food for vultures after triage in the WTC. Of the ORGAN, scrap >12 cm is dumped and is the main source of food for vultures, while scrap <12 cm is transported to an aerobic biological reactor for composting. After the composting treatment, a residual fraction is tipped into the landfill. Of the WASTE, three main residuals are separated: first, materials >18 cm are dumped in the landfill (including food scraps not properly separated in households); the second residue consists of recycled material such as aluminium, light packaging, and iron; and the third residue is biostabilised organic matter which is used as soil for covering the landfill (for more detailed information see https://www.residusosona.cat/circuit-planta/).

We estimated the amount of organic matter tipped in the landfill accessible and available for vulture consumption (hereafter OMA) by quantifying the different types of waste before and after the WTC triage from samples of c.1000 kg, three or four times a year (See Table S2 and Appendix S2 for details). We assessed whether food availability differed between the periods before and after the WTC performing a *t*-test using log-transformed OMA in R version 3.6.3 (R Development Core Team 2020). The yearly OMA values were also used as covariates in the following analyses.

Landfill waste management effect on population parameters

We used a CMR database of Griffon Vultures using the period 2012–2018. Since we aimed to evaluate the effect of the OMA reduction in the Orís landfill on annual visitation probability and abundance, captures were pooled for each year and were treated as a single sampling occasion. We proceeded this way to guarantee the presence of all vultures captured throughout the year to avoid the

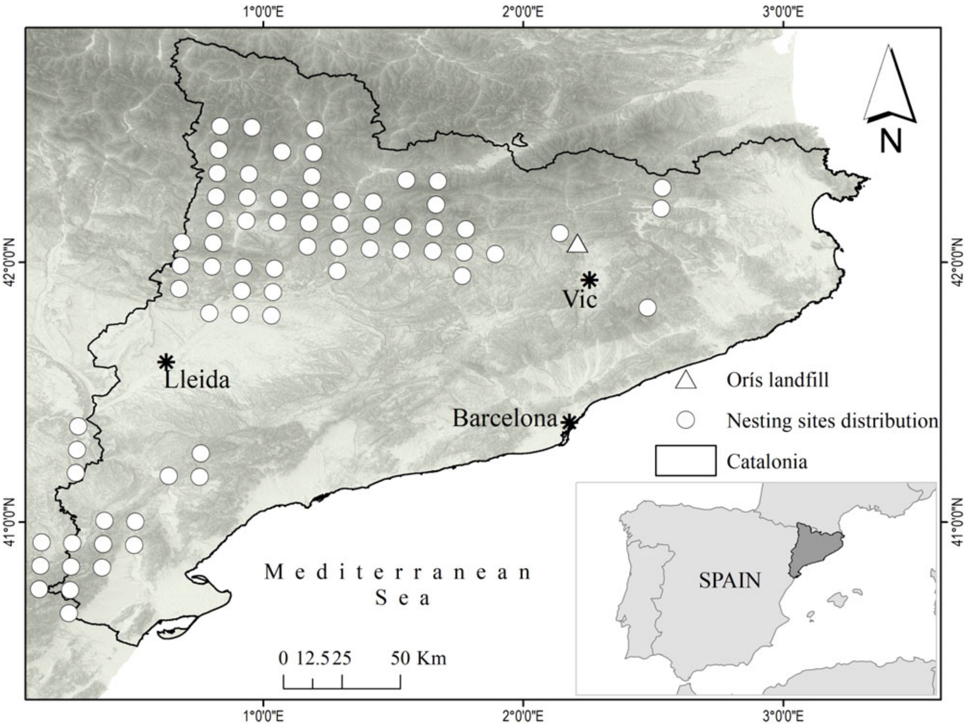

Figure 1. Orís landfill location (triangle) and distribution of Griffon Vulture *Gyps fulvus* nesting sites (white circles) in Catalonia. The distribution of nesting sites is based on data of 10x10 km UTM squares (data provided by Servei de Fauna i Flora, Generalitat de Catalunya 2018). Olive green gradient represent altitude from 0 m (light green) to >3,300 m (dark green). Map was developed in ArcMap 10.3 (ESRI 2014).

potential bias of considering the fraction of birds that use the landfill in a given season (see Discussion; and Smith and Anderson 1987, Hargrove and Borland 1994, O'Brien *et al.* 2005). Despite this, and following other studies based on year-round captures and where part of the data was omitted (Peach *et al.* 2001, Boys *et al.* 2019), we performed the same models using half-year (six months) of captures as a sampling occasion in order to explore the effect on our estimates of shortening the pooling interval (see Appendix S3 for the results of this analysis).

To test whether our data met the model assumptions, we ran the version of the RELEASE test (Burnham *et al.* 1987) performed in program U-CARE (Choquet *et al.* 2009) to detect possible sources of heterogeneity in both visitation and capture probabilities, using a live-encounter Cormack-Jolly-Seber-type (CJS) capture histories structure. Since both Test3.SR and Test2.Ct were significant (see Results), and following Sanz-Aguilar *et al.* (2011), our initial model had to account for both sources of heterogeneity using constraints on visitation and capture probability for transients and trap-dependence, respectively.

We used the Schwarz and Arnason (1996) parameterization of the Jolly-Seber model (or POPAN model), which estimates open-population abundance in terms of a super-population (*N*) and probability of entry (*pent*). The estimated parameters from the POPAN model that we used for inference are: 1) super-population of Griffon vultures (N_{super}), a hypothetical number of vultures entering the study site and available for capturing; 2) visitation probability (ϕ_i), the probability that a vulture alive in year *i* will be alive and present on the landfill in year $i+1$; 3) capture probability (p_i), the probability of capturing a vulture in year *i* given that it is alive and present on the landfill; 4) the probability of entrance ($pent_i$), the probability that a vulture from the super-population entered the study site between year *i* and $i+1$; and 5) the abundance of vultures per year (N_i) as a derived parameter. The visitation (ϕ), capture (*p*), and entry (*pent*) probabilities are the modelling parameters and were modelled as constant (.) or time-dependent (*t*).

To model transient and trap-dependence effects, the PriorCapL function in program MARK 9.0 (White and Burnham 1999) was used. The covariate PriorCapL function was applied to differentiate whether or not a vulture had been previously captured between specified years. To account for transients, PriorCapL (*i,j*) applied to ϕ took the value of 0 if a vulture was not previously captured on years $i, i+1, \ldots, j$, and 1 if the animal was captured during this set of years. To account for trap-dependence, in capture probability, PriorCapL (*i*) was 1 for vultures seen on the preceding occasion *i*-1 and 0 for those not seen on that occasion.

The effect of landfill management was modelled as an additive effect and assessed separately considering two variables: first, the "Landfill Effect" (LE) was coded as a dummy variable indicating two periods, before the WTC (2012 to May 2015) and after (June 2015 to 2018) and was applied to visitation, capture, and entry probabilities. Second, the OMA variable was used to model the effect of landfill management using the OMA values calculated for each year (Table S2, Appendix S2). We modelled the capture probability taking into account the sampling effort. The covariate "Effort" was the total number of sampling days per year (Table S1, Appendix S1). A full explanation of each parameterized component model is shown in Appendix S4.

All the models were fitted with program MARK 9.0 (White and Burnham 1999) and model selection was carried out using Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002) with $\hat{c}$ adjusted for overdispersion (quasi-likelihood AIC_c, $QAIC_c$). Models with $\Delta QAIC_c<2$ were model-averaged in MARK 9.0 (White and Burnham 1999) and used for inferences (mean ± SE).

Determinants of vulture populations present at the landfill

Since the abundance per year (N_i) is not a modelable parameter in POPAN, we conducted a *post-hoc* analysis to evaluate the factors that could determine this parameter in the landfill. We ran linear regressions in R version 3.6.3 (R Development Core Team 2020) using the estimated POPAN model abundance (N_i) as a response variable with two predictive variables: 1) the annual metric tons of OMA discharged into the landfill and 2) the number of breeding pairs of Griffon Vultures estimated in Catalonia in 2012–2018 (N-Census). We evaluated a third model considering the additive effect of both N-Census and OMA. The AIC_c was used for model selection (Burnham and Anderson 2002). The Catalan Griffon Vulture census is only performed every decade and it was provided by Del Moral (2009) in 2008 and by the wildlife service of the local government in 2018 (Servei de Fauna i Flora, Generalitat de Catalunya). N-Census for each year was estimated by regressing the number of breeding pairs against the number of years in each 10x10 UTM square in Catalonia and then summing the values of all grids. For each grid, we only have two observations of the dependent variable and we assumed that number of pairs changed linearly through the period. The first census was completed in 2008 and 2009 so we assumed the same numbers of vultures for these two years and we considered a 9-year period to estimate the yearly increment of pairs (estimate ± SE). By proceeding this way, we also assumed that the number of breeding pairs in Catalonia represents a good measure of the overall population of the individuals at the study site.

Results

Effect of landfill waste management on food availability

During the study period (2012–2018), 234,717.57 metric tons (t) of residuals were received, of which 66,684.15 t of OMA were deposited in the Orís landfill. At least 42% of OMA was dumped into the landfill before WTC (2012–May 2015), followed by a significantly progressive reduction from 27% (2015) to 4% (2018) after it became operational ($t = 18.37$, $n = 7$, $P < 0.01$; Figure 2).

Landfill waste management effect on population parameters

Our data set consisted of 2,937 marked individuals, of which 604 (20%) were recaptured twice or more. As expected, the most general CJS model with visitation and capture probabilities dependent on time (ϕ_t p_t) fitted the data poorly ($\hat{c} = 3.83$, $\chi^2 = 80.53$, df = 21, $P < 0.001$). This lack of fit was due to visitation and capture heterogeneity caused by the presence of transients (Test3.SR: $P < 0.001$) and trap-happiness (Test2.Ct: $P = 0.004$). The other two components (Test3.Sm and Test2.Cl) were not significant (Appendix S5). In order to correct both sources of heterogeneity, our initial model included transience and trap-response constraints in both the visitation and capture probabilities, allowing us thus to greatly decrease overdispersion ($\hat{c} = 1.16$, $\chi^2 = 13.93$, df = 12, $P = 0.30$) (Appendix S5).

Yearly-capture pooling models performed better than half-year pooling models, where the lasts showed lower estimates (and two *pent* equal to zero) and precision (see results of half-year pooling models in Appendix S3). Fourteen models represented the total

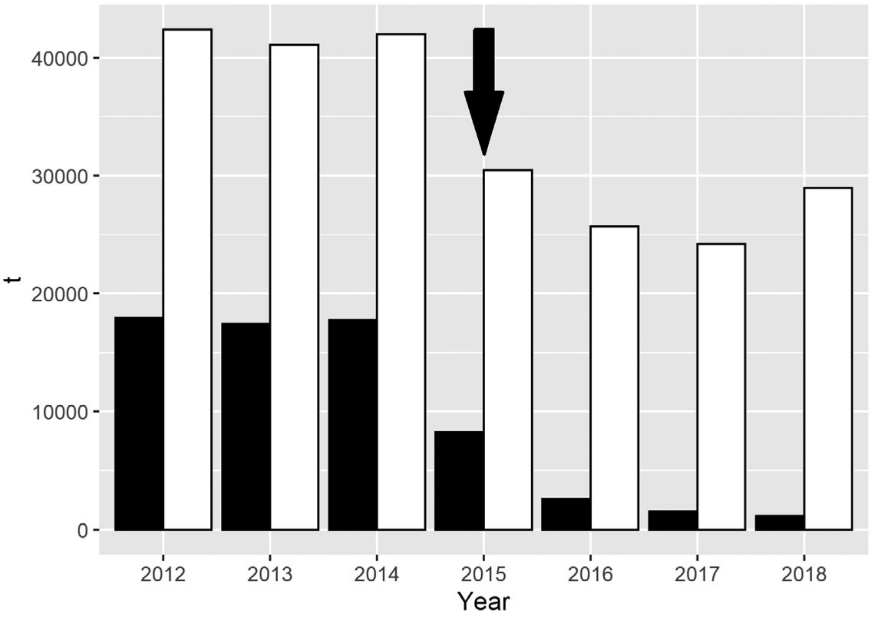

Figure 2. Total metric tonnes (t) of ORGAN+WASTE (the waste fraction and organic fraction of the municipal selective rubbish collection) (white bars) and OMA (organic matter available as food for vultures) (black bars) in Orís landfill during the study period (2012 to 2018). Before the WTC (2012 to mid-2015), WASTE with organic matter were poured into the landfill without separation. After WTC (mid-2015 to 2018), organic matter from WASTE and ORGAN was separated before being poured into the landfill. Arrow indicates the year WTC was implemented.

QAIC$_c$ weight (Table 1 and Appendix S6). The most parsimonious model had 43% support from the data and was 2.53 times greater than the second one (17% of QAIC$_c$ weight). However, both models performed similarly (ΔQAIC$_c$ <2), therefore they were averaged to make inferences about population parameters (Appendix S7). Both models indicated that there is a negative effect on visitation probability due to the decrease in the amount of organic matter dumped in the landfill after the WTC was opened, and that it was modelled by the Landfill Effect (LE) (Table 1). Newly marked vultures had lower visitation probability rates (0.45 ± 0.03) than vultures captured more than once (hereafter residents). Resident vultures experienced a decrease in visitation rates associated to the change in landfill waste management, from 0.82 ± 0.03 in 2012–2015 to 0.76 ± 0.03 in 2015–2018. Applying Pradel *et al.*'s (1997) formula, the proportion of transients in newly marked vultures for both periods were 0.45 ± 0.08 and 0.41 ± 0.05, respectively. The capture probability of vultures not captured at previous periods was lower (0.26 ± 0.03) than those captured at the previous period (0.35 ± 0.02). The super-population size estimated was 5,034 ± 179, while annual abundance increased from 1,520 ± 211 to 2,304 ± 172 during the study period (Figure 3).

Determinants of the vulture population at the landfill

An increase of 720 new breeding pairs of Griffon Vultures was estimated in Catalonia between the two census dates (2008/9 and 2018) (average increase of 80 ± 1.81 pairs/year). The most parsimonious model took the N-Census covariate as the best predictor of annual abundance estimated from POPAN, with 54% of AIC$_c$ weight (Table 2). Both variables were strongly positively related (Intercept = 150.19 ± 605.59, Slope = 1.12 ± 0.38, r = 0.79, r^2 = 0.63, P = 0.03). The second-best model included the OMA covariate as predictor (35% AIC$_c$ weight) and had a strong negative relation with N-POPAN (Intercept = 2150.15 ± 107.5, Slope = –0.02 ± 0.01, r = –0.75, r^2 = 0.57, P = 0.05). The best model coefficient estimates indicate that for every additional breeding pair in the N-Census we can expect the POPAN abundance estimate to increase by an average of 1.12 individuals (y = 150.19 + 1.12N-Census) (Figure 4).

Discussion

We analysed the effect of the amount of organic matter dumped in a landfill on the population parameters of the Griffon Vultures that frequented the site both before and after the installation of a WTC. The amount of organic matter tipped in the landfill fell greatly after the WTC came into operation (from 17,942.03–17,775.45t before WTC to 8,285.73–1,155.06t after WTC). Our results shows that the number of vultures attending the site is high (between 1,520 and 2,304 per year; super-population size = 5,034 individuals) and relevant at a Catalan local population scale (1,628 breeding pairs in 2018; Del Moral and Molina 2018) and close regions (some transients from Spain and France). In agreement with our expectations, the landfill visitation rates of the vultures fell and the overall number of vultures at the landfill increased during the study period. Achieving these results was possible using a remarkable combination in our study: the implementation of a seven-year ringing scheme of c.3,000 captured birds in a landfill where waste management varied drastically the food availability during the study period. In addition, the application of POPAN models allowed us to jointly estimate visitation probability and local abundance while correcting the effects of transience and trap-dependence, two common sources of bias for parameter estimation in capture-recapture studies.

Previous studies on vulture species have shown positive effects of supplementary food (Piper *et al.* 1999) as well as negative effects of food shortage as a consequence of either declines in ungulate populations (Virani *et al.* 2011) or the closure of feeding stations (Martínez-Abraín *et al.* 2012). Griffon Vultures are known to forage

Table 1. Most parsimonious POPAN models that best fit Griffon Vulture *Gyps fulvus* capture-recapture data of Orís landfill during the study period (2012–2018) at Catalonia, Spain (NE Iberian Peninsula). Models in bold were used for parameters inference using model averaging.

Model	QAIC$_c$	ΔQAIC$_c$	w$_i$	Model Likelihood	*k*	QDeviance	Model predictions
ϕ(PriorCapL+LE) p(PriorCapL)pent(t)	**4306.35**	**0.00**	**0.43**	**1.00**	**12**	**−8878.70**	**Visitation probability:** transience and effect of the landfill management on residents' visitation. **Capture probability:** trap-dependence and not time effect for previously caught individuals. **Entrance probability:** time-dependent.
ϕ(PriorCapL+LE) p(PriorCapL+LE)pent(t)	**4308.15**	**1.80**	**0.17**	**0.41**	**13**	**−8878.91**	**Visitation probability:** transience and effect of the landfill management on residents' visitation. **Capture probability:** trap-dependence and effect of the landfill management on previously caught individuals. **Entrance probability:** time-dependent.
ϕ(PriorCapL+LE+t)p(PriorCapL) pent(t)	4308.91	2.56	0.12	0.28	15	−8882.18	Visitation probability: transience and time-dependent effect of the landfill management on residents' visitation. Capture probability: trap-dependence and not time effect for previously caught individuals. Entrance probability: time-dependent.
ϕ(PriorCapL+LE+t)p(PriorCapL+t) pent(.)	4310.18	3.83	0.06	0.15	15	−8880.91	Visitation probability: transience and time-dependent effect of the landfill management on residents' visitation. Capture probability: trap-dependence and time-dependent effect for previously caught individuals. Entrance probability: not time effect.
ϕ(PriorCapL+LE+t)p (PriorCapL+LE)pent(t)	4310.88	4.53	0.04	0.10	16	−8882.23	Visitation probability: transience and time-dependent effect of the landfill management on residents' visitation. Capture probability: trap-dependence and effect of the landfill management on previously caught individuals. Entrance probability: time-dependent.
ϕ(PriorCapL+LE)p(PriorCapL+t) pent(t)	4311.09	4.74	0.04	0.09	17	−8884.04	Visitation probability: transience and time-dependent effect of the landfill management on residents' visitation. Capture probability: trap-dependence and time-dependent effect for previously caught individuals. Entrance probability: time-dependent.
ϕ(PriorCapL)p(PriorCapL)pent(t)	4311.45	5.10	0.03	0.08	11	−8871.58	Visitation probability: transience. Capture probability trap-dependence. Entrance probability: time-dependent.
ϕ(PriorCapL+OMA)p(PriorCapL) pent(t)	4312.93	6.59	0.02	0.04	15	−8878.16	Visitation probability: transience and effect of organic matter poured in the landfill on residents' visitation. Capture probability trap-dependence. Entrance probability: time-dependent.
ϕ(PriorCapL+LE)p (PriorCapL+LE+Effort)pent(t)	4313.05	6.70	0.02	0.04	17	−8882.08	Visitation probability: transience and time-dependent effect of the landfill management on residents' visitation. Capture probability: trap-dependence, effect of the landfill management and capture effort on previously caught individuals. Entrance probability: time-dependent.

(*Continued*)

Table 1. (*Continued*)

Model	QAIC$_c$	ΔQAIC$_c$	w$_i$	Model Likelihood	*k*	QDeviance	Model predictions
ϕ(PriorCapL+LE)p (PriorCapL+Effort)pent(t)	4313.05	6.70	0.02	0.04	17	−8882.07	Visitation probability: transience and time-dependent effect of the landfill management on residents' visitation. Capture probability: trap-dependence and effect of the capture effort on previously caught individuals. Entrance probability: time-dependent.
ϕ(PriorCapL+LE+t)p(PriorCapL+t) pent(t)	4314.05	7.70	0.01	0.02	19	−8885.12	Visitation probability: transience and time-dependent effect of the landfill management on residents' visitation. Capture probability: trap-dependence and time-dependent effect for previously caught individuals. Entrance probability: time-dependent.
ϕ(PriorCapL)p(PriorCapL+Effort) pent(t)	4314.06	7.71	0.01	0.02	16	−8879.05	Visitation probability: transience. accounts for transience and is constant over time for residents. Capture probability: trap-dependence and effect of the capture effort on previously caught individuals. Entrance probability: time-dependent.
ϕ(PriorCapL+LE)p(t)pent(LE)	4314.12	7.78	0.01	0.02	13	−8872.94	Visitation probability: transience and time-dependent effect of the landfill management on residents' visitation. Capture probability: time-dependent. Entrance probability: effect of the landfill management.
ϕ(PriorCapL+LE)p(.)pent(t)	4314.72	8.37	0.01	0.02	11	−8868.32	Visitation probability: transience and time-dependent effect of the landfill management on residents' visitation. Capture probability: not time effect. Entrance probability: time-dependent.
ϕ(.)p(.)pent(.) (Null model)	4478.37	172.02	0.00	0.00	4	−8690.61	Visitation probability: not time effect. Capture probability: not time effect. Entrance probability: not time effect.

w$_i$ = QAIC weight, *k* = number of parameters. Model parameters are: ϕ, landfill visitation probability; *p*, capture probability, *pent*, probability of entry; *t*, variation over time; ., constant over time; PriorCapL, previous capture function; Effort, days of sampling effort per year; LE, effect in time due to change landfill waste management (period 1: 2012 to mid-2015 and period 2: mid-2015 to 2018); and OMA, organic matter available for vulture consumption.

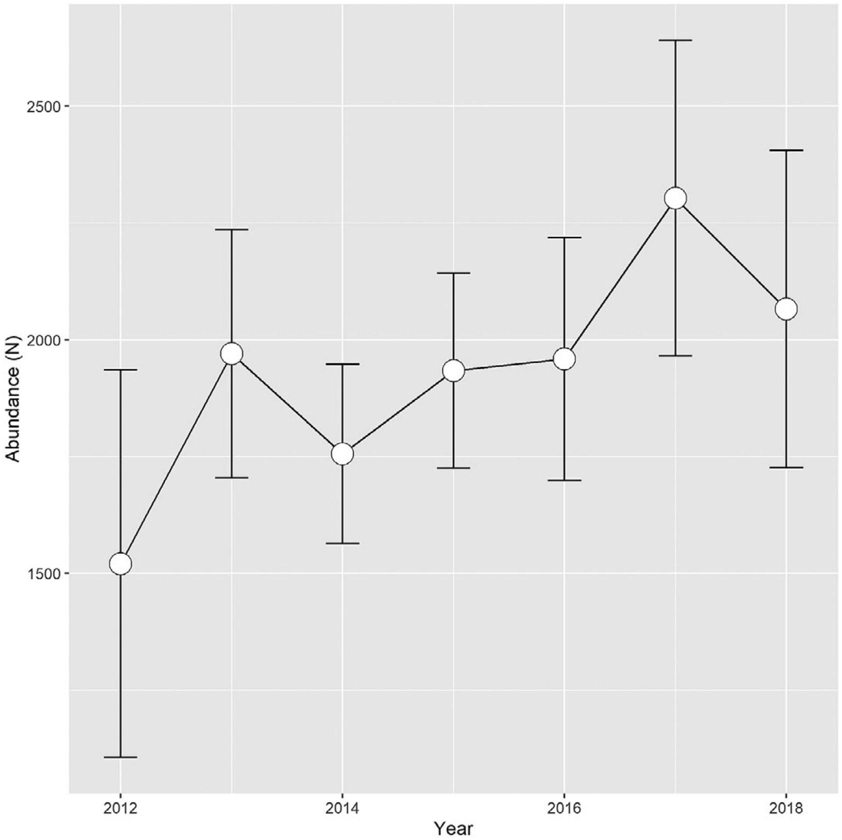

Figure 3. Estimated total abundance per year of the Griffon Vulture population in the Orís landfill based on the model average of the two most fitted POPAN models. Error bars represent the 95% CI.

Table 2. Linear regression models constructed with estimated abundance of POPAN model as response variable and N-Census (number of breeding pairs census) and organic matter available (OMA) in Orís Landfill as predictive variables.

Variable	AIC_c	ΔAIC_c	w_i
N-Census	75.86	0	0.54
OMA	76.96	1.09	0.31
Null	78.72	2.86	0.13
N-Census + OMA	82.84	6.98	0.01

AIC_c = Akaike's information criterion corrected for small sample sizes, w_i = AIC_c weight.

opportunistically and concentrate near reliable food sources such as landfills. It has been also suggested that the survival probabilities of inexperienced Griffon Vultures may increase as they learn to frequent landfills during migration periods characterized by food shortages as it is 'easier' to feed here than forage for carcasses (Garrido *et al.* 2002). Our results suggest that the residents' visitation rate was modulated by the decrease in food resources available at the landfill that caused a permanent emigration of individuals. Previous studies have evaluated responses in population parameters of opportunistic species after a decrease in food availability in landfills. For example, after the closure of an open-air rubbish dump in Kenya, spotted hyenas *Crocuta crocuta* tended to increase their home range size and diminish their near-dump core area groups (i.e. an increase in daily dispersion and a decrease in core-size groups) when foraging for food (Kolowski and Holekamp 2007). Similarly, another over-abundant opportunistic species (Red Fox *Vulpes vulpes*) showed an increase in home range size after a drastic reduction in anthropogenic food availability (Bino *et al.* 2010). Payo-Payo *et al.* (2015) analysed the same effect on Yellow-Legged Gull *Larus michahellis* and showed that after the closure of a landfill, the immediate behavioural response of the species was to disperse and exploit other food resources. On the contrary, Katzenberger *et al.* (2019) found no short-term effect of a landfill closing on reproductive parameters of a local Egyptian Vulture *Neophron percnopterus* population and was explained by the sufficient alternative food sources available around. Griffon Vultures show large home ranges, can travel long distances on foraging trips and visit several feeding sites by day (García-Ripollés *et al.* 2011, Monsarrat *et al.* 2013). The reduction of food availability in a small scale (e.g. a landfill) can lead to increased individual dispersion rates since this species tends to broaden its diet and adapt its foraging movements as a behavioural response to food availability (Donázar *et al.* 2010, Zuberogoitia *et al.* 2013). Therefore, the decrease in the visitation probability we observed is probably explained by a higher permanent emigration rate in search of other food resources as food supply declined in Orís landfill.

One of the expected benefits of a reduction of dumped organic matter is a decrease in the local abundance of opportunistic species that may in turn be involved in wildlife-human conflict, such as vultures (Margalida *et al.* 2014). Interestingly, our results suggest that the methods of waste management applied at Orís landfill, despite drastically reduced available food for scavengers, did not by themselves reduce the local abundance of vultures. One possible

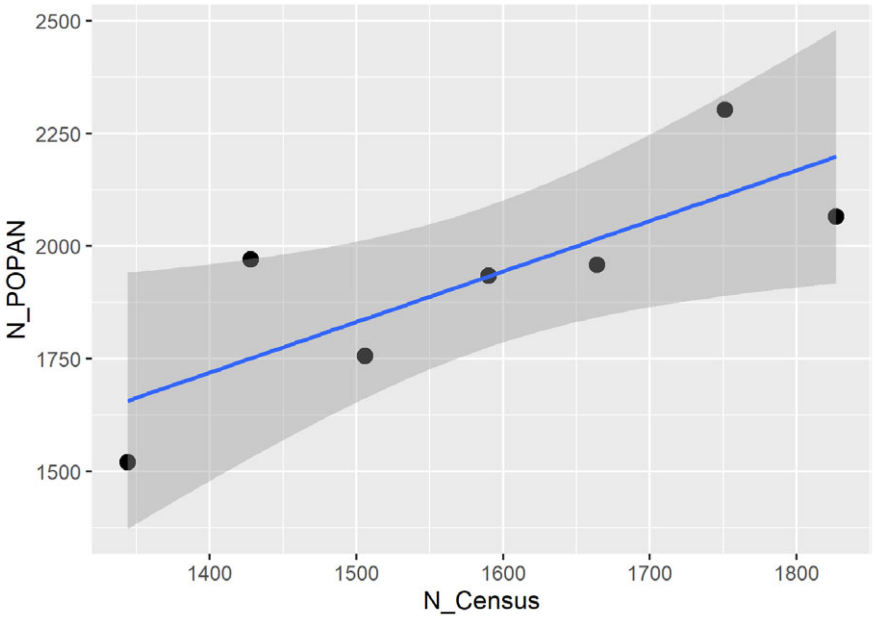

Figure 4. Relation between the estimated POPAN model abundance of vultures attending the landfill (N-POPAN) and number of breeding pairs in Catalonia (N-Census). The relationship trend line between the two variables is shown and the shadowed area represents the 95% CI.

explanation is that the process of waste triage at the WTC is inefficient at separating large pieces of organic matter (all fragments >18 cm of the WASTE and >12 cm of the ORGAN is dumped). These large pieces of food can still be used by very large species like Griffon Vultures. In fact, numbers of smaller scavenger species such as Yellow-legged Gull have markedly decreased in the landfill over the same period (J. Baucells, pers. comm.). In turn, our abundance estimates showed a positive trend during the study period. Previous studies have shown local population declines because of food shortage caused by regulations against TSE at the Ebro Valley in Spain (Camiña and Montelío 2006, Donázar *et al.* 2009). These regulations implied a severe reduction of food available for vultures over the whole country. In our case, though, food shortage occurred very locally and did not affect other food resources in our study area such as vulture restaurants, wild ungulate populations, livestock and other landfills. The fact that the species will travel enormous distances daily to forage (120–300 km according to GPS-tagged vultures, García-Ripollés *et al.* 2011, Harel *et al.* 2016) suggests that a proportion of individuals from the regional population visit the landfill to feed at some point and include the site as part of their frequent foraging areas. In fact, Griffon Vultures may visit several feeding sites in one day and may have dozens of supplementary feeding sites within their home ranges (Monsarrat *et al.* 2013). In addition to this, the decreasing visitation rate we found indicates that a higher number of transients are visiting the landfill, which is proportional to the increasing regional population that is also reflected in our abundance estimate. These results indicate that it is not OMA that determines the abundance of vultures visiting the Orís landfill but, rather, the increasing population of vultures in Catalonia or even at the scale of the Iberian Peninsula. Griffon Vulture has increased steadily during recent decades in Spain achieving 30,946 breeding pairs in 2018 census (c.90% of European population; Del Moral and Molina 2018), warranting its classification as 'Least Concern' globally. Even so, it is a very sensitive species to pre-adult and adult mortality since it has a slow life strategy. In fact, some local populations of Griffon Vulture show high levels of non-natural mortality caused by collisions with wind turbines, power lines and vehicles, electrocutions and poisonings, so it cannot be ruled out that the observed trends of growing local populations result from source-sink dynamics occurring at regional scales (e.g. Hernández-Matías *et al.* 2013). In addition, all vulture species are highly sensitive to diclofenac intoxication which use is legal in Spain (Margalida *et al.* 2014). So even though the breeding population of Griffon Vulture is still markedly increasing in this country, the last census in 2018 revealed that some core populations showed a marked decrease for the first time in decades (i.e. Aragón and Navarra). This might suggest that this species has a more vulnerable status than that derived from a crude interpretation of its abundance. Under such a scenario, it appears relevant to assess the expected effects on vulture populations of a large-scale reduction of the amount of organic matter dumped in landfills in compliance with European directives, which will remarkably decrease food resources for scavenger species (e.g. Margalida and Colomer 2012). In relation to the above, Spain has 182 landfills where about the half of all waste is still dumped, which makes it one of the European countries that has invested the least in circular economy strategies (Eurostat 2021). However, the new agenda contained in Royal Decree 646/2020, of July 7, which regulates the disposal of waste in landfills, suggests that the application of the European directives is underway, although the state-wide synchronous enforcement -which is crucial to foresee a large-scale food reduction for scavengers, is uncertain.

Despite the clear patterns we detected, several methodological considerations are worth discussion. One of the POPAN model assumptions is that recaptures are instantaneous and violating this could lead to a disproportionate survival estimate (in our case, visitation probability) of all members of the marked population over the sampling occasions (Lindberg and Rexstad 2002). Pooling observations violates this assumption; however, it has been proven that can greatly improve population parameter estimates. Smith and Anderson (1987) and Hargrove and Borland (1994) showed that estimates are unbiased as long as survival rates are higher than

50% (our visitation probability is >75%). O'Brien *et al.* (2005) concluded (and recommended) that violating the instantaneous sampling assumption can highly improve the recapture and survival estimates, when: (i) recapture rate is >0.2 (here, 0.32), (ii) a great number of marked individuals (>1,000, the bias is negligible, here, ~3,000) and (iii) the most constant the estimates are, the bias becomes negligible (both visitation and recapture estimates are constant over the two-period tested for the first, and constant over the whole study period for the second parameter). Therefore, and based on these criteria, we believe that our estimates are unbiased and reliable even though not meeting the instantaneous sampling assumption (Appendix S3).

Transience and trap-dependence are common sources of bias when estimating survival and capture probabilities in CMR models (Pradel *et al.* 1993, 1997). For the POPAN model the only available tool for assessing both heterogeneity sources is the PriorCapL function in MARK program and has hardly been used for these purposes (Boys *et al.* 2019). Particularly for transience, several parameterizations have been developed to unravel the underlying biological meaning of this phenomenon when modelling and it has been suggested that is due to differences in age classes, presence of true transients, a permanent emigration due to marking effect or the cost of first reproduction (Genovart and Pradel 2019, Oro and Doak 2020). When using POPAN models, these parameterizations are out of the scope of MARK program, which certainly limits the interpretability of the transient effect. In Orís landfill, vultures of all age classes are captured every ringing session and unpublished analysis using the same capture-recapture data have shown marked differences between age classes (authors' unpubl. data). Similar to the CJS model, in POPAN models not all parameters are identifiable (e.g. final survival and catchability); however, and as we did here using the PriorCapL function, one way to proceed is assuming equal catchability over all sampling occasions to make all parameters identifiable, and importantly, for unbiased abundance estimates (Nichols *et al.* 1984, Schwarz and Arnason 2019). The abundance estimate is particularly sensitive in Jolly-Seber models when there is a trap-response effect in the data (Nichols *et al.* 1984). In our case, trap-happiness was detected and is a frequent phenomenon when baited traps are used (Pradel and Sanz-Aguilar 2012). Trap-happiness can produce serious underestimates of abundance, although improving precision of the survival estimate by decreasing its variance (Nichols *et al.* 1984). In presence of trap-dependence, POPAN models are unbiased when estimating the number of animals using the study area throughout the study period (super-population size) and so provides a good estimate of the pool of vultures that visit the landfill (Arnason and Schwarz 1995, 1999, Schwarz and Arnason 1996). In this way, improving survival (in our case, visitation probability) and catchability with the applications of tools for correcting heterogeneity (PriorCapL accounting for transients and trap-dependence, and applying the variance factor inflation of the first model $\hat{c} = 1.16$), suggest that our estimates are unbiased and accurate, and consequently, the abundance estimates also improved (Nichols *et al.* 1984, Schwarz 2001).

Management implications

Reducing the amount of organic matter dumped in landfills is a desirable goal to reduce the negative impact these can cause on vultures and other species. For example, landfills can alter foraging behavior (Deygout *et al.* 2010), the spatial distribution of nests (Tauler-Ametller *et al.* 2017), and also provide low-quality and dangerously polluted food (Genovart *et al.* 2010, Tauler-Ametller *et al.* 2019, Ortiz-Santaliestra *et al.* 2019). Our findings based on empirical data suggest that vulture populations visiting landfills cannot be reduced by current methods of organic matter reduction because, even if the amount of food available is drastically reduced, there still seems to be enough to support a large local population. In turn, the overall population dynamics of a regional population seems to be a major determinant in the presence of vultures at this type of facilities if resources are still available. Although the Griffon Vulture obtain most of its food from domestic and wild ungulates (Margalida *et al.* 2012), a regional and synchronic application of organic reduction measures in landfills could threaten an alternative feeding source, especially in winter when other resources are scarce and landfills could be supporting the energetic requirements of the species (Garrido *et al.* 2002, Margalida *et al.* 2018). European directives designed to boost the transition to a circular economy aim to reduce the amount of waste dumped in landfills to 10% or less by 2035. In order to maintain the ecosystem services that vultures provide (Whelan *et al.* 2008, Moleón *et al.* 2014) and, given that vultures are currently one of the most globally threatened groups of birds (Ogada *et al.* 2012, Margalida and Ogada 2018, Safford *et al.* 2019), these measures should be accompanied by actions aiming to conserve scavenger birds that currently, to a certain degree, depend on these sites for survival (Garrido *et al.* 2002). For example, the construction of a randomly distributed feeding small-stations network closely resembles natural patterns of carrion discovery by vultures and could be a good alternative management strategy helping to preserve the efficiency of natural scavenging services (Deygout *et al.* 2009, Donázar *et al.* 2009, Cortés-Avizanda *et al.* 2012). Carrion inputs should be in accordance with the needs of all vulture species attending these feeding stations (see Moreno-Opo *et al.* 2015). Likewise, the abandonment of livestock carcasses originating from extensive animal husbandry and transhumance could also help maintain populations of avian scavengers since it promotes natural foraging (Olea and Mateo-Tomás 2009, Margalida *et al.* 2018). The establishment of protection zones for the feeding of necrophagous birds (or ZPAEN zones), a conservation measure based on the European directives that established the 'Protection areas for the feeding of necrophagous species of European interest' is an ongoing strategy that has helped to improve vulture populations and the important ecosystem services they provide (Margalida *et al.* 2012, Morales-Reyes *et al.* 2017). However, efforts should aim to strengthen and expand these ZPAEN zones in the underrepresented areas. For example, the coverage of these zones in Catalonia is the lowest in all of Spain (13% of the territory) and is located in the most forested areas at the northwest of the autonomous community, which does not cover the entire distribution of Griffon Vultures here (see supplementary material in Morales-Reyes *et al.* 2017). In all cases, population monitoring and the estimation of key demographic parameters will be necessary to study population responses to the implemented measures. Finally, this conservation measure for scavenger species must be adopted on a regional basis when sanitary measures are applied to reduce the availability of food in sites such as landfills. Sanitary and environmental policies at European level must be integrated since conservation measures implemented at a smaller scale (e.g. country) are not enough to protect a regional population, especially with these highly-mobile species that cross borders (Arrondo *et al.* 2018).

Acknowledgements. We are deeply grateful to all naturalists of the Grup d'Anellament de Calldetenes-Osona (GACO) and Jordi Baucells of the Institut Català d'Ornitologia (ICO) for providing the database of ringed vultures. We are indebted to Gary White, Jim Hines and Rebecca Boys for guidance and advice with capture-recapture modelling. We also thank J. Baucells of Gestió de Residus i Biodiversitat, SL, Anna Riera of the Consorci per a la Gestió dels Residus Urbans d'Osona, and Verònica Tomàs of Ferrovial for providing landfill waste data. We are very grateful to A. Margalida, D. Oro, and two anonymous referees for their helpful comments which greatly improved an earlier draft of the manuscript. This study was partially funded by the PID2020-117909RB-I00 from the I+D+I National Plan of the Ministry of Science, Innovation and Universities.

Supplementary Materials. To view supplementary material for this article, please visit http://doi.org/10.1017/S0959270922000107.

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Supplementary Material

Reduction of organic waste in a landfill lowers the visitation probability but not the local abundance of a long-lived scavenger species

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Appendix S1

Table S1. Capture-recapture effort (days) of Griffon Vultures *Gyps fulvus* each month and year at the Orís landfill in Catalunya, Spain (NE Iberian Peninsula).

Months	2012	2013	2014	2015	2016	2017	2018	Total
Jan				1		2	1	4
Feb		1	1		1	1	2	6
Mar		4		1	2	1	1	9
Apr	1	2	5	2	1	3	1	15
May	1	1	2	3	2	2	2	13
Jun	2	3		3	1	1	1	11
Jul	2	2	1	2	2	1	1	11
Aug		2	1	3	2	4		12
Sep		2	1	2		2	2	9
Oct		2	1	3	3	3		12
Nov	2	1	1	2	1	1	1	9
Dec	1	2	2	1	1	1	1	9
Total	9	22	15	23	16	22	13	120

Appendix S2

Annual organic matter estimates available for vultures (OMA) at Orís landfill during the 2012 to 2018 period.

To calculate OMA for the 2012-2018 we used data of the *Consorci per a la gestió de residus urbans d'Osona* trimestral reports of 2015 to 2018 (the date where the WTC became operational) and the total entry values of waste to the Orís landfill in 2012-2018. The trimestral reports consist of waste characterizations (in percentages) of ~1000 kg samples taken before and after the WTC triage process to determine what materials the waste is composed of in each stage. The total entry values of waste are the monthly metric tons of WASTE that entered the landfill each year and as of May 2015, also the metric tons of ORGAN. Therefore, to calculate OMA for each year, we departed from the total entry values of ORGAN and WASTE fraction of municipal selective collection before WTC triage, the organic residuals poured in the landfill from ORGAN after WTC triage, and annually averaged organic matter percentages of the trimestral reports of ORGAN and WASTE before and after the WTC triage. The annual value of OMA for the mid-2015 to 2018 period was calculated as follows:

$$OMA = [(TWL - R_{ORGAN}) * \%R_{WASTE}] + (R_{ORGAN} * \%R_{ORGAN})$$

Where TWL=Metric tons of total ORGAN and WASTE, R_{ORGAN}= Metric tons of >12 cm ORGAN residual waste poured into the landfill, and metric tons of <12 cm ORGAN residual waste discarded after composting process and poured into the landfill, $\%R_{WASTE}$=Annual percentage of WASTE organic residuals poured into the landfill, $\%R_{ORGAN}$= Annual percentage of ORGAN organic waste poured into the landfill and R_{ORGAN}=. For 2012 to mid-2015 OMA was estimated as follows:

$$OMA = TWL * \%E_{WASTE}$$

Where $\%E_{WASTE}$= Annual percentage of WASTE organic waste poured into the landfill. The $\%E_{WASTE}$ value calculated for the first two quarters of 2015 (before the WTC was operational) was used to calculate the 2012, 2013 and 2014 OMA's since there is no data available for these years.

Table S2. Summary of Orís landfill waste data during the period 2012 to 2018 in central Catalonia, Spain.

Year	TWL	**OMA**	%OMA	$R_{ORGANpre}$	$R_{ORGANpost}$	$\%R_{WASTE}$	$\%R_{ORGAN}$	$\%E_{WASTE}$
2012	42,366.06	**17,942.03**	42.35					42.35
2013	41,115.42	**17,412.38**	42.35					42.35
2014	41,972.73	**17,775.45**	42.35					42.35
2015	30,440.51	**8,285.73**	27.22	561.42	428.86	14.28	9.49	42.35
2016	25,659.06	**2,603.39**	10.15	788.04	700.62	10.54	7.09	38.42
2017	24,217.15	**1,510.11**	6.24	732.44	959.3	6.51	6.07	27.18
2018	28,946.64	**1,155.06**	3.99	891.14	1250.54	4.17	4.26	26.80

TWL=Metric tons of total ORGAN and WASTE, $R_{ORGANpre}$= Metric tons of >12 cm ORGAN residual waste poured into the landfill, $R_{ORGANpost}$= Metric tons of <12 cm ORGAN residual waste discarded after composting process and poured into the landfill, $\%R_{WASTE}$=Annual percentage of WASTE organic waste poured into the landfill, $\%R_{ORGAN}$= Annual percentage of ORGAN organic waste poured into the landfill, $\%E_{WASTE}$= Annual percentage of WASTE organic waste poured into the landfill. Data used for analysis in bold.

Appendix S3. Estimates of half-year pooling models

Here, we used the half-year of captures and omitted the other part of the data to create the capture histories (following Peach *et al.* 2001 and Boys *et al.* 2019). In order to decrease the effect of transients in our analysis, we considered the data obtained from July to December of each year (from 2012 to 2018) because it represented an interval with fewer individuals that were captured only once (ca. 80 %), and we discarded the data from January to June, when individuals captured only once were almost 90% of the total. The U-CARE goodness-of-fit test using a Cormack-Jolly-Seber-type (CJS) structure detected the presence of transients (Test3.SR: $\chi^2 = 51.48$, df = 5, p-value < 0.001) and trap-response (Test2.CT: $\chi^2 = 15.12$, df = 4, p-value = 0.004). Therefore, we proceeded the same way as the one-year pooling models to account both sources of heterogeneity (See Methods).

The best fitted models were ($\Delta QAIC_c$ < 2): φ(PriorCapL+LE+t)p(PriorCapL)pent(t) and φ(PriorCapL+LE+t)p(PriorCapL+LE)pent(t). Averaged estimates of both models are shown in the table below (Table S3).

Table S3. Real and derived averaged estimates from the best fitted models ($\Delta QAIC_c<2$) using half-year pooling observations.

Parameter	**Estimate±ISE (Low 95%CI – Upper 95%CI)**
ϕ (newly marked vultures)	0.37±0.06 (0.27 – 0.49)
ϕ (after WTC)	0.83±0.04 (0.75 – 0.89) to 0.82±0.05 (0.71 – 0.89)
ϕ (before WTC)	0.77±0.05 (0.65 – 0.86) to 0.67±0.05 (0.57 – 0.76)
p (not captured at previous period)	0.20±0.03 (0.14 – 0.28)
p (captured at previous period and after WTC)	0.30±0.03 (0.25 – 0.35)
p (captured at previous period and before WTC)	0.31±0.03 (0.25 – 0.36)
Pent (2013)	0.27±0.03(0.21 – 0.34)
Pent (2014)	0
Pent (2015)	0.11±0.02 (0.07 – 0.15)
Pent (2016)	0.11±0.03 (0.07 – 0.17)
Pent (2017)	0.20±0.02 (0.16 – 0.24)
Pent (2018)	0
N_{super}	3379.80±198.31 (2991.10 – 3768.49)
N_{2012}	1071.51±194.04 (691.20 –1451.83)
N_{2013}	1308.60±113.26 (1086.61 – 1530.59)
N_{2014}	1094.51±92.43 (913.35 – 1275.67)
N_{2015}	1261.00±94.87 (1075.04 – 1446.95)
N_{2016}	1407.37±109.29 (1193.16 – 1621.59)
N_{2017}	1745.39±128.96 (1492.63 – 1998.15)
N_{2018}	1168.64±118.37 (936.62 – 1400.65)

Model parameters are: ϕ, landfill visitation probability; *p*, capture probability, *pent*, probability of entry; N_{super}=Super-population size, N_i=abundance in year *i*. ISE=Inconditional Standard Error.

Newly-marked vultures' visitation probability is estimated at 0.37 and is time-dependent before and after the waste treatment centre (WTC) with values ranging from 0.83 to 0.67, which are lower compared to one-year pooling models. Capture probabilities decreased 0.05 compared to one-year pooling models (See Table S7) and two Pent estimates are equal to "0" (2014 and 2018), which suggests that we lose information of entrant individuals using half the year of captures. Variances of the visitation, capture and entry probabilities are greater than the 1-year pooling (i.e., higher standard errors), which suggests that we also lose precision when using capture-recapture histories where part of the data was omitted. Finally, and considering that the whole dataset consists in c.3,000 ringed individuals, and that an important fraction of vultures did not wear rings in each ringing session, the estimate of 3,377 individuals for the super-population is clearly unreliable and biased, since we omitted data from vultures captured only once in January to June, and that were an important fraction of the population that attended the landfill during the study period.

Appendix S4. Description of candidate POPAN models

Table S4. Candidate structures for variability in each parameter type in the POPAN model, used to estimate the demographic parameters of the Griffon Vultures *Gyps fulvus* population at Orís landfill during the study period (2012-2018).

Notation	Description
ϕ(PriorCapL+LE)	Landfill visitation probability is differentiated between transients and residents. Residents' visitation is explained by the additive effect of before and after the WTC.
ϕ(PriorCapL+LE+t)	Landfill visitation probability is differentiated between transients and residents. Residents' visitation is explained by the additive effect of before and after the WTC and is time-dependent within both.
ϕ(PriorCapL+OMA)	Landfill visitation probability is differentiated between transients and residents. Residents' visitation is explained by additive effect of the amount of OMA poured into the landfill.
ϕ(PriorCapL+.)	Landfill visitation probability is constant over time for both transients and residents.

ϕ(PriorCapL+t)	Landfill visitation probability is differentiated between transients and residents. Residents' visitation is time-dependent.
ϕ(LE)	Landfill visitation probability is explained by the periods before and after the WTC was installed.
ϕ(OMA)	Landfill visitation probability is explained by the effect of the OMA poured into the landfill.
ϕ(.)	Landfill visitation probability is constant over time.
ϕ(t)	Landfill visitation probability is time-dependent.
p(PriorCapL+Effort)	Capture probability accounts for immediate trap response. Capture probability is explained by the additive effect of sampling effort each year for individuals previously caught.
p(PriorCapL+LE)	Capture probability accounts for immediate trap response. Capture probability is explained by the additive effect of the periods before and after the WTC and is constant within both periods for individuals previously caught.
p(PriorCapL+LE+t)	Capture probability accounts for immediate trap response. Capture probability is explained by the additive effect of the periods before and after the WTC and is time-dependent within both periods for individuals previously caught.
p(PriorCapL+OMA)	Capture probability accounts for immediate trap response. Capture probability is explained by the amount additive effect of OMA poured into the landfill for individuals previously caught.
p(PriorCapL+LE+Effort)	Capture probability accounts for immediate trap response. Capture probability is explained by the additive effects of the periods before and after the WTC and sampling effort each year for individuals previously caught.
p(PriorCapL+OMA+Effort)	Capture probability accounts for immediate trap response. Capture probability is explained by the amount additive effects of OMA poured into the landfill and sampling effort each year for individuals previously caught.
p(PriorCapL+.)	Capture probability accounts for immediate trap response and is constant over time for individuals previously caught.
p(PriorCapL+t)	Capture probability accounts for immediate trap response and is time-dependent for individuals previously caught.
p(LE+Effort)	Capture probability is explained by the periods before and after the WTC and the additive effect of sampling effort each year.
p(OMA+Effort)	Capture probability is explained by the amount of OMA poured into the landfill and the additive effect of sampling effort each year.
p(Effort)	Capture probability is explained by the sampling effort each year.
p(LE)	Capture probability is explained by the periods before and after the WTC and is constant within both periods.
p(LE+t)	Capture probability is explained by the periods before and after the WTC and is time-dependent within both periods.

p(OMA)	Capture probability is explained by the amount of OMA poured into the landfill.
p(.)	Capture probability is constant over time.
p(t)	Capture probability is time-dependent.
pent(.)	The probability that individuals from the super-population enter the study site is constant.
pent(t)	The probability that individuals from the super-population enter the study site is time-dependent.
pent(LE)	The probability that individuals from the super-population enter the study site is explained by the periods before and after the WTC was installed.
pent(LE+t)	The probability that individuals from the super-population enter the study site is explained by the period before and after the WTC was installed, and is time-dependent within both.
pent(OMA)	The probability that individuals from the super-population enter the study site is explained by the effect of the OMA poured into the landfill.

Model parameters are: ϕ, landfill visitation probability; *p*, capture probability, *pent*, probability of entry; *t*, variation over time; ., constant over time; PriorCapL, previous capture function to account for transience and trap-response; Effort, days of sampling effort per year; LE, effect in time due to change landfill waste management (period 1: 2012 to 2015 and period 2: 2015 to 2018); and OMA, organic matter available for consumption.

Appendix S5

Table S5. Goodness of fit (GOF) test for assessing homogeneity assumptions of the Cormack-Jolly-Seber (CJS) model.

GOF components and models assessed	χ^2	df	$\hat{c}$	p-value
Test3.SR	106.66	5		<0.001
Test3.SM	11.42	9		0.24
Test2.CT	25.76	4		<0.001
Test2.CL	7.33	6		0.29
Full time-dependent CJS model (ϕ_t p_t)	151.17	24	6.29	<0.001
Transience and trap-response treated model (ϕ_{a2*t} p_{t+m})	18.75	15	1.25	0.22

Model parameters are: ϕ_t, time-dependent apparent survival probability; ϕ_{a2*t}, two age-class time-dependent apparent survival probability; p_t, time-dependent capture probability; and p_{t+m}, capture probability time-dependent with an additive effect of trap dependence. Apparent survival probability is renamed at the manuscript as 'landfill visitation probability' (See Introduction).

Appendix S6

Table S6. Whole set of POPAN models using the Griffon Vultures *Gyps fulvus* capture-recapture data of Orís landfill during the study period (2012-2018) at Catalonia, Spain (NE Iberian Peninsula). In bold the models that represent the total quasi-likelihood Akaike's information criterion corrected for effective sample sizes (QAIC$_c$) weight.

Model	QAICc	ΔQAICc	w_i	Model Likelihood	*k*	QDeviance
ϕ(PriorCapL+LE)p(PriorCapL)pent(t)	**4306.35**	**0.00**	**0.43**	**1.00**	**12.00**	**-8878.70**
ϕ(PriorCapL+LE)p(PriorCapL+LE)pent(t)	**4308.15**	**1.80**	**0.17**	**0.41**	**13.00**	**-8878.91**
ϕ(PriorCapL+LE+t)p(PriorCapL)pent(t)	**4308.91**	**2.56**	**0.12**	**0.28**	**15.00**	**-8882.18**
ϕ(PriorCapL+LE+t)p(PriorCapL+t)pent(.)	**4310.18**	**3.83**	**0.06**	**0.15**	**15.00**	**-8880.91**
ϕ(PriorCapL+LE+t)p(PriorCapL+LE)pent(t)	**4310.88**	**4.53**	**0.04**	**0.10**	**16.00**	**-8882.23**
ϕ(PriorCapL+LE)p(PriorCapL+t)pent(t)	**4311.09**	**4.74**	**0.04**	**0.09**	**17.00**	**-8884.04**
ϕ(PriorCapL)p(PriorCapL)pent(t)	**4311.45**	**5.10**	**0.03**	**0.08**	**11.00**	**-8871.58**
ϕ(PriorCapL+OMA)p(PriorCapL)pent(t)	**4312.93**	**6.59**	**0.02**	**0.04**	**15.00**	**-8878.16**
ϕ(PriorCapL+LE)p(PriorCapL+LE+Effort)pent(t)	**4313.05**	**6.70**	**0.02**	**0.04**	**17.00**	**-8882.08**
ϕ(PriorCapL+LE)p(PriorCapL+Effort)pent(t)	**4313.05**	**6.70**	**0.02**	**0.04**	**17.00**	**-8882.07**
ϕ(PriorCapL+LE+t)p(PriorCapL+t)pent(t)	**4314.05**	**7.70**	**0.01**	**0.02**	**19.00**	**-8885.12**
ϕ(PriorCapL)p(PriorCapL+Effort)pent(t)	**4314.06**	**7.71**	**0.01**	**0.02**	**16.00**	**-8879.05**
ϕ(PriorCapL+LE)p(t)pent(LE)	**4314.12**	**7.78**	**0.01**	**0.02**	**13.00**	**-8872.94**
ϕ(PriorCapL+LE)p(.)pent(t)	**4314.72**	**8.37**	**0.01**	**0.02**	**11.00**	**-8868.32**
ϕ(PriorCapL+LE)p(PriorCapL+Effort)pent(LE)	4315.78	9.44	0.00	0.01	13.00	-8871.28
ϕ(PriorCapL+LE+t)p(PriorCapL+LE+Effort)pent(t)	4317.52	11.17	0.00	0.00	20.00	-8883.66
ϕ(PriorCapL+LE+t)p(PriorCapL+Effort)pent(t)	4317.52	11.17	0.00	0.00	20.00	-8883.66
ϕ(PriorCapL+OMA)p(PriorCapL+t)pent(t)	4317.62	11.28	0.00	0.00	20.00	-8883.56
ϕ(PriorCapL+LE)p(t)pent(LE+t)	4318.08	11.73	0.00	0.00	16.00	-8875.03
ϕ(PriorCapL+LE)p(t)pent(t)	4318.08	11.73	0.00	0.00	16.00	-8875.03
ϕ(PriorCapL+LE)p(LE+t)pent(t)	4318.08	11.73	0.00	0.00	16.00	-8875.03
ϕ(PriorCapL+LE)p(LE+t)pent(LE+t)	4318.08	11.73	0.00	0.00	16.00	-8875.03
ϕ(PriorCapL+OMA)p(PriorCapL+OMA+Effort)pent(t)	4319.08	12.73	0.00	0.00	20.00	-8882.11
ϕ(PriorCapL+OMA)p(PriorCapL+Effort)pent(t)	4319.10	12.75	0.00	0.00	20.00	-8882.09
ϕ(PriorCapL)p(t)pent(t)	4319.39	13.04	0.00	0.00	15.00	-8871.70
ϕ(PriorCapL)p(.)pent(t)	4319.97	13.63	0.00	0.00	10.00	-8861.05
ϕ(PriorCapL+OMA)p(.)pent(t)	4321.45	15.11	0.00	0.00	14.00	-8867.62
ϕ(PriorCapL+OMA)p(PriorCapL+OMA)pent(t)	4323.06	16.72	0.00	0.00	20.00	-8878.12
ϕ(PriorCapL+t)p(t)pent(t)	4323.11	16.76	0.00	0.00	19.00	-8876.06
ϕ(PriorCapL+LE)p(Effort)pent(t)	4324.37	18.03	0.00	0.00	17.00	-8870.75
ϕ(PriorCapL+LE)p(Effort)pent(LE+t)	4324.37	18.03	0.00	0.00	17.00	-8870.75
ϕ(PriorCapL+OMA)p(t)pent(t)	4324.93	18.58	0.00	0.00	19.00	-8874.23
ϕ(PriorCapL)p(Effort)pent(t)	4326.01	19.67	0.00	0.00	16.00	-8867.09
ϕ(PriorCapL+t)p(Effort)pent(t)	4328.16	21.81	0.00	0.00	20.00	-8873.03
ϕ(PriorCapL+OMA)p(t)pent(OMA)	4329.29	22.95	0.00	0.00	20.00	-8871.89
ϕ(PriorCapL+LE)p(PriorCapL+LE+Effort)pent(.)	4329.54	23.19	0.00	0.00	12.00	-8855.51
ϕ(PriorCapL)p(PriorCapL+Effort)pent(.)	4330.31	23.96	0.00	0.00	11.00	-8852.73
ϕ(PriorCapL+OMA)p(Effort)pent(t)	4330.80	24.45	0.00	0.00	20.00	-8870.39

ϕ(PriorCapL+LE)p(PriorCapL+Effort)pent(.)	4332.23	25.89	0.00	0.00	12.00	-8852.81
ϕ(PriorCapL+OMA)p(PriorCapL+OMA+Effort)pent(OMA)	4332.55	26.21	0.00	0.00	20.00	-8868.63
ϕ(PriorCapL+LE+t)p(PriorCapL+Effort)pent(.)	4333.03	26.68	0.00	0.00	15.00	-8858.06
ϕ(PriorCapL+OMA)p(PriorCapL+OMA+Effort)pent(.)	4335.75	29.40	0.00	0.00	15.00	-8855.35
ϕ(PriorCapL+OMA)p(PriorCapL+Effort)pent(.)	4338.12	31.77	0.00	0.00	15.00	-8852.98
ϕ(PriorCapL+LE)p(PriorCapL)pent(LE)	4352.13	45.78	0.00	0.00	8.00	-8824.88
ϕ(PriorCapL+LE)p(PriorCapL+LE)pent(LE)	4354.06	47.72	0.00	0.00	9.00	-8824.95
ϕ(PriorCapL+LE)p(PriorCapL)pent(.)	4360.40	54.06	0.00	0.00	7.00	-8814.59
ϕ(PriorCapL+LE)p(PriorCapL+LE)pent(.)	4362.10	55.75	0.00	0.00	8.00	-8814.91
ϕ(PriorCapL)p(PriorCapL)pent(.)	4362.84	56.50	0.00	0.00	6.00	-8810.14
ϕ(PriorCapL+OMA)p(PriorCapL)pent(.)	4366.28	59.93	0.00	0.00	10.00	-8814.74
ϕ(PriorCapL+OMA)p(PriorCapL)pent(OMA)	4366.82	60.48	0.00	0.00	15.00	-8824.27
ϕ(PriorCapL+OMA)p(PriorCapL+OMA)pent(OMA)	4373.62	67.27	0.00	0.00	20.00	-8827.57
ϕ(PriorCapL+OMA)p(PriorCapL+OMA)pent(.)	4376.33	69.99	0.00	0.00	15.00	-8814.76
ϕ(PriorCapL+LE)p(LE+Effort)pent(LE)	4379.62	73.27	0.00	0.00	13.00	-8807.44
ϕ(PriorCapL)p(Effort)pent(.)	4380.59	74.24	0.00	0.00	11.00	-8802.45
ϕ(PriorCapL+LE)p(Effort)pent(LE)	4381.54	75.19	0.00	0.00	13.00	-8805.52
ϕ(PriorCapL+LE)p(Effort)pent(.)	4382.54	76.19	0.00	0.00	12.00	-8802.51
ϕ(LE)p(PriorCapL)pent(t)	4384.01	77.66	0.00	0.00	11.00	-8799.02
ϕ(PriorCapL+OMA)p(Effort)pent(.)	4388.07	81.73	0.00	0.00	15.00	-8803.02
ϕ(PriorCapL+OMA)p(OMA+Effort)pent(OMA)	4388.22	81.87	0.00	0.00	20.00	-8812.97
ϕ(LE)p(PriorCapL+Effort)pent(t)	4389.19	82.85	0.00	0.00	16.00	-8803.91
ϕ(.)p(.)pent(t)	4389.46	83.12	0.00	0.00	9.00	-8789.55
ϕ(LE)p(.)pent(t)	4391.37	85.02	0.00	0.00	10.00	-8789.65
ϕ(OMA)p(PriorCapL)pent(t)	4392.18	85.83	0.00	0.00	15.00	-8798.91
ϕ(LE)p(PriorCapL+Effort)pent(.)	4392.28	85.93	0.00	0.00	11.00	-8790.75
ϕ(LE)p(LE)pent(LE+t)	4393.29	86.94	0.00	0.00	11.00	-8789.74
ϕ(t)p(.)pent(t)	4393.51	87.16	0.00	0.00	14.00	-8795.56
ϕ(.)p(t)pent(t)	4394.50	88.15	0.00	0.00	14.00	-8794.58
ϕ(t)p(LE)pent(t)	4395.53	89.18	0.00	0.00	15.00	-8795.56
ϕ(LE)p(t)pent(t)	4396.51	90.17	0.00	0.00	15.00	-8794.58
ϕ(LE)p(LE+t)pent(LE+t)	4396.51	90.17	0.00	0.00	15.00	-8794.58
ϕ(OMA)p(PriorCapL+Effort)pent(t)	4396.97	90.62	0.00	0.00	20.00	-8804.22
ϕ(LE+t)p(LE+t)pent(LE)	4396.98	90.64	0.00	0.00	16.00	-8796.12
ϕ(PriorCapL+OMA)p(Effort)pent(OMA)	4397.63	91.28	0.00	0.00	20.00	-8803.56
ϕ(.)p(Effort)pent(t)	4397.88	91.53	0.00	0.00	15.00	-8793.22
ϕ(LE+t)p(LE+t)pent(t)	4399.35	93.01	0.00	0.00	18.00	-8797.79
ϕ(t)p(LE+t)pent(t)	4399.35	93.01	0.00	0.00	18.00	-8797.79
ϕ(LE+t)p(LE+t)pent(LE+t)	4399.35	93.01	0.00	0.00	18.00	-8797.79
ϕ(LE+t)p(t)pent(LE+t)	4399.35	93.01	0.00	0.00	18.00	-8797.79
ϕ(t)p(t)pent(t)	4399.35	93.01	0.00	0.00	18.00	-8797.79
ϕ(LE+t)p(t)pent(t)	4399.35	93.01	0.00	0.00	18.00	-8797.79
ϕ(t)p(t)pent(LE+t)	4399.35	93.01	0.00	0.00	18.00	-8797.79
ϕ(OMA)p(.)pent(t)	4399.52	93.17	0.00	0.00	14.00	-8789.55
ϕ(LE)p(LE+Effort)pent(LE+t)	4399.60	93.26	0.00	0.00	16.00	-8793.50
ϕ(OMA)p(PriorCapL+Effort)pent(.)	4400.48	94.13	0.00	0.00	15.00	-8790.61

ϕ(OMA)p(t)pent(t)	4404.47	98.12	0.00	0.00	19.00	-8794.70
ϕ(t)p(OMA+Effort)pent(t)	4405.40	99.06	0.00	0.00	20.00	-8795.78
ϕ(t)p(LE+Effort)pent(t)	4405.57	99.22	0.00	0.00	20.00	-8795.62
ϕ(LE+t)p(LE+Effort)pent(t)	4405.57	99.22	0.00	0.00	20.00	-8795.62
ϕ(LE+t)p(LE+Effort)pent(LE+t)	4405.57	99.22	0.00	0.00	20.00	-8795.62
ϕ(t)p(Effort)pent(t)	4405.58	99.23	0.00	0.00	20.00	-8795.61
ϕ(t)p(Effort)pent(LE+t)	4405.58	99.23	0.00	0.00	20.00	-8795.61
ϕ(LE+t)p(Effort)pent(t)	4405.58	99.23	0.00	0.00	20.00	-8795.61
ϕ(LE+t)p(Effort)pent(LE+t)	4405.58	99.23	0.00	0.00	20.00	-8795.61
ϕ(OMA)p(Effort)pent(t)	4407.46	101.11	0.00	0.00	20.00	-8793.73
ϕ(t)p(LE+Effort)pent(LE)	4410.10	103.76	0.00	0.00	16.00	-8783.01
ϕ(LE+t)p(LE+Effort)pent(LE)	4410.10	103.76	0.00	0.00	16.00	-8783.01
ϕ(t)p(LE+Effort)pent(.)	4411.39	105.04	0.00	0.00	15.00	-8779.70
ϕ(.)p(LE+Effort)pent(.)	4411.73	105.38	0.00	0.00	10.00	-8769.30
ϕ(LE)p(LE+Effort)pent(LE)	4412.13	105.78	0.00	0.00	12.00	-8772.92
ϕ(LE)p(Effort)pent(LE)	4412.75	106.40	0.00	0.00	12.00	-8772.30
ϕ(LE)p(LE+Effort)pent(.)	4413.15	106.81	0.00	0.00	11.00	-8769.88
ϕ(LE)p(PriorCapL)pent(.)	4414.09	107.74	0.00	0.00	6.00	-8758.90
ϕ(t)p(OMA+Effort)pent(.)	4414.86	108.51	0.00	0.00	15.00	-8776.23
ϕ(LE)p(Effort)pent(.)	4414.93	108.58	0.00	0.00	11.00	-8768.11
ϕ(t)p(Effort)pent(.)	4415.42	109.07	0.00	0.00	15.00	-8775.67
ϕ(.)p(Effort)pent(.)	4418.48	112.14	0.00	0.00	10.00	-8762.54
ϕ(OMA)p(OMA+Effort)pent(.)	4420.64	114.29	0.00	0.00	15.00	-8770.46
ϕ(OMA)p(PriorCapL)pent(.)	4421.40	115.05	0.00	0.00	10.00	-8759.62
ϕ(t)p(OMA+Effort)pent(OMA)	4422.20	115.85	0.00	0.00	20.00	-8778.98
ϕ(OMA)p(Effort)pent(.)	4424.41	118.06	0.00	0.00	15.00	-8766.68
ϕ(t)p(OMA)pent(t)	4424.74	118.40	0.00	0.00	19.00	-8774.42
ϕ(OMA)p(OMA+Effort)pent(OMA)	4428.51	122.16	0.00	0.00	20.00	-8772.68
ϕ(OMA)p(Effort)pent(OMA)	4432.56	126.21	0.00	0.00	20.00	-8768.62
ϕ(t)p(.)pent(.)	4436.60	130.25	0.00	0.00	9.00	-8742.42
ϕ(t)p(LE)pent(.)	4438.55	132.20	0.00	0.00	10.00	-8742.47
ϕ(t)p(LE)pent(LE)	4439.95	133.60	0.00	0.00	11.00	-8743.09
ϕ(t)p(OMA)pent(.)	4448.51	142.16	0.00	0.00	15.00	-8742.59
ϕ(t)p(OMA)pent(OMA)	4456.70	150.35	0.00	0.00	19.00	-8742.47
ϕ(PriorCapL+LE)p(.)pent(LE)	4458.12	151.77	0.00	0.00	7.00	-8716.87
ϕ(PriorCapL+LE)p(LE)pent(LE)	4458.89	152.54	0.00	0.00	8.00	-8718.11
ϕ(PriorCapL+LE)p(.)pent(.)	4464.00	157.65	0.00	0.00	6.00	-8708.99
ϕ(PriorCapL+OMA)p(OMA)pent(OMA)	4464.92	158.57	0.00	0.00	20.00	-8736.27
ϕ(PriorCapL+OMA)p(.)pent(OMA)	4465.11	158.76	0.00	0.00	14.00	-8723.97
ϕ(PriorCapL+OMA)p(.)pent(.)	4468.46	162.11	0.00	0.00	9.00	-8710.55
ϕ(PriorCapL)p(.)pent(.)	4473.02	166.68	0.00	0.00	5.00	-8697.96
ϕ(.)p(.)pent(LE)	4476.07	169.72	0.00	0.00	5.00	-8694.91
ϕ(.)p(LE)pent(.)	4476.21	169.87	0.00	0.00	5.00	-8694.77
ϕ(LE)p(.)pent(LE)	4477.93	171.58	0.00	0.00	6.00	-8695.06
ϕ(LE)p(.)pent(.)	4478.20	171.86	0.00	0.00	5.00	-8692.78
ϕ(LE)p(LE)pent(.)	4478.20	171.86	0.00	0.00	6.00	-8694.78

ϕ(.)p(.)pent(.)	4478.37	172.02	0.00	0.00	4.00	-8690.61
ϕ(LE)p(LE)pent(LE)	4479.11	172.76	0.00	0.00	7.00	-8695.89
ϕ(OMA)p(.)pent(.)	4485.96	179.61	0.00	0.00	9.00	-8693.05
ϕ(OMA)p(.)pent(OMA)	4491.49	185.14	0.00	0.00	14.00	-8697.58
ϕ(OMA)p(OMA)pent(.)	4492.89	186.54	0.00	0.00	15.00	-8698.20
ϕ(OMA)p(OMA)pent(OMA)	4499.55	193.20	0.00	0.00	20.00	-8701.64

w_i = $QAIC_c$ weight, *k* = number of parameters. Model parameters are: ϕ, landfill visitation probability; *p*, capture probability, *pent*, probability of entry; *t*, variation over time; ., constant over time; PriorCapL, previous capture function; Effort, days of sampling effort per year; LE, effect in time due to change landfill waste management (period 1: 2012 to 2015 and period 2: 2015 to 2018); and OMA, organic matter available for vultures consumption.

Appendix 7

Table S7. Real and derived averaged estimates from the first two models with $\Delta QAIC_c<2$.

Parameter	Estimate	Inconditional SE	Low 95%CI	Upper 95%CI
ϕ (newly marked vultures)	0.45	0.03	0.40	0.51
ϕ (after WTC)	0.82	0.02	0.76	0.86
ϕ (before WTC)	0.76	0.03	0.69	0.82
p (not captured at previous period)	0.26	0.03	0.20	0.33
p (captured at previous period)	0.35	0.02	0.31	0.39
Pent (2013)	0.25	0.02	0.21	0.30
Pent (2014)	0.03	0.02	0.01	0.09
Pent (2015)	0.10	0.01	0.07	0.13
Pent (2016)	0.10	0.02	0.07	0.13
Pent (2017)	0.16	0.01	0.13	0.19
Pent (2018)	0.06	0.01	0.04	0.09
N_{super}	5034.90	179.25	4683.56	5386.24
N_{2012}	1520.48	211.65	1105.64	1935.32
N_{2013}	1970.56	135.64	1704.71	2236.42
N_{2014}	1755.65	98.14	1563.30	1948.01
N_{2015}	1933.56	106.29	1725.22	2141.90
N_{2016}	1958.90	132.48	1699.23	2218.56
N_{2017}	2303.55	172.26	1965.92	2641.18
N_{2018}	2066.96	173.45	1725.99	2405.92

Model parameters are: ϕ, landfill visitation probability; *p*, capture probability, *pent*, probability of entry; N_{super}=Super-population size, N_i=abundance in year *i*.

Appendix S8

Table S8. Summary of newly mark-released cohorts and first recaptures per year. Previously marked individuals are not included in each cohort released per year column.

Year	Newly captured/released	Time of first recapture						Total
		2013	2014	2015	2016	2017	2018	
2012	393	76	19	14	11	3	3	126
2013	634		93	47	14	14	7	175
2014	386			53	19	26	5	103
2015	380				56	15	6	77
2016	353					46	21	67
2017	457						11	11
2018	334							
Total	2,937	76	112	114	100	104	53	559

Table S9. Reduced m-array table of batch released cohorts and first recaptures per year. Previously and newly marked individuals are both included in each cohort released per year.

Year	Batch released	Recaptures per year						Total
		2013	2014	2015	2016	2017	2018	
2012	393	76	19	14	11	3	3	126
2013	710		116	53	18	18	10	215
2014	521			98	29	32	9	168
2015	545				99	31	11	141
2016	510					93	44	137
2017	634						94	94
Total		76	135	165	157	177	171	881

CHAPTER 2

Age-Specific Demographic Response of a Long-Lived Scavenger Species to Reduction of Organic Matter in a Landfill

Photography courtesy of Arnau Soler Costa

Arévalo-Ayala, D. J., Real, J., Mañosa, S., Aymerich, J., Durà, C., & Hernández-Matías, A. (2023). Age-Specific Demographic Response of a Long-Lived Scavenger Species to Reduction of Organic Matter in a Landfill. *Animals*, 13(22), 3529. https://doi.org/10.3390/ani13223529

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Article

Age-Specific Demographic Response of a Long-Lived Scavenger Species to Reduction of Organic Matter in a Landfill

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Simple Summary: Food availability plays a significant role in modulating populations, especially in species relying on human-generated food sources like landfills. Sudden changes in food access can negatively impact vital parameters such as survival. For long-lived scavenger species, understanding how different age groups respond to these changes is essential since landfills are condemned to be closed. We studied the response in terms of apparent survival of griffon vultures to a decline in landfill organic matter after a waste treatment center became operational. The proportion of transients increased in all age groups. Survival dropped in juveniles and adult residents but increased in immature residents. These findings suggest that vultures permanently emigrated at higher rates due to intensified competition after the reduction in food. Intriguingly, immature resident vultures showed resilience, indicating the presence of high-quality individuals despite the food scarcity. The reasons behind reduced survival in adult residents during the final four study years remain unclear but are potentially linked to non-natural mortality. This research highlights the challenges facing scavengers as European landfill sites close, thereby stressing the need for food scarcity studies and timely conservation measures.

Abstract: Food availability shapes demographic parameters and population dynamics. Certain species have adapted to predictable anthropogenic food resources like landfills. However, abrupt shifts in food availability can negatively impact such populations. While changes in survival are expected, the age-related effects remain poorly understood, particularly in long-lived scavenger species. We investigated the age-specific demographic response of a Griffon vulture (*Gyps fulvus*) population to a reduction in organic matter in a landfill and analyzed apparent survival and the probability of transience after initial capture using a Bayesian Cormack-Jolly-Seber model on data from 2012–2022. The proportion of transients among newly captured immatures and adults increased after the reduction in food. Juvenile apparent survival declined, increased in immature residents, and decreased in adult residents. These results suggest that there was a greater likelihood of permanent emigration due to intensified intraspecific competition following the reduction in food. Interestingly, resident immatures showed the opposite trend, suggesting the persistence of high-quality individuals despite the food scarcity. Although the reasons behind the reduced apparent survival of resident adults in the final four years of the study remain unclear, non-natural mortality potentially plays a part. In Europe landfill closure regulations are being implemented and pose a threat to avian scavenger populations, which underlines the need for research on food scarcity scenarios and proper conservation measures.

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Citation: Arévalo-Ayala, D.J.; Real, J.; Mañosa, S.; Aymerich, J.; Durà, C.; Hernández-Matías, A. Age-Specific Demographic Response of a Long-Lived Scavenger Species to Reduction of Organic Matter in a Landfill. *Animals* **2023**, *13*, 3529. https://doi.org/10.3390/ani13223529

Academic Editor: Mathew Crowther

Received: 17 October 2023
Revised: 1 November 2023
Accepted: 11 November 2023
Published: 15 November 2023

Keywords: Cormack-Jolly-Seber model; Bayesian mark-recapture survival analysis; Bayesian hierarchical model; predictable anthropogenic food subsidies; individual random effect; *Gyps fulvus*; vulture conservation; permanent emigration; apparent survival

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1. Introduction

Food availability is a key factor that shapes demographic parameters and influences the life-history evolution of vertebrates by modulating survival, breeding performance, and, ultimately, population dynamics [1]. In general, animals may exhibit improved survival and reproductive rates when food is abundant [2,3]. Conversely, when food is limited, density-dependent processes may operate and increase both intraspecific competition and emigration probability, resulting in a reduction in the apparent survival probability of individuals [1,2,4,5]. Food can also influence age-dependent survival of species. Non-adult individuals naturally exhibit lower survival performance than adults and survival rates usually improve with age due to the selective disappearance of poor-quality phenotypes and an age-related increase in competence [6,7], which is followed by a progressive decline in survival with age due to physiological senescence [8,9]. While acquiring essential foraging and competitive skills, early-age individuals tend to exploit predictable and abundant food resources as density-dependence is relatively low [10–14]. However, during food shortages, density-dependence intensifies and increases the likelihood of early-age individuals becoming transients (i.e., emigrating permanently from the site) [1,4,14].

Ecosystems worldwide have been modified by human food subsidies, which have had the greatest impact in regions where most food is wasted [15]. Food subsidies such as fisheries discards, supplementary feeding stations or landfills are abundant and highly predictable in space and time (also known as predictable anthropogenic food subsidies, hereafter PAFS) and attract large numbers of species [15–17]. Several studies have shown that PAFS can enhance the survival probability of local populations and, above all, that of young individuals [15,18–20]. However, a progressive or drastic food reduction can occur in PAFS due to the application of local or regional regulations that may have negative demographic consequences for species exploiting these resources. Good examples include sanitary regulations that prohibited leaving cattle carcasses in the wild or in supplementary feeding sites for scavengers during the bovine spongiform encephalopathy (BSE) outbreak [21–24], the establishment of trawling moratoriums [1], and, more recently, the reduction in organic waste and the closure of landfills due to the planning of the European circular economy [14,25,26], which are all evidence of the negative effects of food limitation on survival and population dynamics. Even so, the age-specific demographic response to a depletion of food subsidies is still poorly understood [14,23], particularly in PAFS such as landfills.

Landfills acting as PAFS represent a continuous food source that benefits numerous opportunistic species [17]. This surplus food enhances population survival by providing sustenance year-round and, importantly, for specific age cohorts during periods of natural food scarcity (e.g., juvenile vultures during winter since the use of PAFS is energetically less demanding than searching for wild carrion) [15,27–31]. Yet, feeding in landfills though is hazardous, and may only provide low-quality and polluted food, with the associate risk of exposure to solid waste ingestion (e.g., plastic, rubber, glass or metals) and pathogens [32–35]. In addition, in some ecological systems and species, feeding on landfills could have a detrimental effect on chick and juvenile survival since individuals of these ages are more susceptible than adults to the abovementioned risks (e.g., [36,37]. Nevertheless, for long-lived scavengers such as vultures, the overall trade-off seems to be positive, as current evidence supports the idea that landfills represent an important food source that may partially support some populations [27,30,38–40].

Vultures are long-lived vertebrates and are among the most threatened scavenger species, with more than 80% of species listed as Threatened or Near Threatened on the IUCN

Red List [41–43]. In a transitioning scenario towards a worldwide circular economy model that aims to reduce waste and close landfills, it is imperative to evaluate the effects that these regulations may have on the demographic parameters of the vulture populations that have adapted to feed in these infrastructures [26,38]. Previous studies have demonstrated that a drastic reduction in food availability can increase vulture mobility and decrease the apparent survival of adults [44,45]. However, information is still lacking on whether food reduction in landfills may affect individuals in a population in terms of their age, which could have important demographic consequences given that population dynamics are primarily influenced by adult survival [24].

The aim of the present study was to estimate the age-specific apparent survival and the proportion of transients in a local Griffon vulture (*Gyps fulvus*) population in Central Catalonia (NE Iberian Peninsula), where nearly 3500 individuals were banded over an 11-year period (2012–2022 included) at an open landfill that shifted organic waste management. In mid-2015, in accordance with European policies aimed at closing landfills (Directive 2008/98/EC and Directive (EU) 183 2018/850), a waste treatment center (WTC) was opened to reduce the amount of organic matter that is dumped in this landfill, thereby providing a natural experiment for studying the effects of predictable food shortages on the age-specific apparent survival of griffon vultures. Available data suggest that other environmental factors such as food availability did not change in the area of influence around the landfill since sanitary regulations only allow livestock corpses to be left in the field in ZPAEN areas (protection zones for the feeding of scavenging birds), which are mostly concentrated at high altitude in the north-west pre-Pyrenean and Pyrenean Mountains, and wild ungulates seems to form a low fraction of the diet of the griffon vulture population in this area. A previous study [26] reported a decrease in apparent survival from 82% to 76% between 2012–2018 following the installation of the WTC (which led to an 84% reduction in organic matter from mid-2015 to 2018). This was primarily interpreted as being due to increased permanent emigration as the data was collected from a single site. Apparent survival was estimated for the whole resident local population (i.e., individuals recaptured at least once) without distinguishing between adult and non-adult individuals for whom survival is known to vary (e.g., [46]).

Based on available theory and evidence, we formulated several predictions to be tested in the present study. Capture sessions performed at a single site imply that some captured individuals might opportunistically visit the landfill and do not return (hereafter transients; [47,48]). While transients (i.e., individuals that are never recaptured) are usually accounted for to avoid both lack of fit in the model and underestimation of survival probability, they can also be informative of biological processes occurring at the study site [48,49]. Thus, with declining organic waste, we first predicted that the proportion of adult and non-adult (i.e., juveniles and immatures) transients captured in the landfill would increase, meaning that the site would progressively become less attractive and that newly marked individuals would be more prone to becoming transients after the installation of the WTC [49]. Moreover, PAFS tend to attract and benefit non-adult individuals [15,18,30,50–52] since this age fraction is less constrained in their foraging behavior as they are non-breeders and not bound to a specific territory. Consequently, a reduction in food at the landfill may lead to increased density-dependent intraspecific competition at the site, resulting in a higher rate of permanent emigration (reduced site fidelity) since non-adults are less competitive and experienced than adults [52–54]. By contrast, adults typically have more restricted home ranges, exhibit stronger fidelity to their breeding territory and surroundings (i.e., are more knowledgeable of their foraging grounds), and are physically stronger and more experienced than non-adults [51,53]. Even though the reduction in organic waste in the landfill may lead to increased density-dependent intraspecific competition, adults are likely to be less affected since they can more easily monopolize resources over young individuals [52–54]. Hence, our second prediction is that with decreasing organic matter in the landfill, the apparent survival of adults should be less affected than that of non-adults. Additionally, given that experience and competence are expected to increase with age [6,7], we predict that the apparent survival of immatures should be higher and less affected than that of juveniles after the food shortage. To assess these predictions, we employed a Bayesian hierarchical model with the Cormack-Jolly-Seber (CJS) formulation and age-specific effects to produce estimates of the resident apparent survival probability and the proportion of transients at the studied landfill.

2. Materials and Methods

2.1. Study Area and Sampling

Capture-mark-recapture (CMR) sessions were conducted in the Orís open landfill (42.07° N, 2.20° E, Central Catalonia, NE Spain), where an organic waste management shift occurred in 2012–2022. The landfill opened in 1995 and currently receives substantial amounts of waste from approximately 70,000 households in the counties of Osona and El Ripollès. Up to 2015, unsorted organic waste and other recyclable materials were dumped directly in the landfill, providing food for a large number of opportunistic species including common ravens (*Corvus corax*), yellow-legged gulls (*Larus michahellis*), and various vulture species, including the griffon vulture [26,40]. In compliance with European directives (Directive 2008/98/EC and Directive (EU) 183 2018/850), a waste treatment center (WTC) was constructed in mid-2015 to reduce the amount of waste dumped in the landfill, in which led to a significant reduction in the organic matter available for scavengers and other species. The amount of organic waste was drastically reduced with the opening of the WTC, decreasing from 17,942 tons in 2012 to 450 tons in 2022 (Appendix A).

Due to its location and the amount of waste it receives, the Orís landfill annually accommodates a significant proportion of the population from the central-northern Catalonia and surrounding areas, including the south of France. It is estimated that the number of vultures visiting the landfill has increased steadily each year (up to 2300 individuals) in line with the growth that this population has experienced in recent decades [26]. A permanent roosting site exists on cliffs above the landfill, and there are breeding colonies from 18 km to over 200 km away from the site.

Vultures were captured using a walk-in trap located approximately 200 m from the landfill. Bait consisting of 30–50 kg sheep and cattle carcasses was regularly supplied to attract the vultures. When captured, vultures were marked with a metal and distance-reading band and age was determined by molt plumage patterns, eye and bill coloration, and the type of feathers on their ruffs [55,56]. To ensure accurate age assignment, photos of vultures taken in the field were examined a posteriori. The CMR sessions were conducted year-round, usually once or twice a month, with an average of approximately 15 sessions per year.

2.2. Ageing of Vultures and Sampling Interval

Age was initially assigned according to the calendar year, using five age-classes: 1st calendar year (cy), 2nd cy, 3rd cy, 4th cy, and 5th cy or more [56]. Preliminary analyses (not presented here) using the five age-classes showed that some parameters were non-identifiable, particularly during the first years of the study and for the 2nd–4th cy age-classes. This was due to the low number of vultures identified as 2nd–4th cy ages during the initial years of the study (2012, 2013, and 2014). Therefore, we decided to combine these three age classes into one (see [57]). We pooled these three ages based on the assumption that their biology is similar, given that they are all non-breeders and non-territorial (i.e., low site fidelity). This assumption is supported by the known behavior of wild Griffon vultures in Spain, where they typically recruit into a population during their fifth or sixth calendar year and then become territorial (i.e., high site fidelity, [58]). Individuals of unknown ages, of which the majority were captured during 2012 and 2013 and only comprised 8.5% of the database, were removed from the analyses. For the analyses, we pooled captures into six-month periods (January–June and July–December, two semesters per year). It has been shown that for slow-living species such as vultures, the precision of estimates can significantly improve with larger pooling intervals [59–61]. Given the six-month interval, we reassigned ages based on a calendar year that was closer to a biological cycle, in which each individual vulture changes age at the beginning of the second semester. Although in the Mediterranean region mean hatching dates are in spring, nestlings only begin to leave the nest in summer and autumn and so are more likely to be captured in the landfill during the months of the second semester of any given year [62–64]. Thus, the age classes used for analyses were as follows: "juveniles", 1-year-old individuals; "immatures", 2- to 4-year-old individuals; and "adults", individuals aged 5 years and older.

2.3. Apparent Survival Analysis

We initially tested the goodness-of-fit of the full time-dependent CJS model (i.e., apparent survival and recapture probability vary on each occasion) using U-CARE software v2.2 [65]. As suspected, the data fitted the model poorly ($\chi^2 = 413.16$, df = 155, $p < 0.001$). Heterogeneity was mainly due to the presence of transients in apparent survival (Test3.SR, $p < 0.001$) but also for trap-dependence in recapture probability (Test2.CT, $p < 0.001$, trap-happiness: $z = -6.81$), which suggested that our model should account for both effects.

We employed a hierarchical Bayesian state-space Cormack-Jolly-Seber model to estimate age-specific apparent survival and recapture probabilities [66–69]. The state-space formulation provides a framework for explicitly modeling the biological state and the observation process as realizations of Bernoulli trials. The state process is composed of variables $z_{i,t}$ and f_i, where $z_{i,t}$ is a matrix describing the true biological state of individual i at time t, and f_i, a variable that describes the state of individual i on the first capture occasion, being $z_i,f_i = 1$. The states are modeled as Bernoulli trials in subsequent occasions, considering the product of the survival probability of individual i alive at t that survives until occasion $t + 1$ and the state at the previous occasion $z_{i,t}$. To model transients and residents' age-specific apparent survival, we applied a time-varying individual age covariate with five categories: four that account for newly-marked (a mixture of transients and residents), and previously marked individuals (i.e., residents) for immatures and adults age classes, and one category for juvenile individuals. Newly-marked juveniles were not differentiated from previously marked ones to avoid unidentifiable estimates of individuals captured for the first time during the first semester of a given year because, in the following semester, juveniles change to immature state and so a 'juvenile resident' estimate is then non-estimable for these individuals. Therefore, our residents' juvenile parameter was confounded with transient individuals. Age covariate values were stored in matrix $A_{i,t}$, with $i = 1, \ldots, n$, where n is the number of individuals and $t = 1, \ldots, k - 1$, where k is the last capture occasion. Transitions to older ages is deterministic in $A_{i,t}$ covariate, where ages changes from the second semester. Thus, juveniles can only be in the juvenile state from the second semester and change to immature state during the second semester of the following year, and to the adult state after three years of being immature; in this way we guarantee that no reversion from older to younger ages occurs. The probability of an individual alive at the first occasion t that survives until the occasion $t + 1$ is $\phi_{A_{i,t}}$, where $A_{i,t}$ takes the value of 1 if juvenile, 2 or 3 if a newly-marked or resident immature, respectively, or 4 or 5 if a newly-marked or resident adult, respectively. The state process is formally defined as:

$$z_{i,t+1}|z_{i,t} \sim Bernoulli\left(z_{i,t} \times \phi_{A_{i,t}}\right), \tag{1}$$

The information of the observation process is provided by the CMR matrix $y_{i,t}$, being $i = 1, \ldots, n$, where n is the number of individuals, and $t = 1, \ldots, k$, where k is the last capture occasion, and relates with the state matrix as Bernoulli trials in subsequent occasions with probability of $P_{i,t}$ ($t = 2, \ldots, k$). We utilized an individual covariate to model age-specific immediate trap-response in recapture probability $T_{i,t}$ (see [68]). The $T_{i,t}$ matrix contains as many columns as recapture parameters and takes the value of 1, 2 or 3 if the individual i at time t, was captured at the previous occasion ($t - 1$) as juvenile, immature or adult, respectively, and 4, individuals not captured in the previous occasion. Therefore, we identified a 'trap-happy' response if recapture estimates of previously captured juveniles, immatures, or adults were higher than not-previously captured individuals, or 'trap-shy' if they were lower. The equation of the observation process is described as follows:

$$y_{i,t}|z_{i,t} \sim Bernoulli\left(z_{i,t} \times P_{T_{i,t}}\right), \tag{2}$$

To assess how the shift in waste management at the landfill after the opening of the WTC affected the apparent survival and recapture probabilities, we constrained occasions into three periods: (1) the period before the WTC from 2012 to mid-2015, (2) the first after-WTC period from mid-2015 to 2018, and (3) the second after-WTC period from 2018 to 2022. We chose this three-period structure because it provides more accurate estimates than the time-dependent model for some age classes, as well a clearer trend for before and after the opening of the WTC in relation to the reduction of organic matter available as food for scavengers. In the two after-WTC periods there was a reduction by 84.14% (a period of substantial reduction) and 96.42% (a period of extreme reduction) of organic matter dumped in the landfill and relative to the before-WTC period (Appendix A). Therefore, the apparent survival (ϕ) was modeled as follows:

$$logit\left(\phi_{A_{i,t}}\right) = \beta_{A,WTC} + \varepsilon_{A_i,WTC_i}, \tag{3}$$

$$\varepsilon_{A_i,WTC_i} \sim Normal\left(0, \sigma^2_{\phi}\right),$$

where $\phi_{A_{i,t}}$ is the logit apparent survival probability of the ith individual of age A captured in tth interval, and $\beta_{A,WTC}$ is the intercept whose values are the logit mean apparent survival of individuals within each age class A during each period of the WTC implementation. ε_{A_i,WTC_i} is an individual random effect that accounts for heterogeneity among individuals of a given age and σ^2_{ϕ} is the variance of logit apparent survival among individuals of each age and period [68,70,71]. When using an individual random effect, we assume that each individual has its own underlying mortality risk (or 'frailty'). Consequently, individual fitness is considered by incorporating individual variability into the survival estimate. This approach contrasts with age-group-specific classical modelling that assumes that all individuals of a given age are of equal quality [70,72,73]. Thus, the proportion of transients among newly marked individuals for each age class and WTC period was estimated as in [47]:

$$\tau_{A_{WTC}} = 1 - \phi'_{A_{WTC(x)}} / \phi_{A_{WTC(x)}}, \tag{4}$$

where $\phi'_{A_{WTC(x)}}$ and $\phi_{A_{WTC(x)}}$ are the newly marked and previously marked apparent survival estimates of age A, respectively, in a given $WTC(x)$ period.

Recapture probability (P) was modelled as follows:

$$logit\left(P_{T_{i,t}}\right) = \alpha_{T,WTC} + \omega_{T_i,WTC_i}, \tag{5}$$

$$\omega_{T_i,WTC_i} \sim Normal\left(0, \sigma^2_{P}\right),$$

where $p_{T_{i,t}}$ is the logit recapture probability of the ith individual of age-specific trap-response category T on the tth occasion, and α_{T_i,WTC_t} is the intercept with values indicating the logit mean recapture probability of each previously captured individuals of a given age class and mean recapture probability of individuals not-previously captured. Again, we corrected for heterogeneity among individuals with an individual random effect ω_{T_i,WTC_i} to prevent biased survival estimates [74] where σ^2_P was the variance of logit recapture probability among individuals in each trap-response category and period.

We fitted the model using vague priors, including a uniform distribution (0, 1) for values on the probability scale with logit-1(β) and logit-1(α), as well as normal distributions (0, σ^2) for the variances of individual random effects with a uniform distribution (0, 10) in standard deviations [68]. Estimates were obtained by sampling from the posterior probability distribution, taking every 10th sample from 95,000 iterations of three chains, following a burn-in period of 40,000 iterations, using Markov chain Monte Carlo (MCMC) algorithm. Analyses were conducted in JAGS [75] implemented through the R package "jagsUI" [76], in R [77]. To ensure convergence, we inspected chains visually by examining posterior density plots and checking the Gelman-Rubin statistic ($\hat{R}$) for each parameter, where values less than 1.1 suggest convergence [78]. All parameter chains exhibited good mixing ($\hat{R}$ values < 1.1). Estimates are presented as the mean of the posterior samples and 95% Bayesian credible interval probability (95% BCI).

3. Results

A total of 3,414 marked vultures and 1,531 recaptures from 2012 to 2022 were used for modeling. At first capture, 637 were aged as juveniles, 1,104 as immatures, and 1673 as adults (Appendix B). Overall, 66.6% (n = 424) of juveniles, 72.5% (n = 800) of immatures, and 76.2% (n = 1274) of adults were never recaptured, while approximately one-third of juveniles and one quarter of both immatures and adults were recaptured at least once.

Apparent survival of juveniles declined after the opening of the WTC, with a difference of 0.02 (95%BCI: −0.16–0.19) during the first after-WTC period and 0.14 (−0.09–0.38) during the second after-WTC period relative to the before-WTC period (Figure 1). By contrast, immatures' apparent survival tended to increase by 0.07 (−0.007–0.17) during the first after-WTC period and 0.06 (−0.03–0.16) during the second after-WTC period relative to the before-WTC period (Figure 1). Resident adults' apparent survival increased by 0.04 (−0.04–0.10) during the first after-WTC period with a subsequent decrease of 0.14 (0.07–0.21) during the second after-WTC period, and 0.17 (0.13–0.21) relative to the first after-WTC period (Figure 1) (Appendix C).

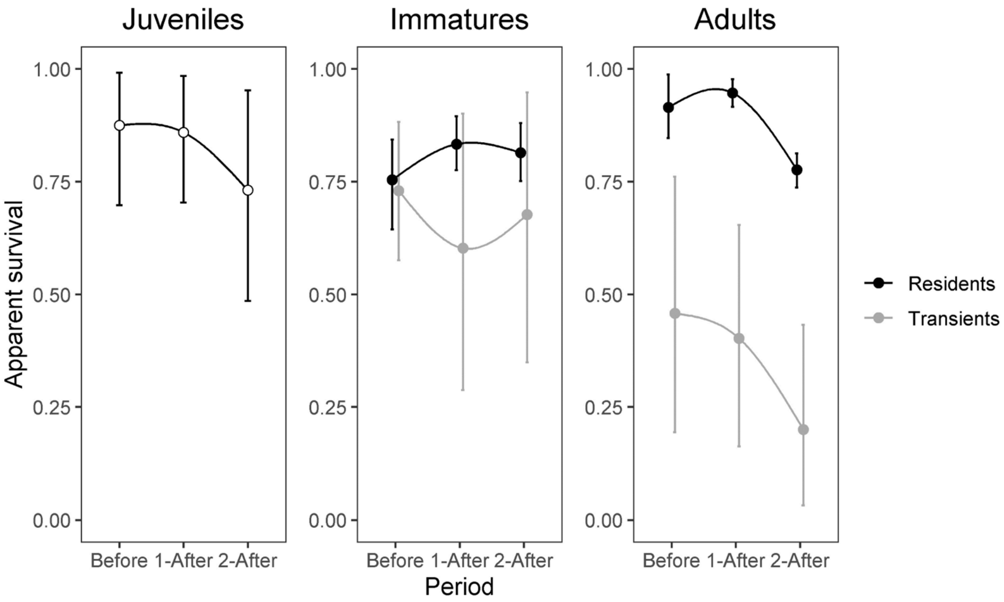

Figure 1. Apparent survival of juveniles, immatures, and adults before (2012–mid 2015), during (mid 2015–2018) and after (2018–2022) the waste treatment center (WTC) was opened. Estimates for newly marked ("Transients") and previously marked ("Residents") individuals are only differentiated for immatures and adults (see Methods). Error bars represent the 95% Bayesian credible interval.

The proportion of transients among newly marked immatures tended to increase by 0.20 (−0.11–0.52) during the first after-WTC period and by 0.13 (−0.15–0.44) during the second after-WTC period, while newly marked adults increased by 0.07 (−0.25–0.42) and 0.24 (−0.12–0.59) during both after-WTC periods (Figure 2) (Appendix C). Recapture probabilities for previously and not-previously captured individuals increased after the WTC was opened (Figure 2). Juveniles' trap-response was similar to not-previously captured individuals before the WTC opened but changed to 'trap-shy' during the first after-WTC period and 'trap-happy' in the second after-WTC period. Immatures behaved 'trap-happy' before the WTC implementation and 'trap-shy' during both after-WTC periods. However, adults were 'trap-happy' before the WTC, 'trap-shy' during the first after-WTC period, and 'trap-happy' in the last after-WTC period (Figure 2) (Appendix C).

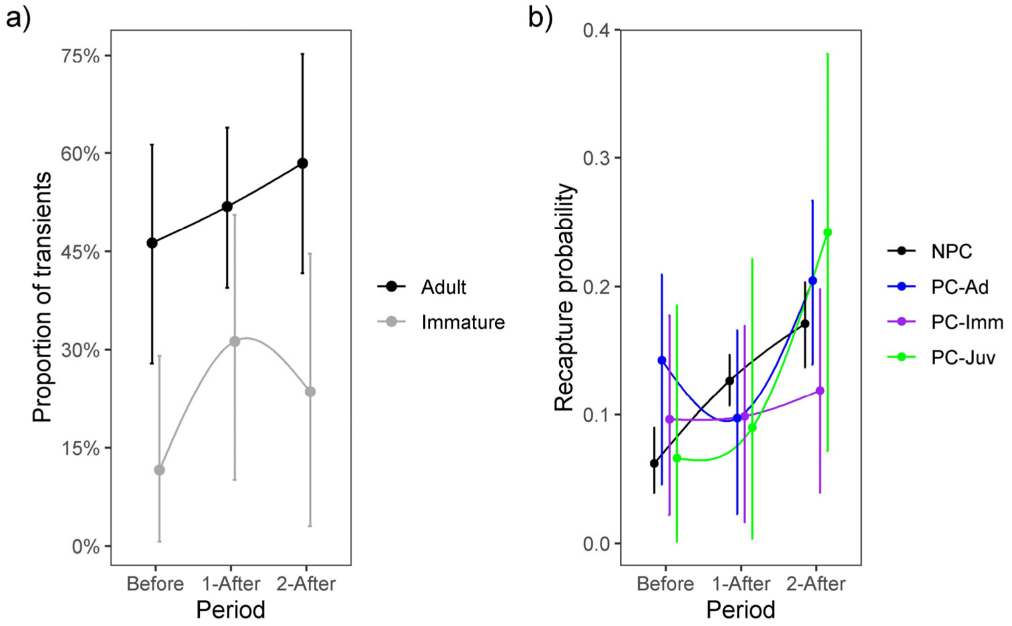

Figure 2. (**a**) Proportion of transients among newly-marked immatures and adults, and (**b**) recapture probability accounting for age-specific trap-response and individual heterogeneity, before (2012–mid 2015) and during the two periods after (mid 2015–2018 and 2018–2022) the waste treatment center (WTC) was opened. NPC = not-previously captured individuals, PC-Ad = previously captured adult individuals, PC-Imm = previously captured immature individuals, and PC-Juv = previously captured juvenile individuals. Error bars represent the 95% Bayesian credible interval.

4. Discussion

We evaluated the age-specific demographic response of a long-lived scavenger species to a drastic reduction in food in a PAFS in terms of its apparent survival and the percentage of individuals that permanently emigrated from the site after the first capture. We used as a natural experiment a local population of ringed griffon vultures that rely on an open landfill where a shift in organic waste management occurred after a waste treatment center (WTC) became operational. This shift caused a progressive reduction from 14,389 to 514 metric tons in the amount of organic matter dumped in the landfill and available as food for vultures during the final four years after the change in waste management (a 96.4% reduction in food availability). In accordance with our first prediction, the proportion of transients among newly marked immature and adult vultures increased over time, thereby indicating that individuals of these ages were more likely to become transients after their first capture due to the diminishing availability of organic matter in the landfill. Regarding our second prediction, the food reduction in the landfill implied a decrease of juveniles' apparent survival. However, immature residents' apparent survival increased after the WTC became operational but decreased for adult residents during the final WTC period. Additionally, we explored the immediate trap-response in the three age classes to the reduction in food in the landfill, where each age class behaved differently after the WTC was opened. These findings were made possible by our long-term (11 years) banding effort, which involved approximately 3500 vultures ringed in the landfill. Furthermore, the versatility of the state-space formulation of the Cormack-Jolly-Seber (CJS) model within a Bayesian framework allowed us to fit complex models with individual covariates [68]. This approach enabled us to simultaneously estimate age-specific apparent survival for resident individuals and recapture probabilities while accounting for common sources of heterogeneity in Capture-Mark-Recapture (CMR) studies such as the presence of transients, immediate trap-response, temporary emigration, and individual heterogeneity among age classes [47,79,80].

The proportion of transients among immature and adults increased after the WTC opened and was particularly high for adults, as has been observed in other long-lived bird species [4,49]. Transients are generally high in number when the study area is relatively small as in our case and in long-lived birds such as vultures that exhibit large home ranges [81–85]. As with stressful environmental conditions, food availability also modulates the probability a bird will become transient after the first capture, with a low probability when food is abundant and a higher one when food is scarce. In this way, the local decrease in food can cause an increase of density-dependent effects such as more intense intraspecific competition leading individuals to permanently emigrate after the first capture, this effect being particularly notable in adults [4,49]. Several hypotheses have been proposed to explain the biological meaning of transients in adults, including the cost of first reproduction, a marking and handling effect, or transiting individuals (true transients). The interpretation varies depending on the specific study system and species [48,49]. In our case, the distances from our marking site to nearby griffon vulture colonies range from 18 km to over 200 km. Given that (i) the landfill is a predictable feeding site that attracts a significant number of individuals, including some from distant populations (e.g., some individuals marked in the landfill have come from as far as France and other parts of Spain), and that (ii) vultures are known to visit multiple feeding sites and cover daily foraging distances of 120 to 300 km, a plausible explanation for transients in our system is that it comprises a mixture of true transients (i.e., individuals passing through without belonging to our study population including dispersing non-territorial adults) and individuals from relatively distant colonies prospecting this feeding site.

Our findings suggest that juveniles were negatively affected by the reduction in food at the landfill. Previous studies have demonstrated the positive influence of PAFS on survival rates of several species, with young individuals often being particularly attracted to these sites due to the relative ease of feeding compared to foraging for natural and unpredictable food sources [10–13,15,18,19]. Typically, after a significant reduction in food availability, it is the juvenile segment of the population that is most affected, resulting in an increased mortality rate or a higher rate of permanent emigration [1,22,23,25]. In our case, however, food reduction was very local and given that juveniles are the most mobile age fraction of the species and not restricted to a specific territory [51,86], the negative apparent survival trend may more likely to be due to a greater permanent emigration rate from the landfill rather than mortality. This suggests a density-dependent effect resulting from reduced food resources, leading to increased intraspecific competition at the site since younger individuals are usually less competitive when compared than their older counterparts; as well, interspecific competition is unlikely as the griffon vulture is typically dominant in the scavenger guild [52–54]. Consequently, the landfill may have become less attractive for these young individuals and made them less likely to return.

Contrary to our prediction, the apparent survival of resident immatures did not decrease despite the reduction in available food. Although immatures are generally more experienced and knowledgeable of alternative foraging grounds than juveniles, it is expected that they will also be negatively affected by a food shortage since they are more dependent of PAFS than older vultures, are not strongly bound to a territory, and are usually subordinate to adults when a food source is poor or scarce [15,87]. Other studies of long-lived species exposed to changes in food availability have yielded results that are similar to our findings, which suggests that individual quality within age classes may play a role. For example, [25] observed that after the closure of landfills, the apparent survival of immature Yellow-legged Gulls (*Larus michahellis*) increased in nearby colonies. Similarly, [24] evaluated the long-term dynamic of a griffon vulture colony before-, during- and after-BSE outbreak in density-dependent and density-independent scenarios, and found that immatures' apparent survival also increased. Both studies and our results suggest that in some systems part of the immature cohort exhibits a demographic response similar to older ages due the disappearance of poor-quality phenotypes of juvenile age. Albeit not restricted to a territory or as experienced as adults, some juveniles may have more knowledge of the foraging grounds and more experience than others, as well a variety of feeding sites within their home ranges that improves their survival probabilities [6,7]. Therefore, among resident immatures, some individuals may behave differently and either revisit the site or permanently leave after the food shortage. Furthermore, the gradual decrease in estimated variances among immature individuals in each period (see Figure A2) suggests that the variability within the resident population lessened after the WTC became operational. This change can be attributed in part to the initial exclusion of transients from residents, as well as the potential persistence of high-quality, experienced individuals that thrive despite the density-dependent effects of a significant food reduction. Hence, a substantial proportion of resident immatures may prefer to frequent and compete for food at the landfill since organic matter may still be enough and available (514 metric tons on average during the last four years of the study) to attract and sustain the large number of vultures that frequent the site each year [26].

The apparent survival of resident adults, on the other hand, partially met our prediction. During the first four years following the food reduction, this parameter remained unaffected and even increased, consistent with findings from prior studies [24,25]. However, during the subsequent four years of extreme food reduction, apparent survival decreased. Although the factors affecting adults are not entirely clear, one reasonable explanation is that the amount of food available at the landfill no longer satisfied the energy requirements of this age class [23]. Thus, the site became less attractive for vultures, especially those nesting at a considerable distance from the landfill that, consequently, shifted their foraging preferences to more viable food sources such as other PAFS and non-predictable (e.g., wild carrion) feeding sites where they can monopolize resources more easily [52–54]. Alternatively, this reduction in apparent survival during the second after-WTC period could also be the product of non-natural mortality of individuals. Adults feed more frequently on unpredictable food sources than young birds, which makes them vulnerable to toxic impacts [18,23]. Adult griffon vultures are potentially susceptible to lead ingestion from game animal carcasses [87], veterinary drugs from extensive livestock production, and anticoagulant rodenticides applied in intensive livestock production facilities and landfills [88–91]. The ingestion of these toxic substances may cause death or induce sub-lethal effects, which may increase the risk of mortality from other causes such as collisions with wind turbines [87,92–94]. For example, 28 out of 42 ringed individuals (67%) in the Orís landfill and found dead elsewhere were adults (individuals excluded from this analysis). However, only in nine of them (32%) was their apparent cause of death identified, being primarily due to electrocution, collision with powerlines, and wind turbines (authors' unpublished data). Recovering and determining the actual cause of death for marked vultures can be challenging due to the difficulty in locating their carcasses, which sometimes may lack markings, thereby rendering them unidentifiable [95,96]. Additionally, when carcasses are found, their partial or extensive deterioration can make necropsy inconclusive, particularly regarding toxic substances. Nevertheless, if non-natural mortality is the cause of the decline of adults' apparent survival in the landfill, it could have serious consequences for the population dynamics of the species as adult mortality can have a substantial impact on population size [24].

Trap-dependence is one of the most common sources of heterogeneity in recapture probability [97]. The trap-happiness observed in our GOF-test was expected because the captures in this study were made using baited traps [97]. Additionally, the presence of transients in the data (for which $p = 0$, significantly differing from individuals recaptured multiple times), along with the scenario of food shortage [98], further contributed to this expectation. Differentiating recapture probability between previously captured and not-previously captured individuals is a widely used method to account for trap-response derived from capture and handling methods, as well as for temporary emigration such as that caused by the possible seasonal movement patterns of our study population [85]). In our analysis, we employed an individual categorical covariate to explore the age-specific trap-response associated with food reduction in the landfill. This approach allowed us to simultaneously address unmeasured individual heterogeneity by incorporating an individual random effect in recapture probability, thereby producing unbiased survival estimates [74]. Our findings indicate that recapture probabilities increased after the implementation of the WTC for both not-previously captured and previously captured individuals in all three age classes (see Figure 2 and Table A3). This trend suggests that vultures were more likely to be recaptured after the food reduction, possibly because the baited walk-in-trap became more attractive and functioned as a predictable feeding site (extrinsic heterogeneity due to the capture method). This shift in behavior has been observed in small mammals [98]. Furthermore, the immediate trap-response for each age class varied during the three periods evaluated and suggests that the trap-response initially diagnosed with the GOF-test (i.e., trap-happiness), may not fully reflect the full nature of this phenomenon. Instead, trap-response can be dynamic in a system, with individuals within groups (e.g., age classes) displaying shifts from 'trap-happy' to 'trap-shy' and vice versa over time [98]. For instance, some immature and adult individuals were 'trap-happy' before the WTC was opened. However, during the next two after-WTC periods, all three ages behaved differently and were 'trap-shy' during the first-WTC period, and 'trap-happy' for juveniles and adults, and 'trap-shy' for immatures during the second-WTC period. Unraveling the reasons for this variability are beyond the scope of our study due to the lack of individual covariates other than age, which could explain part of this heterogeneity during modeling (intrinsic heterogeneity, such as sex, mass, or personality) [73,98], and the absence of temporal environmental covariates that may modulate trap-response at the site (e.g., landfill machinery activities and daily food regimes). However, it is important to emphasize that trap-response can be highly variable over time and among individuals within each age class.

5. Conclusions

In summary, our study provides valuable evidence of the age-specific detrimental impacts of food reduction on the demographic parameters of a long-lived scavenger bird species specialized in feeding on predictable anthropogenic food subsidies. From a conservation perspective, the closure of landfills is a desirable objective that will reduce the adverse effects on both the environment and the species that rely on this food resource. These effects are evident at the level of life history traits [17], health [34,35,87], and human-wildlife conflicts [99]. While our study suggests that the observed negative effect may be largely associated with permanent emigration due to a diminished food supply, it is worth noting that European regulations calling for the reduction of food in landfills are being implemented across the whole of Catalonia (Appendix D, Figure A4). This synchronized reduction in food resources could have significant consequences for demographic rates and ultimately threaten an important food source for numerous species that rely on these facilities and, in particular, for the griffon vulture population in the northeast Iberian Peninsula. These vultures are highly specialized and feed on carcasses originating from extensive livestock farming and landfills [26,38] and younger age classes being particularly dependent on landfills, especially during periods of wild food scarcity such as winter [27,28,30,31,100]. As a result, the reduction in food and the potential closure of landfills may lead to a dramatic shift in trophic strategy among scavenger species, forcing them to rely more on less predictable food sources (and, to some extent, predictable ones like supplementary feeding sites for scavengers), as previously predicted for Egyptian vultures (*Neophron percnopterus*) [40]. To mitigate these impacts, conservation measures should be considered, such as the establishment of a network of randomly distributed supplementary feeding stations to encourage natural foraging [101] or the expansion of protection zones for the feeding of scavenging birds (known as ZPAEN zones) in areas that are currently underrepresented [102]. These efforts should be pursued at a regional level to prevent undesirable negative effects on the population dynamics of these species.

Author Contributions: Conceptualization, D.J.A.-A., J.R. and A.H.-M.; methodology, D.J.A.-A., J.R., S.M., J.A., C.D. and A.H.-M.; formal analysis, D.J.A.-A. and A.H.-M.; investigation, D.J.A.-A., J.R., S.M. and A.H.-M.; data curation, D.J.A.-A. and C.D.; writing—original draft preparation, D.J.A.-A.; writing—review and editing, D.J.A.-A., J.R., S.M., J.A., C.D. and A.H.-M.; visualization, D.J.A.-A.; supervision, A.H.-M. and J.R.; project administration, J.R.; funding acquisition, J.R. All authors have read and agreed to the published version of the manuscript.

Funding: This study was funded by the Ministry of Science and Innovation of Spain (PID2020-117909RB-I00 funded by MCIN/AEI/10.13039/501100011033).

Institutional Review Board Statement: The study was conducted in accordance with relevant national and international guidelines, and conforms to the legal requirements. The animal study protocol has been carried out in compliance with the Ethical Principles in Animal Research and following the standards of the Catalan Institute of Ornithology. Thus, protocols, amendments and other resources have been done according to the guidelines approved by the Catalan Autonomous government following the Real Decreto 1201/2005 (10 October 2005, BOE 21 October 2005) of the Ministry of Presidency of Spain.

Data Availability Statement: The data presented in this study are available in this article and from the corresponding author upon reasonable request.

Acknowledgments: We extend our heartfelt gratitude to all the naturalists of the Grup d'Anellament de Calldetenes-Osona (GACO) who have participated in vulture captures and the Institut Català d'Ornitologia (ICO) for sharing the ringed vulture database. We are in debt to Jaume A. Badia-Boher from Swiss Ornithological Institute for guidance on Bayesian modelling. We thank Jordi Baucells from Gestió de Residus i Biodiversitat, SL, Anna Riera of the Consorci per a la Gestió dels Residus Urbans d'Osona, Verònica Tomàs of Ferrovial and Mar Segret of Consell Comarcal d'Osona for providing Orís landfill waste data.

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

Appendix A

Metric tons of organic matter and total waste data from 2012 to 2018 were obtained from [26], and calculations for 2019 to 2022 were done following supplementary material from [26], and using trimestral reports provided by the Consorci per a la gestió de residus urbans d'Osona (Consortium for the management of urban waste in Osona) corresponding to years 2019, 2020, 2021 and 2022.

After the waste treatment center (WTC) was implemented in mid-2015, organic matter poured into the landfill and available as food for scavengers was drastically reduced (Figure A1). According to the three periods analyzed for modelling apparent survival and recapture probabilities, mean metric tons of organic matter before the WTC implementation (2012 to mid-2015) was 14,388.67, 2282.41 during the first after-WTC period (mid-2015 to 2018), and 513.99 during the second after-WTC (2018 to 2022) period (Table A1). Thus, the reduction of organic matter available as food in the landfill after the WTC implementation was 84.14% and 96.42%, for the first and second after-WTC periods, respectively, and by 77.48% during the second relative to the first after-WTC period.

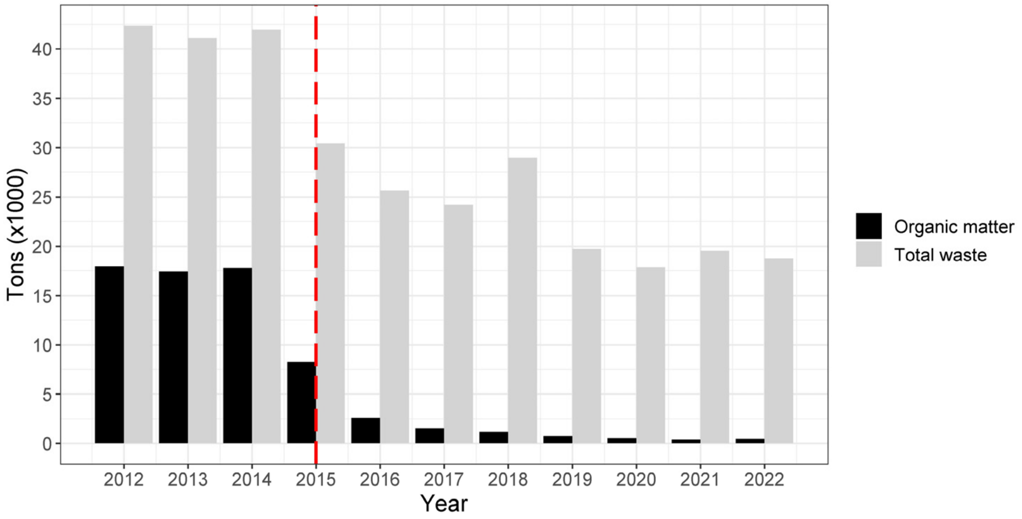

Figure A1. Total metric tons of waste poured into Orís landfill during 2012 to 2022. Red dashed line indicates the year when the WTC was implemented.

Table A1. Summary of Orís landfill organic waste data during the period 2012 to 2022. CJS = Cormack-Jolly-Seber.

Periods for CJS Modelling	Year	Organic Waste *	Mean Organic Waste *
Before WTC	2012	17,942.03	14,388.68
	2013	17,412.38	
	2014	17,775.45	
	2015 (January–June)	4424.85	
1st After WTC	2015 (June–December)	3,861.06	2,282.41
	2016	2,603.39	
	2017	1,510.11	
	2018	1,155.06	
2nd After WTC	2019	723.32	514.00
	2020	524.55	
	2021	355.12	
	2022	452.99	

* Metric tons.

Appendix B

Table A2. Marked and recaptured individuals per WTC period. Note that the total number of marked individuals sum to 3434 and not 3414 as mentioned in Results. We excluded individuals marked in the last occasion (20 individuals) from the modeling, as they do not contribute to the likelihood [68].

Periods for CJS Modelling	Years	Marked	Recaptured
Before WTC	2012 to 2015 (January–June)	1268	239
1st After WTC	2015 (June–December) to 2018	1174	513
2nd After WTC	2019 to 2022	992	779

Appendix C

Statistics of the posterior samples of Markov chain Monte Carlo (MCMC) for each parameter derived from the state-space Cormack-Jolly-Seber. In Table A2, the proportion of transients among newly captured immatures ($\%Tran_{\mathrm{Imm}}$) and newly captured adults ($\%Tran_{\mathrm{Adult}}$) were calculated following the Equation (4). For calculations, we used the MCMC posterior samples of $\phi'_{A_{WTC(x)}}$ and $\phi_{A_{WTC(x)}}$ (and not the means), which allowed us to propagate uncertainty from the samples and thus the estimation of standard deviation and Bayesian credible intervals for these parameters.

Table A3. Mean, posterior standard deviation (SD) and 95% Bayesian credible interval (95%BCI) from the state-space CJS model parameters and derived estimates for the three periods tested: before the WTC implementation (2012 to mid-2015), first after-WTC period (mid-2015 to 2018), and second after-WTC period (2018 to 2022). ϕ_{Juv}, $\phi_{\text{Res-Imm}}$, $\phi_{\text{Res-Adult}}$, $\phi_{\text{Tran-Imm}}$, and $\phi_{\text{Tran-Adult}}$ are apparent survival of juveniles, previously marked immatures, previously marked adults, newly marked immatures, and newly marked adults, respectively. $\%Tran_{\text{Imm}}$ and $\%Tran_{\text{Adult}}$ are the proportion of transients among newly captured immature and adult individuals, respectively. P_{NPC} is the recapture probability of not previously captured individuals, and $P_{\text{PC-Juv}}$, $P_{\text{PC-Imm}}$, $P_{\text{PC-Adult}}$ are the recapture probabilities of previously captured juveniles, immatures, and adults, respectively.

Period	**Parameter**	**Mean**	**SD**	**95%BCI**	
				Lower	**Upper**
Before-WTC (2012 to mid-2015)	ϕ_{Juv}	0.8752	0.0808	0.6983	0.9918
	$\phi_{\text{Res-Imm}}$	0.8139	0.1100	0.5922	0.9796
	$\phi_{\text{Res-Adult}}$	0.9145	0.0360	0.8468	0.9881
	$\phi_{\text{Tran-Imm}}$	0.7539	0.0503	0.6443	0.8434
	$\phi_{\text{Tran-Adult}}$	0.4569	0.1418	0.1944	0.7616
	$\%Tran_{\text{Imm}}$	0.1176	0.0856	0.0058	0.3150
	$\%Tran_{\text{Adult}}$	0.5004	0.1586	0.1662	0.7900
	P_{NPC}	0.0622	0.0126	0.0392	0.0896
	$P_{\text{PC-Juv}}$	0.0663	0.0517	0.0013	0.1853
	$P_{\text{PC-Imm}}$	0.0963	0.0423	0.0220	0.1772
	$P_{\text{PC-Adult}}$	0.1424	0.0416	0.0455	0.2091
1st after-WTC (mid-2015 to 2018)	ϕ_{Juv}	0.8594	0.0778	0.7037	0.9848
	$\phi_{\text{Res-Imm}}$	0.8332	0.0301	0.7758	0.8950
	$\phi_{\text{Res-Adult}}$	0.9468	0.0158	0.9157	0.9775
	$\phi_{\text{Tran-Imm}}$	0.6026	0.1571	0.2878	0.9010
	$\phi_{\text{Tran-Adult}}$	0.4019	0.1233	0.1628	0.6544
	$\%Tran_{\text{Imm}}$	0.3176	0.1688	0.0279	0.6721
	$\%Tran_{\text{Adult}}$	0.5751	0.1313	0.3131	0.8283
	P_{NPC}	0.1264	0.0100	0.1071	0.1466
	$P_{\text{PC-Juv}}$	0.0898	0.0625	0.0036	0.2211
	$P_{\text{PC-Imm}}$	0.0986	0.0394	0.0164	0.1690
	$P_{\text{PC-Adult}}$	0.0971	0.0384	0.0226	0.1655
2nd after-WTC (2018 to 2022)	ϕ_{Juv}	0.7311	0.1205	0.4857	0.9526
	$\phi_{\text{Res-Imm}}$	0.8143	0.0326	0.7513	0.8799
	$\phi_{\text{Res-Adult}}$	0.7764	0.0192	0.7370	0.8131
	$\phi_{\text{Tran-Imm}}$	0.6771	0.1573	0.3490	0.9478
	$\phi_{\text{Tran-Adult}}$	0.2003	0.1132	0.0320	0.4318
	$\%Tran_{\text{Imm}}$	0.2423	0.1588	0.0126	0.6038
	$\%Tran_{\text{Adult}}$	0.7416	0.1463	0.4477	0.9587
	P_{NPC}	0.1708	0.0172	0.1370	0.2032
	$P_{\text{PC-Juv}}$	0.2420	0.0774	0.0719	0.3811
	$P_{\text{PC-Imm}}$	0.1187	0.0411	0.0393	0.1980
	$P_{\text{PC-Adult}}$	0.2046	0.0319	0.1391	0.2667

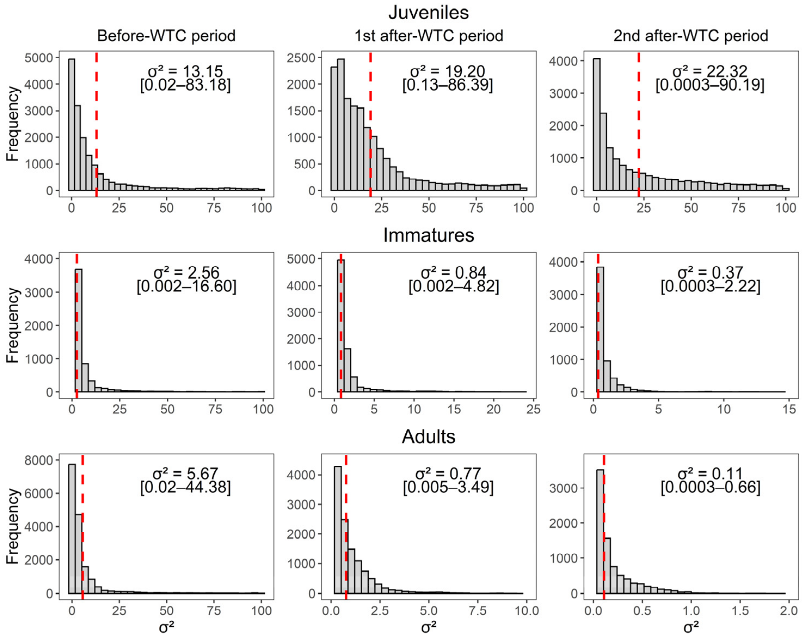

Figure A2. Posterior samples of the apparent survival variance (σ^2_ϕ) among juveniles, resident immatures, and resident adults before the WTC implementation (2012 to mid-2015) and during the two after-WTC periods (mid-2015 to 2018, and 2018 to 2022). Red dashed line represents the mean posterior σ^2 [2.5–97.5% quantiles] in the logit scale.

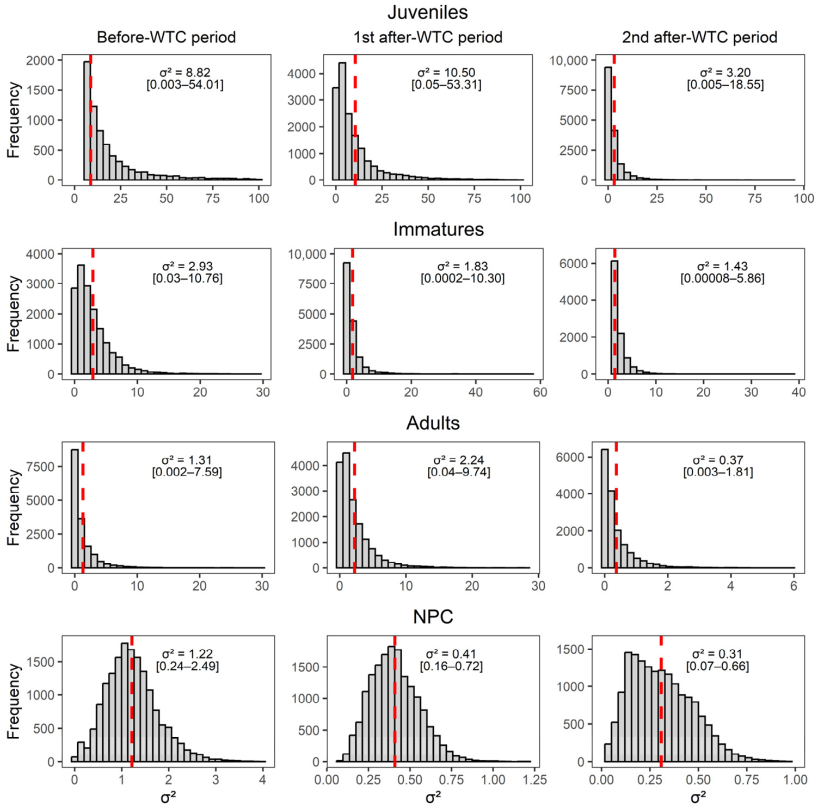

Figure A3. Posterior samples of the recapture probability variance (σ^2_p) among previously captured juveniles, immatures, and adults, and not previously captured individuals (NPC) before the WTC implementation (2012 to mid-2015) and during the two after-WTC periods (mid-2015 to 2018, and 2018 to 2022). Red dashed line represents the mean posterior σ^2 [2.5–97.5% quantiles] in the logit scale.

Appendix D

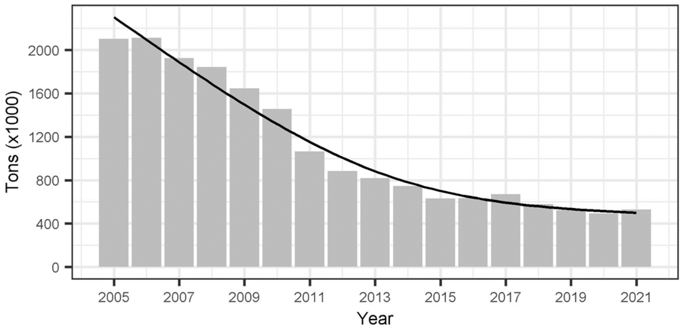

Figure A4. Annual metric tons (×1000) of waste poured into landfills of Catalonia (NE of Spain) from 2005 to 2021. Waste data includes only urban waste generated in households, commercial and non-commercial establishments (excluding construction waste). Data is publicly available from the Agència de Residus de Catalunya (Waste Agency of Catalonia) in: http://estadistiques.arc.cat/ARC/ (accessed on 15 April 2023). The black line shows the timeline trend ($y = 2303.73 - 2899.51x - 1046.99x^2$, Adjusted-$R^2 = 0.97$).

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CHAPTER 3

Multisite integrated population model reveals contrasting vital rates contributions on population dynamics of a highly mobile species

Photography courtesy of Arnau Soler Costa

Arévalo-Ayala, D. J., Real, J., Margalida, A., Badia-Boher, J. A., Mañosa, S., Durà, C., Aymerich, J., Jiménez, J. & Hernández-Matías, A.(2024). Multisite integrated population model reveals contrasting vitalrates contributions on population dynamics of a highly mobile species. *In preparation for submission (Journal of Applied Ecology).*

Multisite integrated population model reveals contrasting vital rates contributions on population dynamics of a highly mobile species

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Abstract

Identifying the key vital rates driving population dynamics in long-lived species is essential for understanding their life-history and to achieve effective conservation management. However, long-term studies often fail to explicitly model dispersal processes such as immigration and emigration, a particularly challenging issue in highly mobile species such as vultures. Additionally, the non-breeding fraction of populations is commonly overlooked despite its prominent role in determining long-lived population trends. We studied three neighbouring populations of griffon vultures (*Gyps fulvus*) in the northeastern Iberian Peninsula and assessed the site-specific population dynamics, while accounting for individual exchanges between these populations using a multisite integrated population model. Results indicated distinct population trends across regions. Catalonia's population exhibited steady growth, the Valencian Community's population stabilized after an initial increase, and Aragon experienced a decline followed by a slight recovery. Adult survival contributed significantly to population growth in Aragon, while the floater-to-breeder ratio and immigration had substantial positive contribution in the Valencian Community. In Catalonia, the floater-to-breeder ratio, immigration, and adult survival were key contributors to population growth. Density dependence was detected in the floater-to-breeder ratio and immigration in both Catalonia and the Valencian Community, indicating that these rates were affected by population size. Additionally, we found density dependence at the population level in the Valencian Community, mainly in Castellón province, likely due to the population approaching its carrying capacity, leading to higher migration probabilities compared to Aragon and Catalonia. Overall, the populations in Aragon and the Valencian Community are relatively stable, while Catalonia continues to grow. Maintaining adult survival in Aragon is crucial, as it is lower compared to the other regions and may be linked to non-natural mortality, such as wind turbine collisions and electrocutions. Our study highlights the importance of multisite integrated population models in understanding complex population dynamics and the need for targeted conservation strategies that consider demographic and spatial heterogeneity. We provided a comprehensive assessment of griffon vulture populations, emphasizing the critical role of dispersal processes and demographic rates in shaping population dynamics, even among closely situated populations.

Introduction

Identifying the key vital rates that drive population dynamics in long-lived species is a complex endeavour, yet critical for understanding both the species-specific life-history and applied conservation. These vital rates include survival, fecundity, immigration, and emigration, and temporal variations of each can have profound impacts on population stability and growth (Sæther and Bakke 2000, Caswell 2001, Margalida et al. 2020). Effective conservation strategies hinge on this understanding, as long-lived species, with their slow life cycles, delayed maturity, and low reproductive rates, are particularly vulnerable to anthropogenic disturbances (Saether and Bakke 2000). These traits make recovery from such impacts especially difficult, as their populations cannot quickly rebound from losses, making them more susceptible to long-term declines (e.g., population crash in Asia, see Green et al. 2004). In addition, adult survival is typically the main driver of population growth rate (Carrete et al. 2009, Genovart et al. 2013), and even small declines in this parameter can have a profoundly negative impact on population growth and viability. For instance, identifying electrocution as the main cause of non-natural mortality in Bonelli's Eagle (*Aquila fasciata*) provided the basis for implementing corrective measures in power lines, which significantly improved survival and conservation outcomes for the species population in south Europe (Real et al. 2001, Tintó et al. 2010, Chevallier et al. 2015, Hernández-Matías et al. 2013, 2015, 2020). Additionally, long-lived species particularly exhibit broad distributions and high mobility, often crossing areas managed by different administrative bodies with varying conservation strategies, which can either support or hinder demographic parameters and the exchange of individuals between populations (i.e., immigration and emigration), which ultimately determine the dynamics of the local population (e.g., Doxa et al. 2013, Lambertucci et al. 2014, Arrondo et al. 2018). In this context, dispersal and population connectivity are critical considerations when studying and managing long-lived and widely distributed species (Oro and Ruxton 2001, Doxa et al. 2013, Hernández-Matías et al. 2013, Zipkin and Saunders 2018, Millon et al. 2019, Badia-Boher et al. 2023).

Conventional population studies typically rely on estimating demographic parameters using capture-recapture methods, which often require substantial effort and investment as many individuals need to be captured, marked and recaptured/resighted to obtain reliable estimates. Consequently, most long-term studies are limited to relatively small spatial extents or a few local populations (Pollock et al. 2002, Sandercock 2006). In contrast, studies aiming to obtain abundance estimates are usually derived from count surveys alone, which can be conducted on a much larger scale (Nichols 2014). However, count surveys do not directly provide estimates of all demographic parameters (Ficetola et al. 2018), which limits the ability to understand the key drivers of local population dynamics comprehensively. Even if both sources of information are gathered, an incomplete understanding of the role of different population fractions, spatial and dispersal processes—such as the presence of immigrants from neighbouring populations and emigrants from the study site—can result in ineffective conservation measures that fail to meet local needs (Schaub et al. 2011, Tavecchia et al. 2016, Millon et al. 2019, Wu et al. 2020), as these processes are difficult to estimate from the separate data sources mentioned, necessitating the use of specific methods to properly assess them (e.g., immigration, Millon et al. 2019; emigration, Badia-Boher et al. 2023). Integrated Population Models (IPM) have emerged as robust analytical tools that combine capture-recapture, counts and productivity information within a unified framework (Besbeas et al. 2002, Schaub and Abadi 2010). These models are flexible enough to account for both demographic and spatial heterogeneity, thereby providing a comprehensive understanding of population dynamics. IPMs enable the estimation of multiple demographic parameters and population fractions for which empirical data is not available (e.g., recruitment, immigration, age-specific population sizes, among others), as well as the contribution of each vital rate on the temporal variation of population growth rate, while properly incorporating parameter uncertainty within a Bayesian framework (Besbeas et al. 2002, Abadi et al. 2010, Kéry and Schaub 2012, Schaub and Kéry, 2021).

Single-site IPMs are currently the most widely utilized analytical approaches (Schaub and Kéry 2022). Depending on the spatial extent of the study area and species, quantifying and incorporating dispersal in the form of emigration or immigration, may significantly impact (usually when spatial extent is small) or minimally influence the dynamics of the local population (Johst and Brandl 1997, Wang et al. 2015). Emigration is informed from the capture-recapture data and often included implicitly in IPMs when estimating apparent survival (which is the product of true survival and site fidelity) or explicitly when including information of dead recoveries inside and outside the study area (Lebreton et al. 1999). Immigration, on the other hand, is notoriously difficult to measure in the field, as it is challenging to distinguish between true immigrants and individuals born inside the study area (Millon et al. 2019). Consequently, immigration is typically estimated as a hidden parameter using the information provided by the other estimates of the IPM (Abadi et al. 2010, Schaub et al. 2013, Schaub and Fletcher 2015). Recent studies suggest that when models are incorrectly specified and rely solely on hidden parameter estimation rather than being informed directly by the data, the estimates of immigration and other parameters may be biased in some cases (and also their contributions to population growth rate; Riecke et al. 2019, Paquet et al. 2021). To address these limitations, a multisite IPM (ms-IPM) framework that explicitly models the movement probability of individuals between populations using a multistate capture-recapture and dead-recovery model, as well as accounting for permanent emigration from the study area, would provide a more comprehensive understanding of the underlying population dynamics since these parameters are directly informed by the data. However, ms-IPMs have been little explored (McCrea et al. 2010, Schaub and Kéry 2022), and scarcely applied in studies of long-lived species such as vultures (Péron et al. 2010, Seward et al. 2019).

Vultures are long-lived, highly mobile species with a wide geographic distribution (Monsarrat et al. 2013, Morant et al. 2023). Despite their vital role for ecosystem balance (Whelan et al. 2008), Old World vultures face a situation of conservation concern, with a staggering 81% of vulture species listed as 'Threatened' or 'Near Threatened' on the IUCN Red List (Margalida and Ogada 2018, Safford et al. 2019). In Europe, vultures face a significant threat from illegal poisonings due to human-wildlife conflicts, as well as indirect exposure to lead, pesticides, rodenticides and veterinary drugs, among others (Margalida 2012, Ogada et al. 2012, Green et al. 2016, Oliva-Vidal et al. 2022, Cook et al. 2024). In addition, current energy policies, amid prevailing climatic conditions, advocate for increased wind farm development globally, posing a new threat to vultures (Carrete et al. 2012, De Lucas et al. 2012, Serrano et al. 2020, Morant et al. 2024). Despite these challenges, vulture populations in southwestern Europe have exhibited remarkable growth, with the griffon vulture (*Gyps fulvus*) experiencing a notable 200% increase over the past fifteen years (Safford et al. 2019). In addition, Spain serves as the stronghold for 90% of the European griffon vulture population, with between 30,946 to 37,134 breeding pairs as of 2018 (Del Moral and Molina, 2018). Nevertheless, griffon vulture populations in some of the northern areas of Spain have shown a slight decline according to the last national census (Del Moral and Molina 2018), which may be attributed to high levels of landscape anthropization and higher mortality (Arrondo et al. 2020). In addition, differential conservation management and environmental policy integration at the regional level (Lambertucci et al. 2014, Arrondo et al. 2018), such as the development of renewable energy and the application of sanitary regulations on landfills (Ramírez et al. 2018, Arévalo-Ayala et al. 2023a, 2023b), among others, could be also influencing local population dynamics.

In this study, we focused on the griffon vulture populations located in northeastern Iberian Peninsula. Our aim was to provide an assessment of the site-specific population dynamics, including breeding and non-breeding fractions of the population, while explicitly accounting for the exchange of individuals between local populations. The specific objectives of our study were to estimate the (a) key demographic rates such as survival, productivity, immigration, and emigration for each vulture population; (b) identify the demographic rates that contributed most significantly to the temporal variance in population growth rates; and (c) assess whether density dependence was affecting any of the demographic rates. We combined population counts, productivity, and capture-recapture data from the three autonomous communities to construct the ms-IPM. This model allowed us to include movement probabilities between sites and elsewhere, enhancing our understanding of the demographic drivers behind the temporal variability in population growth rates of griffon vultures in this region. In addition, this information appears crucial to inform management and conservation strategies for highly mobile long-lived species that crosses administrative boundaries.

Materials and methods

Griffon vulture populations

Our study focuses on the griffon vulture populations of Catalonia, Valencian Community and Aragon, three autonomous communities of Spain located in the northeast of the Iberian Peninsula (**Figure 1**). These populations inhabit open environments characterized by sparse tree cover, the presence of rocky cliffs suitable for nesting and roosting, and abundant food sources mainly consisting of carrion from livestock and organic matter dumped in landfills (Margalida et al. 2007, Arévalo-Ayala et al. 2023a, 2023b, Arrondo et al. 2023). In Aragon and Catalonia, the breeding population is predominantly distributed throughout the Pyrenean and pre-Pyrenean regions, as well as the Iberian System and its foothills in the south of Aragon and the south part of the Catalan precoastal mountain range. Conversely, within the Valencian Community, the population primarily breeds in the Iberian System. Notably, since 2004, there has been a recent colonization in the Betic System in the southernmost of this autonomous community, facilitated by a reintroduction program (Jiménez and Seguí 2009). The species is notably absent in depressions and low-lying areas of the three autonomous communities (**Figure 1**).

These three autonomous communities account for approximately 23% of the total breeding pairs of Spain according to 2018 census, with Catalonia and Valencian Community experiencing a marked increase over the past decade. In contrast, Aragon, where 16% of Spain's pairs inhabit, has apparently shown a slight decrease from 5,174 in 2008 to 4,832 in 2018 (Del Moral 2009, Del Moral and Molina 2018). The delimitation of these three populations is political-administrative, as each autonomous administration is responsible for managing and internally coordinating the population monitoring of the species (Del Moral and Molina 2018). Therefore, the classification of populations by autonomous community may not have a biological connotation, as breeding pairs in some areas may occupy the same mountain range but be administratively divided (**Figure 1**). Instead, this classification represents the areas covered during the breeding pairs counts, the capture-recapture campaigns and the reproductive monitoring (Del Moral and Molina 2018), but our approach to movement between populations of these regions remains unaffected. However, as the monitoring scheme and conservation measures are specific to each autonomous community, these will be referred to as "populations" in the manuscript.

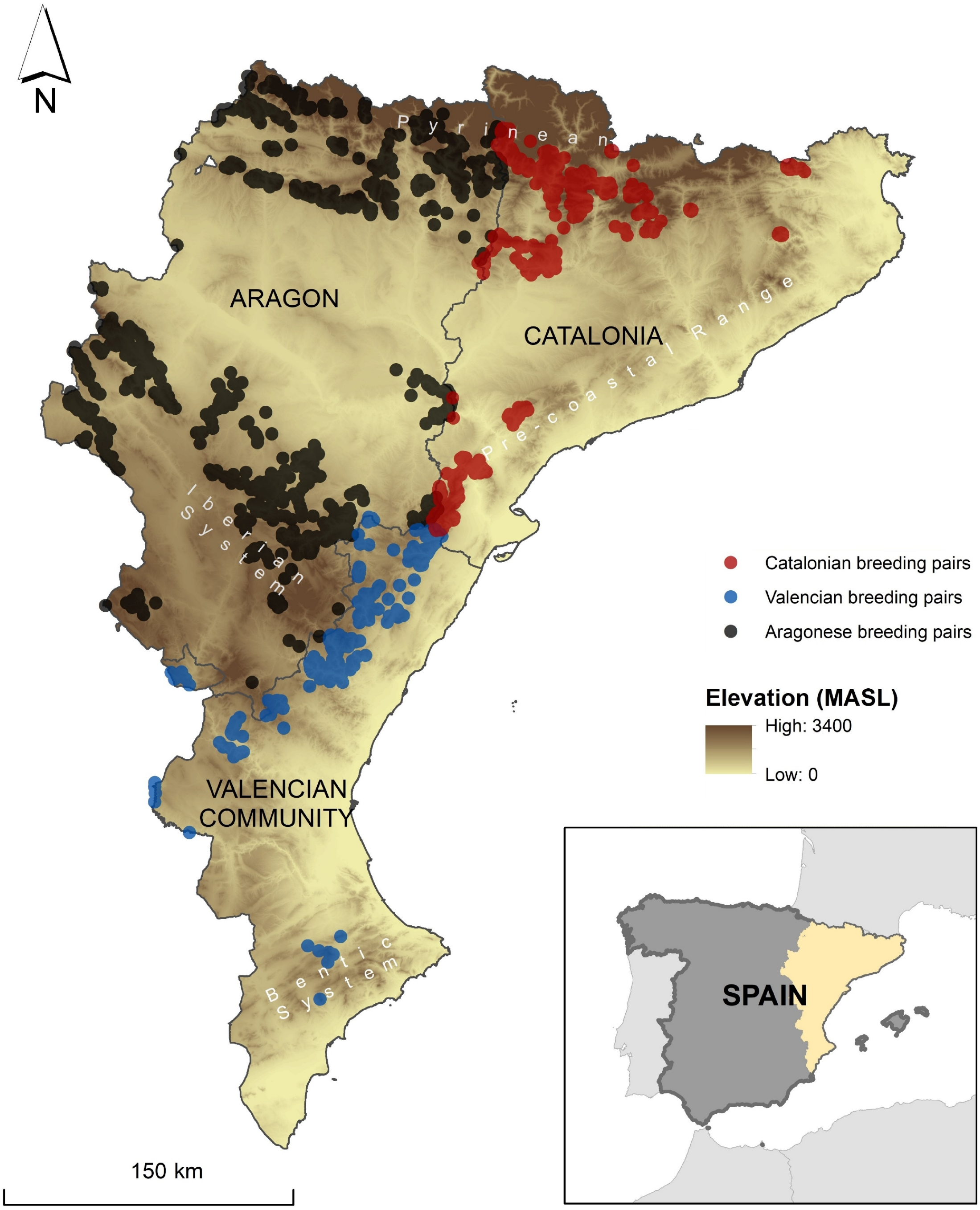

Figure 1. Study area showing the distribution of breeding pairs according to the 2018 griffon vulture census in Aragon, Catalonia and Valencian Community, northeast of the Iberian Peninsula (Del Moral and Molina 2018).

Data collection

The study covers a 14-year period from 2008 to 2021, a timeframe that reasonably aligns with the coverage of breeding pairs counts, capture-recapture campaigns, and productivity assessment for the three autonomous communities (**Appendix S1**, **Figure S1**).

Population monitoring data

Since 1979, breeding pair counts have been conducted every 10 years nationwide with the coordination of the Sociedad Española de Ornitología (SEO - Birdlife) and performed by trained volunteers and mostly by technical personnel from the autonomous administrations (Del Moral 2009, Del Moral and Molina 2018). In the Valencian Community, censuses have been carried out annually since 1989 under the direction of the regional government, providing full coverage for the study period except for the year 2020. In Catalonia and Aragon, the counts have been conducted in the years 1979, 1989, 1999, 2008, and 2018. Therefore, for both autonomous communities, we counted with two censuses, 2008 and 2018. Field efforts could vary by year and autonomous community, but the rule was to conduct observations on all known cliffs and crags housing nesting sites or isolated pairs, as well as those with suitable conditions for the species. The censuses were systematized into three stages: the first, from mid-January to mid-March, to monitor formed, forming, or non-breeding pairs; the second, from mid-March to mid-April, to monitor breeding pairs; and the third, from mid-May to mid-June, to monitor fledgling chicks (Del Moral 2009, Del Moral and Molina 2018).

Productivity data

In the Valencian Community, the number of fledglings was obtained from the third visit of the breeding pair census, except for 2020; thus, productivity represents the total new recruits produced annually in this area. In Aragon, the number of breeding pairs and fledglings was monitored from random subsamples selected from the known breeding colonies of the autonomous community in years 2008, 2010 to 2014, 2018, 2019 and 2021. In Catalonia, fledging chicks and breeding pairs from the south of the autonomous community were monitored during the study period except in 2021.

Mark-recapture/resighting and recovery data

Capture and marking campaigns began in 2006, 2008, and 2011 in the Valencian Community (although here we used only individuals marked from 2008 onwards), Aragon, and Catalonia, respectively. In all three autonomous communities, juvenile, immature, and adult individuals were captured using various methods such as walk-in traps and cannon-nets powered by compressed air. Only in Aragon were some chicks marked in their nests (n = 47), and several individuals from a wildlife rehabilitation centre were marked and released post-rehabilitation (n = 98). During the marking sessions, each individual was marked with a metal band, a plastic band, and a patagial wing mark on each wing, and their age was determined based on moult plumage patterns, eye and bill coloration, and the type of feathers on their ruffs (Duriez et al. 2011, Zuberogoitia et al. 2013). In Catalonia, patagial wing marks were not used from 2013 onwards and marking campaigns have been ongoing to the present day, conducted approximately each month per year. In Aragon, capture-mark campaigns took place at any time of the year from 2008 to 2014, 2019, and 2021, whereas in the Valencian Community, marking occurred between April and December, since 2006 and with the last individuals marked in 2016. Overall, 4,892 individuals were marked (735, 3,353 and 804 in, respectively, Aragon, Catalonia and Valencia). Recaptures comprised physical captures of previously marked individuals during capture-mark sessions (n = 3,362). Resightings were the observation of marked individuals seen at supplementary and natural feeding sites, landfills, roosting and nesting sites, and in flight, and recorded by environmental personnel from the autonomous administrations and birdwatcher's that uploaded their records on the portals of the Ringing Office of Estación Biológica de Doñana and ornitho.cat (Institut Català d'Ornitologia) (n = 45,727). Photographs of marked individuals by camera traps installed in supplementary feeding sites were also included in the analyses. Recovery of marked dead individuals included those found within the three autonomous communities and elsewhere (n = 152).

Integrated Population Model

Population dynamics model

We developed a pre-breeding stage-structured female-based Bayesian ms-IPM to estimate demographic parameters, population sizes, immigration and floater-to-breeder ratios, and population growth rate by integrating capture-recapture and dead-recoveries (CRDR), productivity and breeders count data of the three autonomous communities to describe the within and between population dynamics of the three populations (Besbeas et al. 2002, McCrea et al. 2010, Schaub and Abadi 2011, Schaub and Kéry 2022) (**Figure 2**). Our IPM was built under the well-known life-history traits of griffon vultures. Briefly, we assumed that some individuals could start reproducing at age two (Sarrazin et al. 1996, Demerdzhiev et al. 2014), the nestling sex ratio is even (Gómez-López et al. 2023), and survival differs only by age (Gouar et al. 2008).

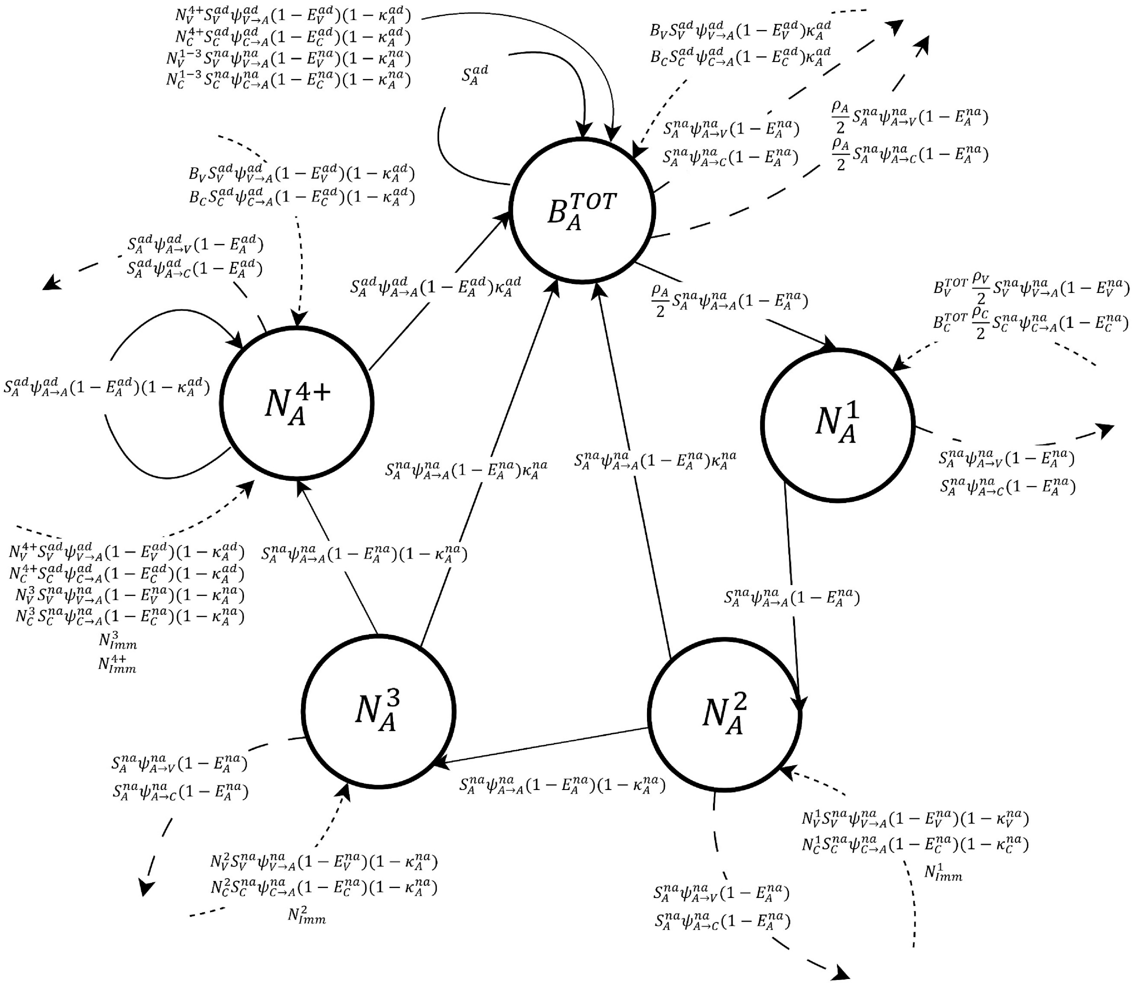

Figure 2. Life-cycle graph of the multi-site griffon vulture Integrated Population Model (ms-IPM) in the Northeast of the Iberian Peninsula. The griffon vulture population of Aragon (A) is shown as reference and modelled in function of the immigrants and emigrants between the three populations on each stage. B and N stands for breeding and non-breeding populations, respectively, and for each population (V, Valencian Community; C, Aragon). S, ρ, ψ, κ, and E denote true survival, productivity, movement probability, and recruitment, respectively. Superscripts 1 to 4+ indicates age-stages for non-breeding population sizes and na and ad in probabilities stands for non-adults and adults, respectively. Imm indicates immigrants from elsewhere (i.e., outside of our study system), and it was applied only in the state process of the population in Aragon (see Materials and Methods and Appendix S2 for more details).

We employed a state-space model to decompose the variance in the observed breeder population counts into two components: a state process (or population model) that captures the underlying true population sizes over time linked to the demographic rates, and an observation process that accounts for observation error associated with the true state in each year (Kéry and Schaub 2012) (see **Appendix S2**). In the state process, we distinguished specific stages for yearlings (N^1), non-recruited two- (N^2), three- (N^3), four-year-old (N^4), and older individuals ($N^{>4}$), a breeding stage composed of two- (R^2), three- (R^3), four-year-old (R^4) and older individuals ($R^{>4}$) that are recruited, and individuals that are already part of the breeding population (B). Based on existent evidence, we assumed two age-classes for survivals: S^{na}, for one- to three-year old individuals (hereafter non-adults), and S^{ad}, for four-year-old and older (hereafter adults), as previous studies suggest survivals improve substantially from age four onwards (Chantepie et al. 2015, Arévalo-Ayala et al. 2023b). We allowed for movements of individuals between populations in each stage, therefore, each stage in a given population included immigrants from the other two neighbour populations. Thus, movement probabilities between sites were differentiated for non-adults (ψ^{na}) and adults (ψ^{ad}). As we lack recruitment information, we estimated this probability as a hidden parameter to link the non-breeding stage of two- to four-year-old and older, and breeders that dispersed from the other two populations to a given breeder population. We assumed a time constant age-specific recruitment probability for each population, categorized by ages two to three years (κ^{na}), and four years and older (κ^{ad}).

Since our study system is open, we accounted for both emigration from the study area and immigration from elsewhere. We estimated permanent emigration probabilities in the capture-recapture model for non-adults (E^{na}) and adults (E^{ad}), considering the high mobility of this species (García-Ripollés et al. 2011, Monsarrat et al. 2013, Harel et al. 2016), which likely results in some individuals permanently emigrating beyond our study area (i.e., outside of the three autonomous communities). Immigration, on the other hand, was estimated using informative priors, as the high prevalence of missing count values in Aragon and Catalonia prevent proper *hidden estimates* and also because we are already estimating recruitment as a hidden parameter and estimating more than one is not possible (Schaub and Kéry 2022). We assumed that immigrants from elsewhere primarily enter through Aragon, with minimal entry into Catalonia and the Valencian Community due to their geographical locations (**Figure 1**). To prevent overestimating the immigrant fraction in the breeding population, we assumed immigrants first enter as non-breeders in time t. Their numbers were proportional to the volume of immigrants coming from Catalonia and Valencian Community, multiplied by the ratio between breeding pairs from neighbouring provinces (Guadalajara, Cuenca, Soria, La Rioja, and Navarra) to those in Aragon (see **Appendix S2** for details). Consequently, immigrants entering the non-breeding population in Aragon were available for recruitment into the breeding population in time $t+1$ and were also implicitly included withing the non-breeders emigrating from Aragon to Catalonia and the Valencian Community, thereby accounting for immigration from elsewhere in these regions too (see **Appendix S2** for details).

Finally, the observation process in each autonomous community was modelled using the breeding pairs count data (y_i) drawn from a Poisson distribution. In 2018, the census in Aragon achieved 90.6%

territorial coverage (Del Moral and Molina 2018). We accounted for this percentage in our population modelling to prevent a possible underestimation of the population due to the census's incomplete coverage.

Productivity submodel

We estimated productivity (ρ) from the number of nestlings produced by breeding pairs in each autonomous community. We assumed that the number of fledglings followed a Poisson distribution and estimated as the product of the number of breeding pairs and productivity. Productivity was modelled with random time effects (**Appendix S2**).

Survival, movement and permanent emigration probabilities between sites submodel

Survival, movement and permanent emigration probabilities were estimated using a multistate model with the summarized CRDR data in a m-array format and multinomial likelihood (Lebreton et al. 1999, Kéry and Schaub 2012). We estimated site- and age-class specific probabilities of true survival (S^{na} and S^{ad}), movements between sites (ψ^{na} and ψ^{ad}), and permanent emigration from the study system (E^{na} and E^{ad}), while accounting for wing tag and plastic band loss, dead-recoveries inside and outside our study system, and immediate trap-dependence. Survival, permanent emigration and recapture probabilities were modelled as time-varying with a random time effect, and recovery and movement probabilities as constant over time. See **Appendix S2** for more details of the multistate model parameterization.

Retrospective and density dependence analyses

We examined the correlation between demographic rates (survival, productivity, permanent emigration, floaters-to-breeder ratio and immigrant ratio) and population growth rate using the posterior parameter samples to assess their contributions to population dynamics (Schaub and Kéry 2022). The stronger the correlation, the more the variability in a demographic rate contributed to the variability in population growth rate (Robinson et al. 2004, Schaub et al. 2013). By using posterior samples, we addressed parameter uncertainties, allowing us to compute 95% credible intervals for correlation coefficients (*r*) and the probability of *r* being positive or negative (Genovart et al. 2018, Schaub and Kéry 2022).

To assess density dependence in demographic parameters, we calculated correlations between posterior samples of the estimates of each vital rate and breeding populations sizes. Similarly, for population-level density dependence assessment, we correlated the population growth rate with breeding population sizes (Abadi et al. 2012). Given the interdependence between estimated breeding population sizes and population growth rate (the latter derived from the former), we compared density dependence estimates from a model with simulated population sizes devoid of density dependence to those derived from the actual model, as detailed in Schaub and Kéry (2022). Briefly, we first fitted a model of exponential population growth without density dependence and random noise using the estimated population sizes in the IPM. Then, we used the resulting population growth parameters to simulate a new population trajectory initiating from the estimated population size in year 1 of the IPM. A density-dependent model was then fitted to the simulated population trajectories to obtain a reference distribution of the slope that determines density dependence (i.e., a null model without density dependence). By comparing the density dependence estimates from the simulated and actual data, we determined the probability that the observed effect of density dependence was more negative than expected compared to the null model without density dependence (Schaub and Kéry 2022).

Model implementation

Models were fitted using JAGS through the *jagsUI* package within R (Kellner et al. 2018) to sample from the posterior distribution of each parameter using Markov chain Monte Carlo (MCMC) methods. We ran three chains of 1,000,000 iterations each, applying a burn-in of 100,000 iterations and keeping every 150th sample. Convergence diagnostics for each parameter relied on visually inspecting the chains traceplots and checking the Gelman-Rubin statistic ($\hat{R}$, Brooks and Gelman, 1998). Convergence was achieved for all the parameters ($\hat{R} < 1.01$). Estimates are presented as posterior means and Bayesian credible intervals (95% CRI).

Results

The estimated breeding population sizes in Catalonia experienced an increasing linear growth from 1,113 (1,067–1,160 95%CRI) in 2008 to 1,779 (1,590–1,984) in 2021 (**Figure 3**). In the Valencian Community, the population showed an increasing trend from 263 (244–285) in 2008 to 565 (534–598) in 2015, after which it maintained apparent stability, ranging between 559 (526–593) and 593 (554–633) (**Figure 3**). On the other hand, in Aragon, a population decline was estimated starting in 2008 with 5,138 (5,040–5,237), reaching a minimum in 2012 of 4,932 (4,563–5,316), and slightly increasing from 4,978 (4,604–5,362) to a maximum of 5,447 (5,039–5,875) in 2020 (**Figure 3**). The population growth rate (λ) was relatively constant in Catalonia for the 14-year period, with a geometric mean of 1.04 (0.98–1.09), indicating steady growth (**Figure 3**). In the Valencian Community, λ decreased from 1.19 (1.09–1.30) in 2008 to relatively stable values between 0.97 (0.91–1.04) and 1.06 (0.99–1.13) from 2016 onwards (**Figure 3**). The geometric mean in the whole period was 1.07 (0.94–1.24). Meanwhile, in Aragon, the λ geometric mean was 1.003 (0.94–1.05), indicating stability (**Figure 3**).

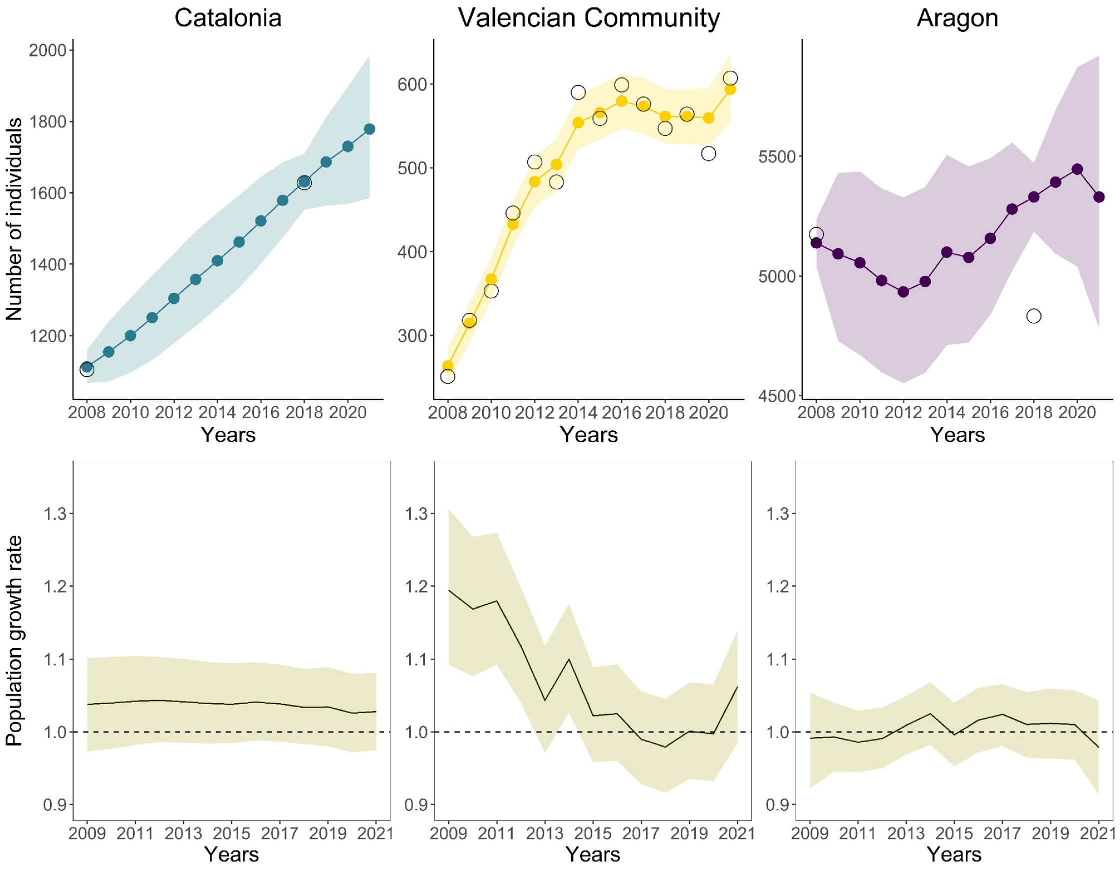

Figure 3. Estimated population sizes (filled circle) and observed breeding pair counts (open circle) (above). Note that in Aragon, the observed count is lower than the estimated population size, as the observation process of the state-space model accounted for the lack of a complete census during 2018 (see Appendix S2 for details). Below, population growth rates in each autonomous community. Coloured shaded areas represent 95% credible intervals.

The floater-to-breeder ratio exhibited a steady decline in the Valencian Community, dropping from 5.71 (5.18–6.27) in 2008 to 2.61 (1.99–3.47) in 2021. In Catalonia, this ratio decreased slightly from 3.60 (3.41–3.78) to 2.60 (1.86–3.54) over the same period (Figure 4). In contrast, Aragon maintained a relatively constant ratio throughout the study period, with values of 1.36 (1.32–1.40) in 2008 and 1.42 (0.91–2.13) in 2021. Similarly, the number of immigrants recruited per local breeder followed similar trends. The Valencian Community showed a marked decrease from 0.17 (0.12–0.22) in 2008 to 0.06 (0.03–0.09) in 2021, while Catalonia experienced a slight decline from 0.03 (0.02–0.04) to 0.017

(0.008–0.027). In Aragon, the ratio remained relatively constant at 0.01 (0.008–0.02) (**Figure 4**).

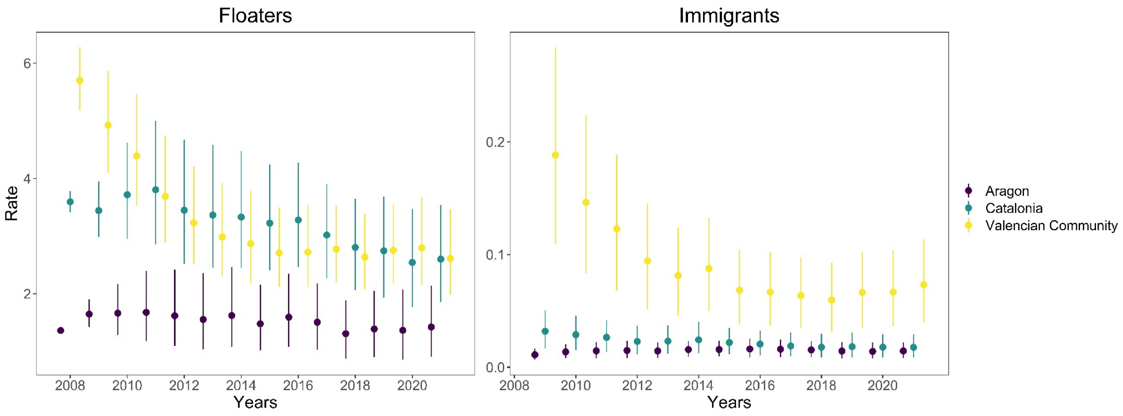

Figure 4. Floater-to-breeder and immigration rates in the three studied populations. Error bars represent the 95% credible intervals.

Mean survival probability of adults in Catalonia was relatively higher at 0.98 (0.96–0.99) compared to non-adults at 0.92 (0.78–0.99). Similarly, in the Valencian Community, adults had mean survival of 0.97 (0.93–0.99), higher than the 0.87 (0.64–0.99) for non-adults. In Aragon, adult survival was lower at 0.95 (0.90–0.99), while non-adults had a similar probability of 0.94 (0.84–0.99). Temporal variation was almost nil for adults in Catalonia and minimal in the Valencian Community (**Figure 5**). In Aragon, survival was apparently lower from 2009 to 2012 compared to subsequent years (**Figure 5**). Non-adults in Catalonia showed greater variability from 2009 to 2014, while those in the Valencian Community exhibited the most variability and highest uncertainty compared to the other populations (**Figure 5**). In Aragon, non-adults had less variability, with trends similar to adults but with greater uncertainty (**Figure 5**).

The mean productivity in Valencia was 0.66 (0.63–0.69) fledglings per pair, higher than in Catalonia at 0.59 (0.52–0.67) and Aragon at 0.59 (0.49–0.68). Temporal variations in productivities were greater in Aragon and Catalonia, and relatively lower in the Valencian Community with a slight increase from 2008 to 2020 in the latter. Uncertainties in years without data were relatively high in Aragon as expected (**Figure 5**).

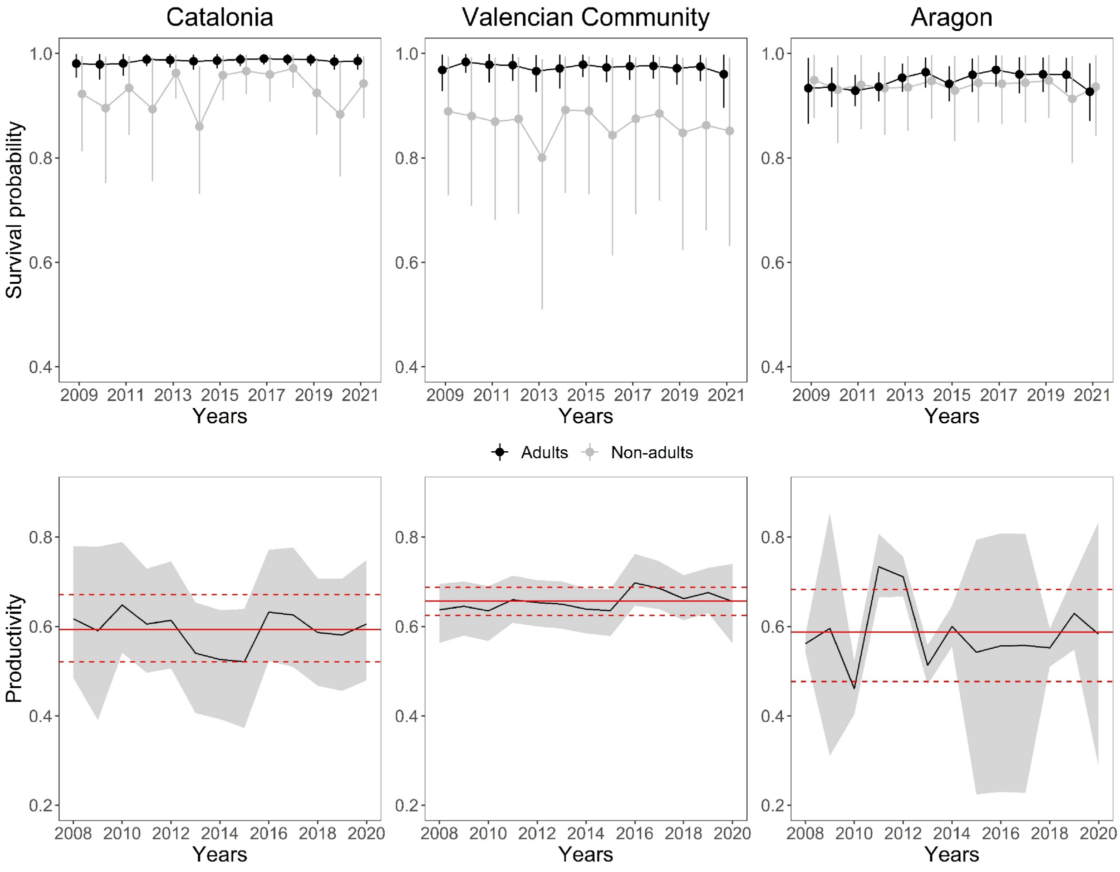

Figure 5. Year-specific survival estimates for non-adults and adults (above) and productivities (below) in each autonomous community. Continuous red line in productivities indicates the mean. Error bars in survivals, and shaded areas and dashed red lines in productivities represent 95% credible intervals.

The between-populations movement probabilities of adult and non-adult griffon vultures in Catalonia were very similar, with non-adults having a slightly higher probability of staying within the site (0.83 [0.80–0.86]) compared to adults (0.81 [0.80–0.83]) (Figure 6). Both ages were more prone to emigrate to Aragon than to the Valencian Community. In the Valencian Community, both ages showed a higher probability of emigrating to Aragon, with 0.35 (0.20–0.51) and 0.56 (0.54–0.59) probabilities for adults and non-adults, respectively, than to Catalonia. The probability of staying in Valencian Community was 0.56 (0.54–0.59) and 0.34 (0.20–0.27) in adults and non-adults, respectively (Figure 6). In Aragon, non-adults and adults had probabilities of 0.53 (0.46–0.59) and 0.76 (0.74–0.78) of staying, respectively. Adults were more likely to emigrate to Catalonia, while non-adults had a higher probability of moving to the Valencian Community (**Figure 6**).

The probability of permanent emigration from our study site varied by age class and region (**Figure 6**). In Catalonia, non-adults had a mean probability of 0.08 (0.006–0.21), slightly lower than the 0.11 (0.01–0.29) estimated for adults. In the Valencian Community, non-adults exhibited a higher mean emigration probability of 0.24 (0.02–0.57) compared to 0.09 (0.01–0.25) in adults (**Figure 6**). Conversely, in Aragon, non-adults had a mean emigration probability of 0.17 (0.03–0.34), while adults had a much lower probability of 0.03 (0.001–0.10) (**Figure 6**). The temporal variation of this parameter over the study period was variable for both age groups across the three populations, except for adults in Aragon, where it remained relatively constant. The uncertainties were greater for non-adults and were especially high for the population in the Valencian Community (**Figure 6**).

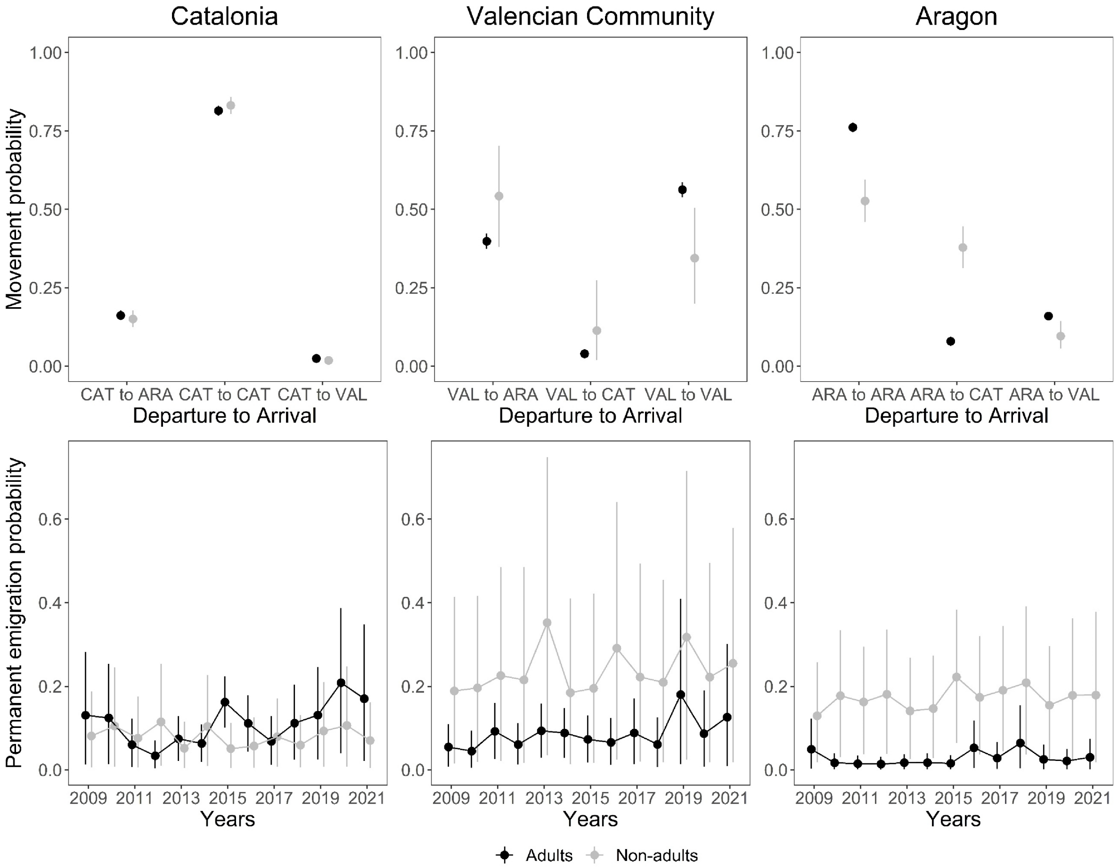

Figure 6. Movement between sites (above) and year-specific permanent emigration probabilities (below) for non-adults and adults in each autonomous community. CAT, ARA and VAL stands for Catalonia, Aragon and Valencian Community, respectively. Error bars represent 95% credible intervals.

The recruitment probability for non-adult and adult griffon vultures was similarly low across the three autonomous communities. In Catalonia, the probabilities were 0.02 (0.001–0.04) for non-adults and 0.02 (0.001–0.03) for adults. In the Valencian Community, the probabilities were slightly higher for non-adults at 0.05 (0.001–0.16), while adults had a probability of 0.02 (0.01–0.04). In Aragon, the recruitment probabilities were the highest among the three regions, at 0.09 (0.004–0.20) for non-adults and 0.06 (0.004–0.12) for adults.

Recapture/resighting probabilities varied across regions. In Catalonia, the mean probability of previously captured (P^{pc}) individuals was 0.39 (0.26–0.54), and for not previously captured (P^{npc}) individuals, it was 0.22 (0.18–0.27). In the Valencian Community, mean values were higher: 0.53 (0.25–0.80) for P^{pc} individuals and 0.29 (0.09–0.62) for P^{npc} ones. In Aragon, these probabilities were even higher: 0.68 (0.41–0.87) for P^{pc} individuals and 0.38 (0.21–0.61) for P^{npc} ones. Temporal variations were notable in the Valencian Community and Aragon, with initially high values for both P^{pc} and P^{npc} individuals, followed by a marked decline in the later years (**Appendix S2**, **Figure S2**). In Catalonia, P^{pc} individuals showed a decline from 2013 onwards, stabilizing around 0.25, while the probabilities for P^{npc} individuals remained constant (**Appendix S2**, **Figure S2**). The probabilities of losing wing tags and plastic bands increased from 0.02 (0.003–0.03) and 0.01 (0.001–0.03) in the first year to 0.71 (0.62–0.80) and 0.09 (0.04–0.15) by the thirteenth year, respectively (**Appendix S2**, **Figure S3**). The probability of recovering a dead individual remained constant at 0.16 (0.10–0.27) across all regions.

Retrospective and density dependence analyses

The correlations of demographic parameters to the population growth rate varied in magnitude across the three populations (**Figure 7**). In Catalonia, the primary positive contributions, were the floater-to-breeder ratio with an 84.3% probability (*r* = 0.26, -0.28 to 0.70), followed by the immigration ratio with an 81% probability (*r* = 0.24, -0.32 to 0.71), and adult survival with an 80% probability (*r* = 0.24, -0.35 to 0.71) (**Figure 7**). In the Valencian Community, the floater-to-breeder and immigration ratio had both 100% probability of having positive contributions (*r* = 0.81, 0.64–0.92, and *r* = 0.80, 0.58–0.93, respectively), while productivity (*r* = -0.32, -0.73 to 0.21) and permanent adult emigration (*r* = -0.20, -0.57 to 0.27) contributed negatively with 89% and 82% probabilities, respectively (**Figure 7**). In Aragon, the primary positive contribution was adult survival (100% of probability, *r* = 0.82, 0.56–0.95), followed by the immigration ratio (83% of probability, *r* = 0.28, -0.32 to 0.74) (**Figure 7**).

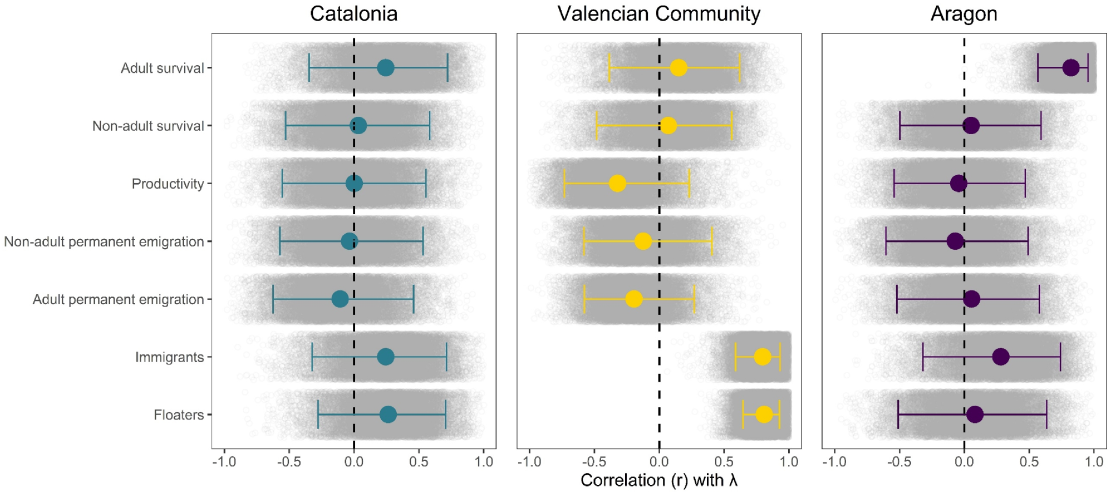

Figure 7. Correlations between posterior samples of demographic parameters with population growth rate (λ) for assessing contributions on population dynamics. Dashed lines indicate zero correlation. Values close to 1 or -1, represent positive or negative contribution, respectively. Jittered grey points represent each posterior sample. Coloured point with error bars indicates mean values and 95% credible intervals.

A strong negative effect of density-dependence with 99% probability was found on the floater-to-breeder ratio (*r* = -0.77, -0.95 to -

0.31) and the immigrant ratio (*r* = -0.65, -0.90 to -0.19) in Catalonia (**Figure 8**). Positive (correlation) effects with 91% probability were observed on permanent emigration (*r* = 0.36, -0.19 to 0.76). Similarly, in the Valencian Community, a strong negative effect with 100% probability was estimated on the floater-to-breeder ratio (*r* = -0.96, -0.98 to -0.90) and the immigrant ratio (*r* = -0.90, -0.97 to -0.76). A positive effect with 91% was found on permanent emigration (*r* = 0.35, -0.19 to 0.76). In Aragon, there were little density-dependence effects on demographic parameters (**Figure 8**).

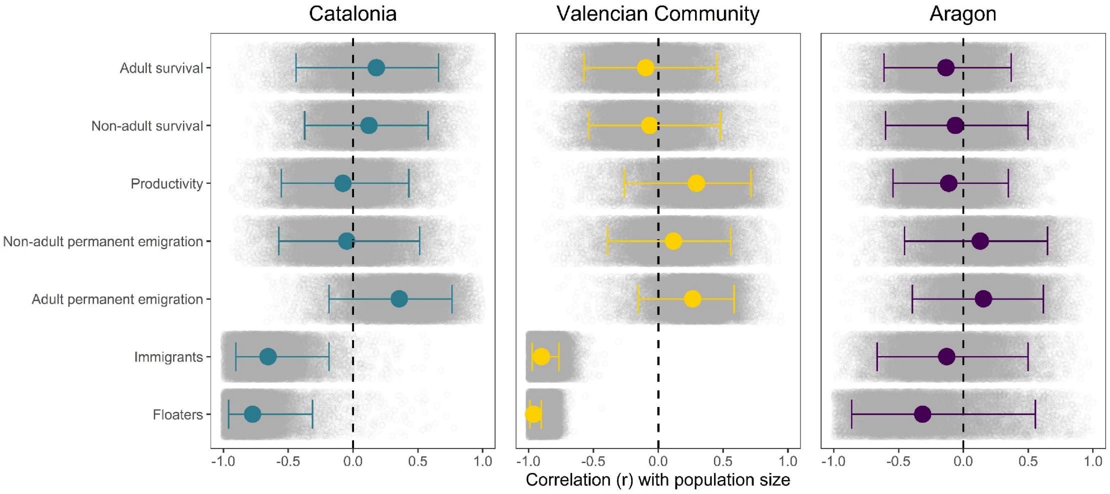

Figure 8. Correlations between posterior samples of demographic parameters with breeder population sizes for assessing density-dependence. Dashed lines indicate zero correlation. Values close to 1 or -1, represent positive or negative contribution, respectively. Jittered grey points represent each posterior sample. Coloured point with error bars indicates mean values and 95% credible intervals.

A negative density-dependence effect at the population level was found in the Valencian Community population with a 94% probability (**Figure 9**). No evidence of density-dependence at the population level was found in the other populations.

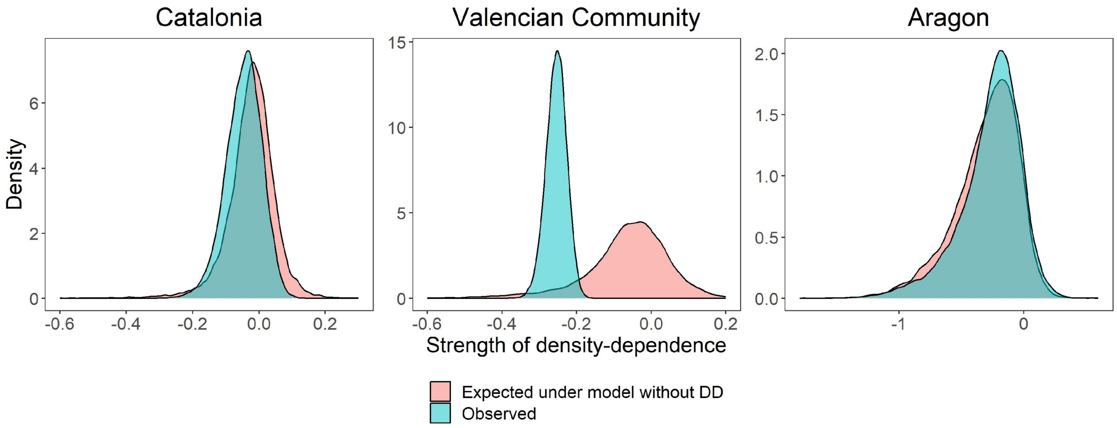

Figure 9. Coefficients of regression models testing the strength of density dependence (i.e., the magnitude of the effect of population size on population growth rate) at the population level. We compared the slopes of a regression model simulated using posterior samples of our population size estimates, assuming no density dependence (DD), with the slope of the regression model based on our actual estimated population sizes. The probability that the observed slope was smaller than the expected slope under no density dependence was high at 0.94 in the Valencian Community, while there were no signs of density dependence in the other two populations.

Discussion

Our study reveals significant demographic variation, contributions to population dynamics, and movement probabilities among three neighbouring populations of griffon vultures in the northeast Iberian Peninsula. Utilizing a multisite IPM approach allowed us to integrate spatial structure and connectivity into our assessment, emphasizing the importance of multipopulational models for estimating true survival and explicitly incorporating emigration and immigration into the model to understand the population dynamics of wide-ranging, highly mobile species like vultures (Arrondo et al. 2020, Dobrev et al. 2022). Collaboration among autonomous administrations, researchers, volunteer networks, and ringing programs facilitated large-scale multi-site monitoring data despite heterogeneous data collection and temporal coverage challenges. Applying IPMs within a Bayesian framework enabled us to estimate several vital rates (including recruitment as a hidden parameter) and quantify population fractions that so far have received very little attention, such as non-breeders, which are challenging to monitor in the field but crucial for maintaining stable populations by buffering sudden declines in adult numbers and expanding to new territories (Penteriani et al. 2011). This approach also allowed us to assess critical contributions of demographic rates to population change while effectively accounting for uncertainty and data heterogeneity (Schaub and Kéry 2022).

The breeding population sizes of griffon vultures showed distinct regional patterns. In Catalonia, the estimated breeding population exhibited a constant linear growth during the study period. This continuous increase suggests that the carrying capacity has not yet been reached, allowing for sustained population growth. For instance, a natural repopulation in the province of Girona was discovered in 2008-2009 (three breeding pairs) and monitored its growth during 2018 census (35 breeding pairs), indicating the continuous expansion of the species in this autonomous community and increasing the global distribution of the species to the most Eastern part of the Iberian Peninsula (Del Moral and Molina 2018). In the Valencian Community, the population showed a steady increase over the past three decades, achieving relative stability in recent years. This suggests that the population may be approaching it carrying capacity, at least within the main population area in Castellón province (Del Moral and Molina 2018). However, and similar to the situation in Catalonia, a slight expansion has also been recorded in Valencia and Alicante provinces during the 2018 census (Del Moral and Molina 2018). Aragon, on the other hand, showed a slight population decline observed between 2008 and 2012, followed by a gradual recovery with a fluctuating trend. Nevertheless, the overall growth rate remained relatively stable, indicating a balanced population trend.

One suspected cause of the observed decline in Aragon's population sizes and adult survival from 2008 to 2013 was the implementation of sanitary measures that prohibited leaving dead livestock in extensive farming areas for the Bovine Spongiform Encephalopathy (BSE) outbreak (Donázar et al. 2009, Margalida et al. 2010), which significantly reduced food availability for vultures that could led to population decline as occurred in other colonies of vultures (Almaraz et al. 2022). The recovery observed from 2013 onwards corresponds with the revert of the sanitary measures and the establishment of Protected Areas for Feeding of Scavengers (PAFS), which have been shown to support vulture populations (Morales-Reyes et al. 2017). Nevertheless, in Catalonia, the impact of BSE-related food shortages does not appear to have been evident as population sizes were increasing, and survival and productivity was relatively constant with little temporal variation, potentially mitigated by the use of natural carrion and predictable food sources like landfills, carcass dumping sites, intensive farms and supplementary feeding stations (Margalida and Colomer 2012, Fernández-Gómez et al. 2022). Additionally, it is likely that some carcasses were left available in the field during the sanitary measures, that could sustain these vulture populations (Cabrera-García et al. 2020). In the Valencian Community, BSE-related food shortages occurred just before our study period began in 2006-2007, following the closure of a key supplementary feeding site in Aragón, near the population of Castellón (Del Moral and Molina 2018). This, combined with the operation of a nearby wind farm, led to a population decline that year (Martínez-Abraín et al. 2012). However, after the wind farm issue was resolved and the feeding sites were reopened, the population began to grow again (Martínez-Abraín et al. 2012, Del Moral and Molina 2018). According to our estimates, this growth continued starting in 2008, when our study period began.

The floater-to-breeder ratio and immigration rates in the griffon vulture populations provide further insights into their population dynamics. In Catalonia and the Valencian Community, the floater-to-breeder ratio was a key driver of population growth rate (84.3% and 100% of chance to positively contributing, respectively). Immigration rate was also an important contributor to the dynamics of the three populations (Millon et al. 2019), but was stronger in the Valencian Community (again, with 100% of probability). Overall, the high values of floaters per breeders across the three populations suggest a stable demographic structure that can support continuous recruitment (*buffer effect*), which is crucial for the long-term persistence of long-lived species with low productivity (Hunt et al. 1998; Penteriani et al. 2011). Similarly, the low immigration rates indicates that the populations are largely self-sustaining, with local recruitment playing a primary role rather than relying heavily on immigration (Schaub et al. 2010, Millon et al. 2014). In our case, however, the recruitment estimates may not directly reflect the true recruitment probability into the breeding population. Instead, it may represent a combination of the percentage of the non-breeding population that joined the breeding population, as well as other unmodeled demographic processes (e.g., breeding propensity). As such, these recruitment estimates should be interpreted with caution and considered as a 'correction term' that accounts for multiple unmodeled demographic parameters as it happens in some IPMs (Robinson et al. 2014, Schaub and Kéry 2022). Specifically, our recruitment rate was around 2% in Catalonia for both age classes, 5% and 2% for non-adults and adults in the Valencian Community, and 9% and 6% for both age groups in Aragon. These values are lower than the known recruitment for the species, although, available estimates are only for a closed and reintroduced population of griffon vultures in Grand Causses during it establishment period, making it difficult to compare with our results (Sarrazin et al. 1996). Nonetheless, in the Valencian Community, the floater-to-breeder ratio decreased significantly from 5.71 floaters per breeding female in 2008 to 2.61 in 2021, while Catalonia saw a modest decline from 3.60 to 2.60. In contrast, Aragon maintained a relatively constant ratio at 1.36. Similarly, the number of recruited immigrants per breeder followed these trends, with significant decreases in the Valencian Community and minor changes (i.e., relatively constant) in Catalonia and Aragon. This indicates that the Valencian Community may be experiencing a saturation effect, where the population is stabilizing as it approaches the carrying capacity of the habitat, while Catalonia's modest decline and Aragon's stable ratios suggest that these populations are maintaining a balance between floaters, immigrants and breeders, which is crucial for long-term stability (Schaub et al. 2010, Penteriani et al. 2011, Millon et al. 2014).

Adult survival was also an important driver of population growth rates, as is commonly observed for long-lived species (Margalida et al. 2020, Almaraz et al. 2022). This was particularly strong in Aragon, where adult survival had a 100% probability of contributing positively to the population growth rate. Survival estimates indicated that adult griffon vultures in all three regions exhibited higher probabilities compared to non-adults, aligning with the species' life-history characteristics (Chantepie et al. 2016). Adults have lower mortality rates due to their greater experience, access to resources, and ability to cope with environmental challenges. In contrast, non-adults are more susceptible to fluctuations in food availability, non-natural mortality, and landscape anthropization (Arrondo et al. 2020; Arévalo-Ayala et al. 2023b). However, among the three populations, adult survival in Aragon was lower, which could be attributed to higher rates of non-natural mortality such as electrocution and collisions with wind turbines, as this species is highly vulnerable to these threats (Carrete et al. 2012; De Lucas et al. 2012; Serrano et al. 2020; Morant et al. 2024). In this sense, and compared to the other autonomous communities, Aragon has developed wind energy more extensively, and the number of griffon vulture collisions with turbines is already the leading cause of their entry into rescue centres (**Appendix S3 Figure S6**). Given that this species is highly vulnerable to wind turbines and that population dynamics are driven by adult survival, it is crucial to focus on improving this vital parameter as the number of wind farms has been increasing since 2019 (**Appendix S3 Figure S6**).

Productivity was higher in Valencian Community (0.66) compared to Catalonia and Aragon (0.59). Temporal variations were more pronounced in Aragon and Catalonia, with a slight decrease trend in the first, indicating fluctuating environmental conditions or resource availability but also the incremental population density (Carrete et al. 2006; Cortés-Avizanda et al. 2009). In Valencian Community, on the other hand, showed little variations in productivity with a slight increase trend and may be due to the increased availability of food from supplementary feeding stations (author's unpublished data). This parameter had very little contribution to population dynamics in Catalonia and Aragon, as observed in other long-lived species (Genovart et al. 2018; Margalida et al. 2020). In contrast, the negative contribution to population dynamics in Valencian Community suggests that while feeding stations support high productivity levels, thus contributing to the production of new potential recruits, these individuals have a high probability of emigrating to other regions, such as Aragon and Catalonia, but also outside our study region, as shown by our movement and permanent emigration probabilities. This means that the new recruits nowadays are not contributing significantly to the long-term growth of the Valencian Community population, and instead are supporting the other neighbouring populations through emigration (Margalida et al. 2013, Fay et al. 2019). Additionally, as this population appears to be reaching it carrying capacity, mostly in Castellón province, density-dependent effects may manifest and drive the observed high dispersal probabilities (Matthysen 2005, Tavecchia et al. 2007, Bona et al. 2019). Moreover, the proximity of the nesting sites to the other autonomous communities' results in higher emigration rates of both adults and non-adults moving to Aragon, Catalonia and elsewhere. In contrast, in Catalonia, the high probability (over 80%) of non-adults and adults remaining within the site suggests that local resources have been sufficient to support the resident population, contributing to the region's steady population growth. Similarly, adults in Aragon showed a strong preference for staying within the autonomous community due to established breeding sites and known foraging grounds that offer stable resources (Moreno-Opo et al. 2015; Morant et al. 2023), while non-adults were more likely to move between regions, especially to the Valencian Community. In general, in Catalonia and the Valencian Community, both adults and non-adults showed a higher propensity to emigrate to Aragon. This highlights Aragon’s role as a key habitat with foraging opportunities for dispersing vultures from both populations. However, Aragon also poses dangers, as wind energy is expanding within the region, potentially turning it into an ecological trap for these vultures (**Appendix S3 Figure S6**) (Hale and Swearer 2016).

The analysis of density dependence revealed a strong negative effect on the floater-to-breeder and immigration ratios in both Catalonia and the Valencian Community, indicating that as population density increases, the availability of resources per individual decreases, leading to increased competition and emigration (Tavecchia et al. 2007, Seward et al. 2019). This was also corroborated by the positive correlation between population sizes and permanent emigration and more particularly in adults. Moreover, density-dependent effect at the population level was significant in the Valencian Community, with a 94% probability. This finding highlights the critical role of density dependence in regulating population size and growth in this autonomous community (Tavecchia et al. 2007, Schaub and Kéry 2022). In fact, the last national census recorded new expansions in the Valencian Community, suggesting the critical role of floaters on colonizing new available sites (Hunt 1998, Penteriani et al. 2011). In contrast, Aragon showed minimal density-dependent effects on demographic parameters and at the population level. However, this result should be interpreted with caution, as there are small signs that the population may be experiencing a saturation phase (e.g., permanent emigration rates for non-breeders are similar to those in the Valencian Community, and philopatry in this fraction is very low, around 53% of probability). Our retrospective analysis may have missed the pre-saturation effects, potentially giving a false impression of population stability during the study period. In other words, this outcome may be influenced by the length of the time series used for correlation analysis. Indeed, the Aragon population has stabilized since the 2008 census, with its growth phase documented from 1978 to 2008 in national censuses (Del Moral and Molina 2018), indicating it may now be experiencing apparent density-dependent effects, particularly through emigration, as population sizes have started to oscillate.

Conservation implications

Our study comprehensively examines griffon vulture population dynamics and demographic processes in three regions, emphasizing the importance of regional conservation efforts and coordinated management strategies. Spain's decentralized governance delegates conservation authority to autonomous communities, sometimes resulting in varied implementation of policies and potential coordination challenges (Agranoff 2007, Ferraro and Failler 2024). An example of this was the reversion of sanitary measures for the bovine spongiform encephalopathy outbreak, leading to the establishment of Protected Areas for Feeding of Scavengers under European regulation (EC) No 1069/2009, and implemented with different criteria at temporally and spatial level across regions that may not adequately cover the feeding requirements of scavenger species (Morales-Reyes et al. 2017; Mateo-Tomás et al. 2018, 2019). Aragon established them in 2013, Catalonia in 2012, and the Valencian Community in 2009. Furthermore, each region designed its Protected Areas for Feeding of Scavengers zones differently—Aragon selected specific municipalities covering 50% of the region, Catalonia focused on public forests above 1400 meters and specific municipalities, ultimately covering only 13% of its area, while the Valencian Community targeted Special Protection Areas (SPAs) within the Natura 2000 network, encompassing 20% of its territory. Additionally, current circular economy policies aiming to close landfills, a predictable food source to which many vulture species have adapted (Arrondo et al. 2020), could potentially have a negative impact on demography and local populations through emigration (Arévalo-Ayala et al. 2023a; 2023b). Although landfill closures might shift vultures towards less predictable food sources (Ceredo-Iglesias et al. 2023), integral, standardize and regional solutions are needed (Morales-Reyes et al. 2017; Mateo-Tomás et al. 2018). Catalonia is progressing with landfill closures, but the implementation status in other Spanish regions remains uncertain (Arévalo-Ayala et al. 2023a; 2023b). This lack of coordination among administrations can influence local vulture populations, potentially prompting migration to areas with better feeding conditions or emigration from areas with poorer conditions (Lieury et al. 2015; Arévalo-Ayala et al. 2023a; 2023b).

Another risk to vulture populations is the wind energy development. In the Valencian Community, installing wind farms in vulture foraging areas initially led to high mortality and reduced productivity that provoked a population decline in 2007, later improving after corrective measures were implemented to keep vultures away from the turbines (Martínez-Abraín et al. 2012, Oro et al. 2012). While Catalonia and Valencian Community have minimally developed wind energy, Aragon and other regions have expanded significantly (**Appendix S3 Figure S6**), threatening vultures, particularly the griffon vulture, and other species (Carrete et al. 2012; De Lucas et al. 2012; Serrano et al. 2020; Morant et al. 2024). In Aragon, turbine collisions are now the main cause of vultures entering rescue centres, threatening their regional populations (**Appendix S3 Figure S6**). Furthermore, it is alarming that the European Commission and EU member states have recently promoted the REPower EU Plan (Regulation (EU) 2022/2577) to fast-track renewable energy projects by reducing or eliminating environmental assessments and public participation in the approval process (Bolonio et al. 2024). This regulation was implemented in Spain through an urgent and exceptional measure in the same year (Royal Decree-Law 20/2022). A key concern is that this acceleration of the "permit-granting process" could allow projects in areas previously protected or restricted, putting vulnerable species like the griffon vulture at greater risk of mortality and ultimately their populations.

We conclude that integrating comprehensive environmental and biodiversity conservation strategies across sectors is crucial. Future research should focus on how environmental changes affect vulture demographics and movement patterns explicitly. Addressing indirect exposure to contaminants like lead, pesticides, veterinary drugs and rodenticides (Margalida 2012; Green et al. 2016; Oliva-Vidal et al. 2022; Cook et al. 2024; Serratosa et al. 2024) requires interregional measures and standardized monitoring at national levels. Improved communication among autonomous governments is essential for effective conservation of species that cross administrative borders.

Acknowledgements

We are immensely grateful to all the ornithologists, bird watchers, researchers, volunteer networks, and ringing programs who have contributed their observations to the capture-recapture databases over the years. In particular, we extend our thanks to all the people of the Grup d'Anellament de Calldetenes-Osona in Catalunya, Sara Ferreras of the Centre de Recuperació de Fauna Forn del Vidre Castellón (Valencian Community), and the Government of Aragon. We are indebted to the Generalitat Valenciana; to Manuel Alcántara, and Francisco Hernández of the Biodiversity Service of the Government of Aragon; and Joan Mestre, Diego García, Ricard Casanovas, Joan Mayné and Rafael Molina of the Generalitat de Catalunya for providing crucial information regarding reproductive parameters data, censuses of breeding pairs, marked and re-sighted vultures, and causes of admission of griffon vultures to recuperation centres for each of the three autonomous communities. A heartfelt appreciation goes to the members of the Hierarchical Modelling group for their assistance in clarifying doubts related to the IPM modelling, especially Michael Schaub, José Jiménez García, and Thomas Riecke. This study is part of the project funded by the Ministry of Science and Innovation of Spain (PID2020-117909RB-I00 funded by MCIN/AEI/10.13039/501100011033).

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Supporting information

Appendix S1. Datasets temporal coverage.

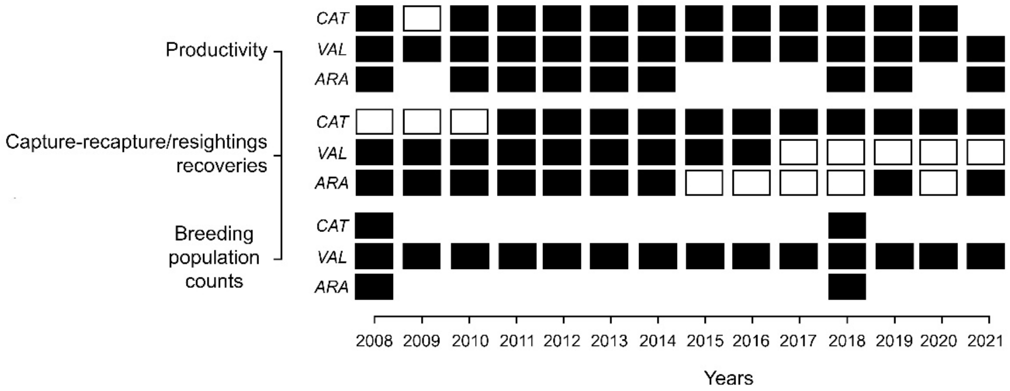

Figure S1. Dataset used to develop the griffon vulture (*Gyps fulvus*) multi-site Integrated Population Model in Catalonia (*CAT*), Valencian Community (*VAL*), and Aragon (*ARA*). For each year, filled rectangles represents complete data and the absence of rectangle no data collected or available. Open rectangles represent that only the number of breeding pairs were recorded for productivity and that only resightings (no markings) were performed for the capture-recapture data.

Appendix S2. The multi-site Integrated population model

S2.1. Population dynamics model

We employed a state-space formulation to separate the observation process from the state process of the breeding count data of each population (Catalonia, Valencian Community, and Aragon) to model changes in population sizes of griffon vultures from year t to t+1. We modelled each population stage with demographic stochasticity using both Poisson and Binomial distributions.

State process in Catalonia

For Catalonia, the number of one-year-old population (N_C^1) in t+1was modelled as the sum of individuals of the same age that were born in Catalonia, survived, and stayed in Catalonia, along with those who were born, survived, and migrated from the Valencian Community and Aragon to Catalonia as:

$$N^1_{C\to C_{t+1}} \sim Pois\left(B^{TOT}_{C_t}\frac{\rho_{C_t}}{2}S^{na}_{C_t}\psi^{na}_{C\to C}(1-E^{na}_{C_t})\right)$$

$$N^1_{V\to C_{t+1}} \sim Pois\left(B^{TOT}_{V_t}\frac{\rho_{V_t}}{2}S^{na}_{V_t}\psi^{na}_{V\to C}(1-E^{na}_{V_t})\right)$$

$$N^1_{A\to C_{t+1}} \sim Pois\left(B^{TOT}_{A_t}\frac{\rho_{A_t}}{2}S^{na}_{A_t}\psi^{na}_{A\to C}(1-E^{na}_{A_t})\right)$$

$$N^1_{C_{t+1}} = N^1_{C\to C_{t+1}} + N^1_{V\to C_{t+1}} + N^1_{A\to C_{t+1}}$$

Where N^1 are the one-year-old individuals with subscripts indicating the source population ($_{C\to C}$, $_{V\to C}$, and $_{A\to C}$, indicating staying in Catalonia, immigrants from the Valencian Community and immigrants from Aragon, respectively), B_C^{TOT}, B_V^{TOT}, and B_A^{TOT}, indicating the site-specific breeding populations, ρ_C, ρ_V, and ρ_A, indicating site-specific productivities, S_V^{na}, S_V^{na}, and S_A^{na} site-specific non-adult survival probabilities, $\psi^{na}_{C\to C}$, $\psi^{na}_{V\to C}$, and $\psi^{na}_{A\to C}$ the site-specific non-adult movement probabilities, and $E^{na}_{C_t}$, $E^{na}_{V_t}$, and $E^{na}_{A_t}$ the site-specific non-adult permanent emigration probabilities.

The number of two- (N^2) and three-year-old (N^3) individuals in Catalonia were calculated as the sum of individuals that stayed in Catalonia and immigrants from Valencian Community and Aragon, while assuming the same site-specific non-adult survival, permanent emigration and movement probabilities as above, but now allowing that can either not recruit and become part of the two- or three year-old non-breeding population (N^2 and N^3, respectively) with probability $(1-\kappa_C^{na})$, or recruit and become part of the breeding population (R^2 and R^3) with probability κ_C^{na}:

$$N^2_{C\to C_{t+1}} \sim Bin\left(N^1_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to C}(1-E^{na}_{C_t})(1-\kappa^{na}_C)\right)$$

$$N^2_{V\to C_{t+1}} \sim Bin\left(N^1_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to C}(1-E^{na}_{V_t})(1-\kappa^{na}_C)\right)$$

$$N^2_{A\to C_{t+1}} \sim Bin\big(N^1_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to C}(1-E^{na}_{A_t})(1-\kappa^{na}_C)\big)$$

$$N^2_{C_{t+1}} = N^2_{C\to C_{t+1}} + N^2_{V\to C_{t+1}} + N^2_{A\to C_{t+1}}$$

$$N^3_{C\to C_{t+1}} \sim Bin\big(N^2_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to C}(1-E^{na}_{C_t})(1-\kappa^{na}_C)\big)$$

$$N^3_{V\to C_{t+1}} \sim Bin\big(N^2_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to C}(1-E^{na}_{V_t})(1-\kappa^{na}_C)\big)$$

$$N^3_{A\to C_{t+1}} \sim Bin\big(N^2_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to C}(1-E^{na}_{A_t})(1-\kappa^{na}_C)\big)$$

$$N^3_{C_{t+1}} = N^3_{C\to C_{t+1}} + N^3_{V\to C_{t+1}} + N^3_{A\to C_{t+1}}$$

$$R^2_{C\to C_{t+1}} \sim Bin\big(N^1_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to C}(1-E^{na}_{C_t})\kappa^{na}_C\big)$$

$$R^2_{V\to C_{t+1}} \sim Bin\big(N^1_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to C}(1-E^{na}_{V_t})\kappa^{na}_C\big)$$

$$R^2_{A\to C_{t+1}} \sim Bin\big(N^1_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to C}(1-E^{na}_{A_t})\kappa^{na}_C\big)$$

$$R^2_{C_{t+1}} = R^2_{C\to C_{t+1}} + R^2_{V\to C_{t+1}} + R^2_{A\to C_{t+1}}$$

$$R^3_{C\to C_{t+1}} \sim Bin\big(N^2_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to C}(1-E^{na}_{C_t})\kappa^{na}_C\big)$$

$$R^3_{V\to C_{t+1}} \sim Bin\big(N^2_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to C}(1-E^{na}_{V_t})\kappa^{na}_C\big)$$

$$R^3_{A\to C_{t+1}} \sim Bin\big(N^2_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to C}(1-E^{na}_{A_t})\kappa^{na}_C\big)$$

$$R^3_{C_{t+1}} = R^3_{C\to C_{t+1}} + R^3_{V\to C_{t+1}} + R^3_{A\to C_{t+1}}$$

During the fourth year of life, we again assumed that Catalonian vultures comprised individuals that stayed from year t to t+1 and immigrants from the other two sites, but now allowing that can either not recruit and become part of the four-year-old non-breeding population (N^4) with probability $(1-\kappa^{ad}_C)$, or recruit and become part of the breeding population (R^4) with probability κ^{ad}_C, while consistently assuming the same site-specific non-adult survival, permanent emigration and movement probabilities:

$$N^4_{C\to C_{t+1}} \sim Bin\Big(N^3_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to C}(1-E^{na}_{C_t})\big(1-\kappa^{ad}_C\big)\Big)$$

$$N^4_{V\to C_{t+1}} \sim Bin\left(N^3_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to C}(1-E^{na}_{V_t})(1-\kappa^{ad}_C)\right)$$

$$N^4_{A\to C_{t+1}} \sim Bin\left(N^3_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to C}(1-E^{na}_{A_t})(1-\kappa^{ad}_C)\right)$$

$$N^4_{C_{t+1}} = N^4_{C\to C_{t+1}} + N^4_{V\to C_{t+1}} + N^4_{A\to C_{t+1}}$$

$$R^4_{C\to C_{t+1}} \sim Bin\left(N^3_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to C}(1-E^{na}_{C_t})\kappa^{ad}_C\right)$$

$$R^4_{V\to C_{t+1}} \sim Bin\left(N^3_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to C}(1-E^{na}_{V_t})\kappa^{ad}_C\right)$$

$$R^4_{A\to C_{t+1}} \sim Bin\left(N^3_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to C}(1-E^{na}_{A_t})\kappa^{ad}_C\right)$$

$$R^4_{C_{t+1}} = R^4_{C\to C_{t+1}} + R^4_{V\to C_{t+1}} + R^4_{A\to C_{t+1}}$$

Individuals older than four years in Catalonia included those who survived and remained in Catalonia with an adult survival ($S^{ad}_{C_t}$), site fidelity to the study area ($1 - E^{ad}_{C_t}$), and movement probability ($\psi^{ad}_{C\to C}$), non-breeding immigrants from the other two sites who survived from the four-year-old population (N^4, with survival probabilities: $S^{ad}_{V_t}$, $S^{ad}_{A_t}$; movement probabilities: $\psi^{ad}_{V\to C}$, $\psi^{ad}_{A\to C}$; site fidelities: $(1-E^{ad}_{V_t})$, $(1-E^{ad}_{A_t})$), and dispersing breeders from other breeding populations. As a result, the non-breeding population of older individuals in Catalonia ($N^{>4}$) encompassed all these individuals with a probability of not recruiting $(1-\kappa^{ad}_C)$, while the breeding population comprised individuals recruited with probability κ^{ad}_C, in addition to those already part of the breeding population (B_C). Note that B_C population fraction lacks a recruitment, permanent emigration and movement probability, since we assume that the annual breeding population sizes are primarily composed of breeders who consistently reproduce in the same site. In addition to this, previous studies suggest that breeding populations from northern and central Spain show smaller home-range areas and shorter cumulative distances compared to those from the south (Morant et al. 2023), and data on 29 GPS-tagged adult individuals captured at the marking site in Catalonia showed that 89.7% (n=26) concentrate their movements inside the autonomous community all year round, whereas 6.9% (n=2), have permanently emigrated to south of Spain and 3.4% (n=1) to south of France (authors' unpublished data), so we can assure a high site fidelity of territorial adults.

$$N^{>4}_{C\to C_{t+1}} \sim Bin\left(N^{4}_{C_t}, S^{ad}_{C_t}\psi^{ad}_{C\to C}(1-E^{ad}_{C_t})(1-\kappa^{ad}_{C})\right)$$

$$N^{>4}_{V\to C_{t+1}} \sim Bin\left(N^{4}_{V_t}, S^{ad}_{V_t}\psi^{ad}_{V\to C}(1-E^{ad}_{V_t})(1-\kappa^{ad}_{C})\right)$$

$$N^{>4}_{A\to C_{t+1}} \sim Bin\left(N^{4}_{A_t}, S^{ad}_{A_t}\psi^{ad}_{A\to C}(1-E^{ad}_{A_t})(1-\kappa^{ad}_{C})\right)$$

$$N^{>4}_{C_{t+1}} = N^{>4}_{C\to C_{t+1}} + N^{>4}_{V\to C_{t+1}} + N^{>4}_{A\to C_{t+1}}$$

$$R^{>4}_{C\to C_{t+1}} \sim Bin\left(N^{4}_{C_t}, S^{ad}_{C_t}\psi^{ad}_{C\to C}(1-E^{ad}_{C_t})\kappa^{ad}_{C}\right)$$

$$R^{>4}_{V\to C_{t+1}} \sim Bin\left(N^{4}_{V_t}, S^{ad}_{V_t}\psi^{ad}_{V\to C}(1-E^{ad}_{V_t})\kappa^{ad}_{C}\right)$$

$$R^{>4}_{A\to C_{t+1}} \sim Bin\left(N^{4}_{A_t}, S^{ad}_{A_t}\psi^{ad}_{A\to C}(1-E^{ad}_{A_t})\kappa^{ad}_{C}\right)$$

$$R^{>4}_{C_{t+1}} = R^{>4}_{C\to C_{t+1}} + R^{>4}_{V\to C_{t+1}} + R^{>4}_{A\to C_{t+1}}$$

$$N^{B}_{V\to C_{t+1}} \sim Bin\left(B_{V_t}, S^{ad}_{V_t}\psi^{ad}_{V\to C}(1-E^{ad}_{V_t})(1-\kappa^{ad}_{C})\right)$$

$$N^{B}_{A\to C_{t+1}} \sim Bin\left(B_{A_t}, S^{ad}_{A_t}\psi^{ad}_{A\to C}(1-E^{ad}_{A_t})(1-\kappa^{ad}_{C})\right)$$

$$R^{B}_{V\to C_{t+1}} \sim Bin\left(B_{V_t}, S^{ad}_{V_t}\psi^{ad}_{V\to C}(1-E^{ad}_{V_t})\kappa^{ad}_{C}\right)$$

$$R^{B}_{A\to C_{t+1}} \sim Bin\left(B_{A_t}, S^{ad}_{A_t}\psi^{ad}_{A\to C}(1-E^{ad}_{A_t})\kappa^{ad}_{C}\right)$$

$$B_{C_{t+1}} \sim Pois\left(B^{TOT}_{C_t}, S^{ad}_{C_t}\right)$$

Finally, the breeding population of Catalonia (B^{TOT}_{C}) comprised the breeding individuals that always reproduce and are permanent (B_C), dispersant breeders that were recruited ($R^{B}_{V\to C}$ and $R^{B}_{A\to C}$) and the two- (R^2), three- (R^3), four-year-old (R^4) and older ($R^{>4}$) breeders that were recruited:

$$B^{TOT}_{C_t} = B_{C_t} + R^{B}_{V\to C_t} + R^{B}_{A\to C_t} + R^{>4}_{C_t} + R^{4}_{C_t} + R^{3}_{C_t} + R^{2}_{C_t}$$

State process in Valencian Community

The state process in Valencia Community is basically the same for Catalonia, with little changes in site transitions. Thus, $_{V \to V}$, $_{C \to V}$, and $_{A \to V}$, indicate staying in Valencian Community, immigrants from Catalonia and immigrants from Aragon, respectively.

For non-breeders:

$$N^1_{V \to V_{t+1}} \sim Pois\left(B^{TOT}_{V_t} \frac{\rho_{V_t}}{2} S^{na}_{V_t} \psi^{na}_{V \to V} (1 - E^{na}_{V_t})\right)$$

$$N^1_{C \to V_{t+1}} \sim Pois\left(B^{TOT}_{C_t} \frac{\rho_{C_t}}{2} S^{na}_{C_t} \psi^{na}_{C \to V} (1 - E^{na}_{C_t})\right)$$

$$N^1_{A \to V_{t+1}} \sim Pois\left(B^{TOT}_{A_t} \frac{\rho_{A_t}}{2} S^{na}_{A_t} \psi^{na}_{A \to V} (1 - E^{na}_{A_t})\right)$$

$$N^1_{V_{t+1}} = N^1_{V \to V_{t+1}} + N^1_{C \to V_{t+1}} + N^1_{A \to V_{t+1}}$$

$$N^2_{V \to V_{t+1}} \sim Bin\left(N^1_{V_t}, S^{na}_{V_t} \psi^{na}_{V \to V} (1 - E^{na}_{V_t})(1 - \kappa^{na}_V)\right)$$

$$N^2_{C \to V_{t+1}} \sim Bin\left(N^1_{C_t}, S^{na}_{C_t} \psi^{na}_{C \to V} (1 - E^{na}_{C_t})(1 - \kappa^{na}_V)\right)$$

$$N^2_{A \to V_{t+1}} \sim Bin\left(N^1_{A_t}, S^{na}_{A_t} \psi^{na}_{A \to V} (1 - E^{na}_{A_t})(1 - \kappa^{na}_V)\right)$$

$$N^2_{V_{t+1}} = N^2_{V \to V_{t+1}} + N^2_{C \to V_{t+1}} + N^2_{A \to V_{t+1}}$$

$$N^3_{V \to V_{t+1}} \sim Bin\left(N^2_{V_t}, S^{na}_{V_t} \psi^{na}_{V \to V} (1 - E^{na}_{V_t})(1 - \kappa^{na}_V)\right)$$

$$N^3_{C \to V_{t+1}} \sim Bin\left(N^2_{C_t}, S^{na}_{C_t} \psi^{na}_{C \to V} (1 - E^{na}_{C_t})(1 - \kappa^{na}_V)\right)$$

$$N^3_{A \to V_{t+1}} \sim Bin\left(N^2_{A_t}, S^{na}_{A_t} \psi^{na}_{A \to V} (1 - E^{na}_{A_t})(1 - \kappa^{na}_V)\right)$$

$$N^3_{V_{t+1}} = N^3_{V \to V_{t+1}} + N^3_{C \to V_{t+1}} + N^3_{A \to V_{t+1}}$$

$$N^4_{V \to V_{t+1}} \sim Bin\left(N^3_{V_t}, S^{na}_{V_t} \psi^{na}_{V \to V} (1 - E^{na}_{V_t})\left(1 - \kappa^{ad}_V\right)\right)$$

$$N^4_{C \to V_{t+1}} \sim Bin\left(N^3_{C_t}, S^{na}_{C_t} \psi^{na}_{C \to V} (1 - E^{na}_{C_t})\left(1 - \kappa^{ad}_V\right)\right)$$

$$N^4_{A \to V_{t+1}} \sim Bin\left(N^3_{A_t}, S^{na}_{A_t} \psi^{na}_{A \to V} (1 - E^{na}_{A_t})\left(1 - \kappa^{ad}_V\right)\right)$$

$$N^4_{V_{t+1}} = N^4_{V \to V_{t+1}} + N^4_{C \to V_{t+1}} + N^4_{A \to V_{t+1}}$$

$$N_{V\rightarrow V_{t+1}}^{>4} \sim Bin\left(N_{V_t}^{4}, S_{V_t}^{ad}\psi_{V\rightarrow V}^{ad}(1-E_{V_t}^{ad})\left(1-\kappa_V^{ad}\right)\right)$$

$$N_{C\rightarrow V_{t+1}}^{>4} \sim Bin\left(N_{C_t}^{4}, S_{C_t}^{ad}\psi_{C\rightarrow V}^{ad}(1-E_{C_t}^{ad})\left(1-\kappa_V^{ad}\right)\right)$$

$$N_{A\rightarrow V_{t+1}}^{>4} \sim Bin\left(N_{A_t}^{4}, S_{A_t}^{ad}\psi_{A\rightarrow V}^{ad}(1-E_{A_t}^{ad})\left(1-\kappa_V^{ad}\right)\right)$$

$$N_{V_{t+1}}^{>4} = N_{V\rightarrow V_{t+1}}^{>4} + N_{C\rightarrow V_{t+1}}^{>4} + N_{A\rightarrow V_{t+1}}^{>4}$$

$$N_{C\rightarrow V_{t+1}}^{B} \sim Bin\left(B_{C_t}, S_{C_t}^{ad}\psi_{C\rightarrow V}^{ad}(1-E_{C_t}^{ad})\left(1-\kappa_V^{ad}\right)\right)$$

$$N_{A\rightarrow V_{t+1}}^{B} \sim Bin\left(B_{A_t}, S_{A_t}^{ad}\psi_{A\rightarrow V}^{ad}(1-E_{A_t}^{ad})\left(1-\kappa_V^{ad}\right)\right)$$

For breeders:

$$R_{V\rightarrow V_{t+1}}^{2} \sim Bin\left(N_{V_t}^{1}, S_{V_t}^{na}\psi_{V\rightarrow V}^{na}(1-E_{V_t}^{na})\kappa_V^{na}\right)$$

$$R_{C\rightarrow V_{t+1}}^{2} \sim Bin\left(N_{C_t}^{1}, S_{C_t}^{na}\psi_{C\rightarrow V}^{na}(1-E_{C_t}^{na})\kappa_V^{na}\right)$$

$$R_{A\rightarrow V_{t+1}}^{2} \sim Bin\left(N_{A_t}^{1}, S_{A_t}^{na}\psi_{A\rightarrow V}^{na}(1-E_{A_t}^{na})\kappa_V^{na}\right)$$

$$R_{V_{t+1}}^{2} = R_{V\rightarrow V_{t+1}}^{2} + R_{C\rightarrow V_{t+1}}^{2} + R_{A\rightarrow V_{t+1}}^{2}$$

$$R_{V\rightarrow V_{t+1}}^{3} \sim Bin\left(N_{V_t}^{2}, S_{V_t}^{na}\psi_{V\rightarrow V}^{na}(1-E_{V_t}^{na})\kappa_V^{na}\right)$$

$$R_{C\rightarrow V_{t+1}}^{3} \sim Bin\left(N_{C_t}^{2}, S_{C_t}^{na}\psi_{C\rightarrow V}^{na}(1-E_{C_t}^{na})\kappa_V^{na}\right)$$

$$R_{A\rightarrow V_{t+1}}^{3} \sim Bin\left(N_{A_t}^{2}, S_{A_t}^{na}\psi_{A\rightarrow V}^{na}(1-E_{A_t}^{na})\kappa_V^{na}\right)$$

$$R_{V_{t+1}}^{3} = R_{V\rightarrow V_{t+1}}^{3} + R_{C\rightarrow V_{t+1}}^{3} + R_{A\rightarrow V_{t+1}}^{3}$$

$$R_{V\rightarrow V_{t+1}}^{4} \sim Bin\left(N_{V_t}^{3}, S_{V_t}^{na}\psi_{V\rightarrow V}^{na}(1-E_{V_t}^{na})\kappa_V^{ad}\right)$$

$$R_{C\rightarrow V_{t+1}}^{4} \sim Bin\left(N_{C_t}^{3}, S_{C_t}^{na}\psi_{C\rightarrow V}^{na}(1-E_{C_t}^{na})\kappa_V^{ad}\right)$$

$$R_{A\rightarrow V_{t+1}}^{4} \sim Bin\left(N_{A_t}^{3}, S_{A_t}^{na}\psi_{A\rightarrow C}^{na}(1-E_{A_t}^{na})\kappa_V^{ad}\right)$$

$$R_{V_{t+1}}^{4} = R_{V\rightarrow V_{t+1}}^{4} + R_{C\rightarrow V_{t+1}}^{4} + R_{A\rightarrow V_{t+1}}^{4}$$

$$R_{V\rightarrow V_{t+1}}^{>4} \sim Bin\left(N_{V_t}^{4}, S_{V_t}^{ad}\psi_{V\rightarrow V}^{ad}(1-E_{V_t}^{ad})\kappa_V^{ad}\right)$$

$$R^{>4}_{C\to V_{t+1}} \sim Bin\left(N^{4}_{C_t}, S^{ad}_{C_t}\psi^{ad}_{C\to V}(1-E^{ad}_{C_t})\kappa^{ad}_{V}\right)$$

$$R^{>4}_{A\to V_{t+1}} \sim Bin\left(N^{4}_{A_t}, S^{ad}_{A_t}\psi^{ad}_{A\to V}(1-E^{ad}_{A_t})\kappa^{ad}_{V}\right)$$

$$R^{>4}_{V_{t+1}} = R^{>4}_{V\to V_{t+1}} + R^{>4}_{C\to V_{t+1}} + R^{>4}_{A\to V_{t+1}}$$

$$R^{B}_{C\to V_{t+1}} \sim Bin\left(B_{C_t}, S^{ad}_{C_t}\psi^{ad}_{C\to V}(1-E^{ad}_{C_t})\kappa^{ad}_{V}\right)$$

$$R^{B}_{A\to V_{t+1}} \sim Bin\left(B_{A_t}, S^{ad}_{A_t}\psi^{ad}_{A\to V}(1-E^{ad}_{A_t})\kappa^{ad}_{V}\right)$$

$$B_{V_{t+1}} \sim Pois\left(B^{TOT}_{V_t}, S^{ad}_{V_t}\right)$$

$$B^{TOT}_{V_t} = B_{V_t} + R^{B}_{C\to V_t} + R^{B}_{A\to V_t} + R^{>4}_{V_t} + R^{4}_{V_t} + R^{3}_{V_t} + R^{2}_{V_t}$$

State process in Aragon

The state process in Aragon follows the same logic as the other two sites, with movement transitions subscripts $_{A\to A}$, $_{C\to A}$, and $_{V\to A}$, indicating staying in Aragon, immigrants from Catalonia and immigrants from Valencian Community, respectively. Given the low number of immigrants from Catalonia and the Valencian Community, assuming a closed system led to an underestimation of the non-breeding population in Aragon (results not shown here). To address this, we allowed for the inclusion of immigrants from other regions. Since we are already estimating recruitment as a hidden parameter (estimating more than one hidden parameter is not feasible due to identifiability issues, Shaub and Kéry, 2021) and given the significant number of missing values in the count data, we estimated immigrants from other regions using informative priors and strong, yet plausible, assumptions about their numbers.

We assumed that immigrants from other regions primarily enter through Aragon, with minimal entry into Catalonia and the Valencian Community due to their geographical locations on the easternmost part of the Iberian Peninsula, bordered by the Mediterranean Sea to the east (Figure 1 in manuscript). To prevent overestimating the proportion of immigrants in the breeding population of Aragon, we assumed that immigrants initially enter as non-breeders in time *t* and then available to be recruited from the pool of non-breeders in time *t*+1 at each stage. We deliberately assumed their numbers were proportional to the volume of immigrants coming from Catalonia ($N_{C\to A}$) and Valencian Community ($N_{V\to A}$) at each stage. This calculation is very conservative about the immigrant numbers and implicitly involves assuming the same survival and dispersal probabilities from both autonomous communities but numbers adjusted by the ratio of breeding pairs (*BPR*) from the neighbouring provinces (y_I) of Guadalajara, Cuenca, Soria, La Rioja, and Navarra to those in Aragon (y_A). We considered these provinces as the closest populations to Aragon, assuming that individuals from these areas would be more likely to emigrate to Aragon, while those from more distant locations would be less likely. To illustrate, GPS-tagged individuals from Segovia (n = 15), the province west of Guadalajara and Soria, showed movements exclusively to the autonomous community of Andalucía (south of Spain), whereas individuals from Andalucía (n = 42) showed very little movement to the south of Aragon according to Morant et al. (2023). Similarly, a study of several GPS-tagged griffon vultures (n=48) captured in Andalucía demonstrated almost no movement to the Valencian Community and Aragon (Delgado-González et al. 2022). Therefore, our assumption of a higher probability of individuals emigrating from neighbouring western provinces to Aragon appears to be very plausible. Since griffon vulture censuses were conducted in 2008 and 2018 (Del Moral 2009, Del Moral and Molina 2018), we calculated the ratios in both years and applied them following a uniform distribution (*Imm*) on immigrant numbers $N_{C\to A}$ and $N_{V\to A}$ as:

$$Imm \sim Uniform(BPR_{2008}, BPR_{2018})$$

$$BPR_{2008} = \frac{y_{I_{2008}}}{y_{A_{2008}}};\ BPR_{2018} = \frac{y_{I_{2018}}}{y_{A_{2018}}}$$

Non-breeders:

$$N^{1}_{A\to A_{t+1}} \sim Pois\left(B^{TOT}_{A_t}\frac{\rho_{A_t}}{2}S^{na}_{A_t}\psi^{na}_{A\to A}(1-E^{na}_{A_t})\right)$$

$$N^1_{C\to A_{t+1}} \sim Pois\left(B^{TOT}_{C_t}\frac{\rho_{C_t}}{2}S^{na}_{C_t}\psi^{na}_{C\to A}(1-E^{na}_{C_t})\right)$$

$$N^1_{V\to A_{t+1}} \sim Pois\left(B^{TOT}_{V_t}\frac{\rho_{V_t}}{2}S^{na}_{V_t}\psi^{na}_{V\to A}(1-E^{na}_{V_t})\right)$$

$$N^1_{A_{t+1}} = N^1_{A\to A_{t+1}} + N^1_{C\to A_{t+1}} + N^1_{V\to A_{t+1}} + N^1_{Imm_{t+1}}$$

$$N^1_{Imm_{t+1}} \sim Pois\left(\left(N^1_{C\to A_{t+1}} + N^1_{V\to A_{t+1}}\right)Imm\right)$$

$$N^2_{A\to A_{t+1}} \sim Bin\left(N^1_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to A}(1-E^{na}_{A_t})(1-\kappa^{na}_A)\right)$$

$$N^2_{C\to A_{t+1}} \sim Bin\left(N^1_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to A}(1-E^{na}_{C_t})(1-\kappa^{na}_A)\right)$$

$$N^2_{V\to A_{t+1}} \sim Bin\left(N^1_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to A}(1-E^{na}_{V_t})(1-\kappa^{na}_A)\right)$$

$$N^2_{A_{t+1}} = N^2_{A\to A_{t+1}} + N^2_{C\to A_{t+1}} + N^2_{V\to A_{t+1}} + N^2_{Imm_{t+1}}$$

$$N^2_{Imm_{t+1}} \sim Pois\left(\left(N^2_{C\to A_{t+1}} + N^2_{V\to A_{t+1}}\right)Imm\right)$$

$$N^3_{A\to A_{t+1}} \sim Bin\left(N^2_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to A}(1-E^{na}_{A_t})(1-\kappa^{na}_A)\right)$$

$$N^3_{C\to A_{t+1}} \sim Bin\left(N^2_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to A}(1-E^{na}_{C_t})(1-\kappa^{na}_A)\right)$$

$$N^3_{V\to A_{t+1}} \sim Bin\left(N^2_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to A}(1-E^{na}_{V_t})(1-\kappa^{na}_A)\right)$$

$$N^3_{A_{t+1}} = N^3_{A\to A_{t+1}} + N^3_{C\to A_{t+1}} + N^3_{V\to A_{t+1}} + N^3_{Imm_{t+1}}$$

$$N^3_{Imm_{t+1}} \sim Pois\left(\left(N^3_{C\to A_{t+1}} + N^3_{V\to A_{t+1}}\right)Imm\right)$$

$$N^4_{A\to A_{t+1}} \sim Bin\left(N^3_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to A}(1-E^{na}_{A_t})\left(1-\kappa^{ad}_A\right)\right)$$

$$N^4_{C\to A_{t+1}} \sim Bin\left(N^3_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to A}(1-E^{na}_{C_t})\left(1-\kappa^{ad}_A\right)\right)$$

$$N^4_{V\to A_{t+1}} \sim Bin\left(N^3_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to A}(1-E^{na}_{V_t})\left(1-\kappa^{ad}_A\right)\right)$$

$$N^4_{A_{t+1}} = N^4_{A\to A_{t+1}} + N^4_{C\to A_{t+1}} + N^4_{V\to A_{t+1}} + N^4_{Imm_{t+1}}$$

$$N^4_{Imm_{t+1}} \sim Pois\left(\left(N^4_{C\to A_{t+1}} + N^4_{V\to A_{t+1}}\right)Imm\right)$$

$$N^{>4}_{A\to A_{t+1}} \sim Bin\left(N^{4}_{A_t}, S^{ad}_{A_t}\psi^{ad}_{A\to A}(1-E^{ad}_{A_t})(1-\kappa^{ad}_{A})\right)$$

$$N^{>4}_{C\to A_{t+1}} \sim Bin\left(N^{4}_{C_t}, S^{ad}_{C_t}\psi^{ad}_{C\to A}(1-E^{ad}_{C_t})(1-\kappa^{ad}_{A})\right)$$

$$N^{>4}_{V\to A_{t+1}} \sim Bin\left(N^{4}_{V_t}, S^{ad}_{V_t}\psi^{ad}_{V\to A}(1-E^{ad}_{V_t})(1-\kappa^{ad}_{A})\right)$$

$$N^{>4}_{A_{t+1}} = N^{>4}_{A\to A_{t+1}} + N^{>4}_{C\to A_{t+1}} + N^{>4}_{V\to A_{t+1}} + N^{>4}_{Imm_{t+1}}$$

$$N^{>4}_{Imm_{t+1}} \sim Pois\left((N^{>4}_{C\to A_{t+1}} + N^{>4}_{V\to A_{t+1}})Imm\right)$$

$$N^{B}_{C\to A_{t+1}} \sim Bin\left(B_{C_t}, S^{ad}_{C_t}\psi^{ad}_{C\to A}(1-E^{ad}_{C_t})(1-\kappa^{ad}_{A})\right)$$

$$N^{B}_{V\to A_{t+1}} \sim Bin\left(B_{A_t}, S^{ad}_{A_t}\psi^{ad}_{V\to A}(1-E^{ad}_{A_t})(1-\kappa^{ad}_{A})\right)$$

Breeders:

$$R^{2}_{A\to A_{t+1}} \sim Bin\left(N^{1}_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to A}(1-E^{na}_{A_t})\kappa^{na}_{A}\right)$$

$$R^{2}_{C\to A_{t+1}} \sim Bin\left(N^{1}_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to A}(1-E^{na}_{C_t})\kappa^{na}_{A}\right)$$

$$R^{2}_{V\to A_{t+1}} \sim Bin\left(N^{1}_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to A}(1-E^{na}_{V_t})\kappa^{na}_{A}\right)$$

$$R^{2}_{A_{t+1}} = R^{2}_{A\to A_{t+1}} + R^{2}_{C\to A_{t+1}} + R^{2}_{V\to A_{t+1}}$$

$$R^{3}_{A\to A_{t+1}} \sim Bin\left(N^{2}_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to A}(1-E^{na}_{A_t})\kappa^{na}_{A}\right)$$

$$R^{3}_{C\to A_{t+1}} \sim Bin\left(N^{2}_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to A}(1-E^{na}_{C_t})\kappa^{na}_{A}\right)$$

$$R^{3}_{V\to A_{t+1}} \sim Bin\left(N^{2}_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to A}(1-E^{na}_{V_t})\kappa^{na}_{A}\right)$$

$$R^{3}_{A_{t+1}} = R^{3}_{A\to A_{t+1}} + R^{3}_{C\to A_{t+1}} + R^{3}_{V\to A_{t+1}}$$

$$R^{4}_{A\to A_{t+1}} \sim Bin\left(N^{3}_{A_t}, S^{na}_{A_t}\psi^{na}_{A\to A}(1-E^{na}_{A_t})\kappa^{ad}_{A}\right)$$

$$R^{4}_{C\to A_{t+1}} \sim Bin\left(N^{3}_{C_t}, S^{na}_{C_t}\psi^{na}_{C\to A}(1-E^{na}_{C_t})\kappa^{ad}_{A}\right)$$

$$R^{4}_{V\to A_{t+1}} \sim Bin\left(N^{3}_{V_t}, S^{na}_{V_t}\psi^{na}_{V\to A}(1-E^{na}_{V_t})\kappa^{ad}_{A}\right)$$

$$R^{4}_{A_{t+1}} = R^{4}_{A\to A_{t+1}} + R^{4}_{C\to A_{t+1}} + R^{4}_{V\to A_{t+1}}$$

$$R^{>4}_{A\to A_{t+1}} \sim Bin\left(N^{4}_{A_t}, S^{ad}_{A_t}\psi^{ad}_{A\to A}(1-E^{ad}_{A_t})\kappa^{ad}_{A}\right)$$

$$R^{>4}_{C\to A_{t+1}} \sim Bin\left(N^{4}_{C_t}, S^{ad}_{C_t}\psi^{ad}_{C\to A}(1-E^{ad}_{C_t})\kappa^{ad}_{A}\right)$$

$$R^{>4}_{V\to A_{t+1}} \sim Bin\left(N^{4}_{V_t}, S^{ad}_{V_t}\psi^{ad}_{V\to A}(1-E^{ad}_{V_t})\kappa^{ad}_{A}\right)$$

$$R^{>4}_{A_{t+1}} = R^{>4}_{A\to A_{t+1}} + R^{>4}_{C\to A_{t+1}} + R^{>4}_{V\to A_{t+1}}$$

$$R^{B}_{C\to A_{t+1}} \sim Bin\left(B_{C_t}, S^{ad}_{C_t}\psi^{ad}_{C\to A}(1-E^{ad}_{C_t})\kappa^{ad}_{A}\right)$$

$$R^{B}_{V\to A_{t+1}} \sim Bin\left(B_{V_t}, S^{ad}_{V_t}\psi^{ad}_{V\to A}(1-E^{ad}_{V_t})\kappa^{ad}_{A}\right)$$

$$B_{A_{t+1}} \sim Pois\left(B^{TOT}_{A_t}, S^{ad}_{A_t}\right)$$

$$B^{TOT}_{A_t} = B_{A_t} + R^{B}_{C\to A_t} + R^{B}_{V\to A_t} + R^{>4}_{A_t} + R^{4}_{A_t} + R^{3}_{A_t} + R^{2}_{A_t}$$

Observation process

The observation process of each population was modelled with a Poisson distribution as:

$$y_{C_t} \sim Pois\left(B^{TOT}_{C_t}\right)$$

$$y_{V_t} \sim Pois\left(B^{TOT}_{V_t}\right)$$

$$y_{A_t} \sim Pois\left(B^{TOT}_{A_t}\right)$$

Where y and B^{TOT} are the breeder counts and the estimated number of breeding females, respectively, in Catalonia ($_C$), Valencian Community ($_V$), and Aragon ($_A$).

In 2018, the census in Aragon achieved 90.6% territorial coverage, recording 4,832 pairs distributed across 562 colonies and 127 isolated pairs (Del Moral and Molina 2018). To account for this information and prevent potential bias by underestimating the breeding population for that year, we modelled the observed count as:

$$y_{A_2} \sim Pois\left(\frac{B^{TOT}_{A_2}}{0.906}\right)$$

S2.2. Productivity model

We estimated productivity (ρ) from the number of fledglings (J) produced by breeding pairs (R) in year t in each autonomous community. We assumed that in each site, the number of J_t followed a Poisson distribution and was estimated as the product of R_t and ρ_t as:

$$J_t \sim Pois(R_t * \rho_t),$$

For the missing years ($_{my}$) in Aragon, the number of breeding pairs (R_A) were assumed to be the mean number of breeding pairs in the whole study period drawn from a Poisson distribution. Thus, for years 2009, 2015, 2016, 2017 and 2020, the number of breeding pairs were estimated as:

$$R_{A_{my}} \sim Pois\left(\bar{x}_{R_{2008-2021}}\right),$$

Productivity was modelled as a generalised linear mixed model (GLMM) using a logit link function and a random time effect:

$$\text{logit}(\rho_t) = \beta_0 + \varepsilon_{\rho,t},$$

$$\varepsilon_{\rho,t} \sim Normal\left(0, \sigma_\rho^2\right),$$

Where β_0 is the overall mean (intercept) of productivity in the logit scale and $\varepsilon_{\rho,t}$ is the deviation from the overall mean (or temporal residual) and σ_ρ^2 the temporal variance (Kéry and Schaub 2012). Applying the logit link function allowed us to bound productivity values to 0 and 1, as griffon vultures rarely lay more than one egg (see Xirouchakis 2010).

S2.3. Multistate model

Survival and movement probabilities were estimated using a multi-site multistate model with the summarized capture-mark-recapture and dead-recovery data in a m-array format and multinomial likelihood (Lebreton et al. 1999, Kéry and Schaub 2012). Occasions comprised 9-month intervals (January to September) as it has been shown that pooled data improves precision of estimates in long-lived species (Hargrove and

Borland 1994, O'Brien et al. 2005, Dupont et al. 2019). Data from different sources (camera traps, resightings and captures) were used without distinction as provide more accurate and unbiased estimates than separated (Santangeli et al. 2020). In total, 804 individuals were marked in the Valencian Community, 3,353 in Catalonia, and 735 in Aragon, with recaptures and resightings within the three autonomous communities exceeding 45,000 records, and the recoveries of dead individuals throughout Spain and France totalling 152.

We had 37 observed states, denoting three sites (Catalonia, Aragon or Valencian Community), age (1-year-old, 2- year-old, 3- year-old, and ≥4-year-old), mark status (seen with both wing tag and plastic band, wing tag only or plastic band only) and recovery of dead individuals. See **doi.10.17632/smf4zc5ysw.1** for details of states coding and transition matrix. We estimated site-specific probabilities of non-adult (S^{na}: 1- to 3-year-old) and adult (S^{ad}: ≥ 4- year-old) true survivals, non-adult (E^{na}) and adult (E^{ad}) permanent emigration from the study area, and non-adult (ψ^{na}) and subadult/adult (ψ^{ad}) movements between sites. We distinguished these two age-classes assuming that at age four, individuals are more likely to become territorial (although 2- and 3- year-old can recruit also, but less likely) and survivals improves significantly from this age onwards (Sarrazin et al. 1996, Chantepie et al. 2015, Arévalo-Ayala et al. 2023). A common probability (i.e., without site distinction) for wing tag loss, plastic band loss, and recovery was estimated as marks were made of the same materials and recoveries were done anywhere (inside and outside of the study area). Recapture probabilities were estimated as site-specific without age distinction as previous models (not shown here) indicated 'non-significant' differences between ages. As goodness-of-fit showed a lack of fit of the data due to the presence of transients and trap-dependence (see *Goodness-of-fit* below), we accounted for these sources of heterogeneity by applying, respectively, the structures developed by Lebreton et al. (1999) and detailed in Kéry and Schaub (2012) and Shaub and Kéry (2021) to estimate a permanent emigration probability (which is the complement of site fidelity), as jointly dead-recovery probability allowed us to separately estimate true survival from permanent emigration, and the multistate structure of Pradel and Sanz-Aguilar (2012) to estimate recapture probabilities for previously (P^{pc}) and not-previously captured (P^{npc}) individuals.

Survival, permanent emigration, and recapture probabilities were modelled as time-varying with a random time effect in each autonomous community as:

$$\mathrm{logit}(S_t^{na}) = \beta_1 + \varepsilon_{S^{na},t},$$

$$\mathrm{logit}(S_t^{ad}) = \beta_2 + \varepsilon_{S^{ad},t},$$

$$\mathrm{logit}(E_t^{na}) = \beta_3 + \varepsilon_{E^{na},t},$$

$$\mathrm{logit}(E_t^{ad}) = \beta_4 + \varepsilon_{E^{ad},t},$$

$$\mathrm{logit}(P_t^{pc}) = \beta_5 + \varepsilon_{P^{pc},t},$$

$$\mathrm{logit}(P_t^{npc}) = \beta_6 + \varepsilon_{P^{npc},t},$$

$$\varepsilon_{S^{na},t} \sim Normal(0, \sigma^2_{S^{na},t})$$

$$\varepsilon_{S^{ad},t} \sim Normal(0, \sigma^2_{S^{ad},t})$$

$$\varepsilon_{E^{na},t} \sim Normal(0, \sigma^2_{E^{na},t})$$

$$\varepsilon_{E^{ad},t} \sim Normal(0, \sigma^2_{E^{ad},t})$$

$$\varepsilon_{P^{pc},t} \sim Normal(0, \sigma^2_{P^{pc},t})$$

$$\varepsilon_{P^{npc},t} \sim Normal(0, \sigma^2_{P^{npc},t})$$

Where $\beta_{1,}$ β_2, β_3, β_4, β_5, and β_6, are the overall means (intercepts) of survival, permanent emigration and recapture probabilities in the logit scale, $\varepsilon_{S^{na},t}$, $\varepsilon_{S^{ad},t}$, $\varepsilon_{E^{na},t}$, $\varepsilon_{E^{ad},t}$, $\varepsilon_{P^{pc},t}$, and $\varepsilon_{P^{npc},t}$ are the deviations from the overall mean (or temporal residual) and $\sigma^2_{S^{na},t}$, $\sigma^2_{S^{ad},t}$, $\sigma^2_{E^{na},t}$, $\sigma^2_{E^{ad},t}$, $\sigma^2_{P^{pc},t}$, and $\sigma^2_{P^{npc},t}$ the temporal variances (Kéry and Schaub 2012).

Recovery and movement probabilities were modelled as constant over time, as preliminary analyses showed little temporal variation, using a uniform uninformative prior (0,1) for the first and a Dirichlet distribution for the second to constrain the three movement probabilities for each site (e.g., from site A to A, from site A to B, and from site A to C) to sum to one as (Royle and Dorazio, 2008):

$$\psi_j^{na} = \alpha_j / \textstyle\sum_{i=1}^{n} \alpha_i,$$

$$\psi_j^{ad} = \gamma_j / \textstyle\sum_{i=1}^{n} \gamma_i,$$

$$\alpha_j \sim gamma(1,1)$$

$$\gamma_j \sim gamma(1,1)$$

Where ψ_j^n and ψ_j^a are the movement probabilities of non-adults and adults between the three autonomous communities (*j*), respectively, and α_j and γ_j the gamma hyperpriors.

Wing tag loss and plastic band were modelled as time-since-marking and using as informative priors the means and standard deviations of estimates from studies of Santageli et al. (2020, *Torgos tracheliotos*) and Rousteau et al. (2022, *Aegypius monachus*), respectively, using normal distributions as:

$$ml_t \sim Normal(\mu_{prior,t}, \sigma^2_{prior,t}),$$

Where m_t represents either wing tag or plastic band probability, and $\mu_{prior,t}$ and $\sigma^2_{prior,t}$ the mean and variance of the informative priors applied in each year. We proceeded this way to prevent biased survival estimates as the state and type of mark read from distance was not always reported and because previous analyses without these informative priors showed unrealistically low wing tag and plastic band loss probabilities, rendering distrustful low survival estimates. The resulting posterior estimates were sensitive to the chosen priors as we expected to 'correct' the estimates from our data.

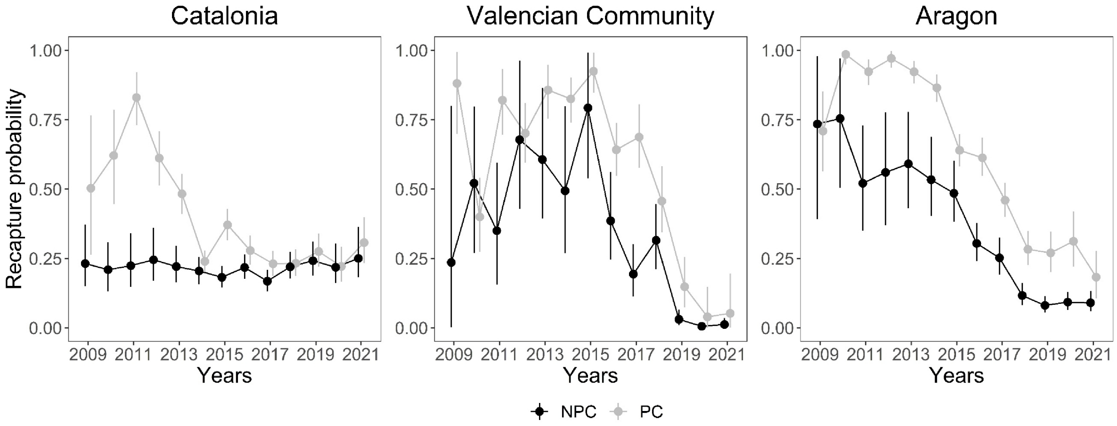

Figure S2. Yearly estimates of recapture probability for previously captured (PC) and not previously captured (NPC) vultures in the three autonomous communities in the northeast of the Iberian Peninsula.

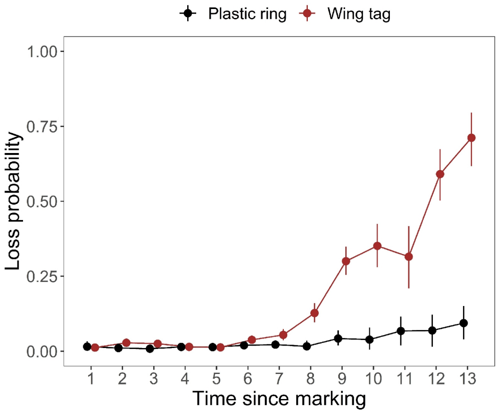

Figure S3. Probabilities of plastic ring and wing tag loss over time since marking in the three populations of griffon vulture in the northeast of the Iberian Peninsula.

S2.4. Derived estimates

We estimated the annual population growth rates of the breeding pairs of each population by dividing the size of the total breeding population size in year *t*+1 by the total population size in year *t* as:

$$\lambda_t = B_{t+1}^{TOT} / B_t^{TOT}$$

We calculated the number of floaters per breeding female (floater-to-breeder ratio) in each autonomous community by diving the number of non-recruited individuals of age two and older per the total breeding population size in year *t*. Similarly, we calculated the immigration rate by dividing the number of recruited immigrants of age two and older that come from the neighbour populations in time *t*+1 per the total number of surviving breeders and local recruits in year *t* (Schaub and Kéry 2022).

S2.5. The IPM likelihood

Integrated Population Models are usually fitted in a single jointly likelihood of the three datasets. Here, we developed our IPM using a sequential analysis approach. This involved fitting a separate likelihood for one of the datasets, and then integrating its estimates as informative priors into the IPM to incorporate significant computational benefits (Schaub and Kéry 2022). Thus, we initially fitted the mark-recapture multistate model alone, given the significant structural complexity required to account several sources of heterogeneity, thus rendering the model computationally demanding. We used three chains of 20,000 iterations each, a burn-in of 8,000 iterations and a thinning rate of six, which had a computational running time of ~20 days. Then, the posterior means and standard deviations of parameters were used as informative priors to inform the IPM about survival, permanent emigration and movement probabilities and their uncertainties using normal for the first two, and a Dirichlet distribution for the latter (Kéry and Schaub 2012, Schaub and Kéry 2022).

S2.6. Goodness-of-fit of the IPM

Currently, there is no goodness-of-fit test (GoF) specifically for IPMs, so the most feasible approach is to evaluate the potential lack of fit of each submodel separately (Besbeas and Morgan 2014, Schaub and Kéry 2022). The state-space count and Poisson productivity models were assessed using the Posterior Predictive Check, which involves comparing observed data with simulated expected data. Bayesian p-values indicated a good fit for the productivity and count models in all three autonomous communities (**Figures S4** and **S5**). For the multistate model, we employed the GoF test of the Jolly-Move model using sites as states with U-CARE (Choquet et al. 2009). The GoF test revealed lack of fit (p-value < 0.001) with a strong influence of transients and trap-dependence, which was corrected with the definitive parametrization of the multi-state model (see the *Survival, movement and permanent emigration probabilities between sites submodel* section in Materials and Methods).

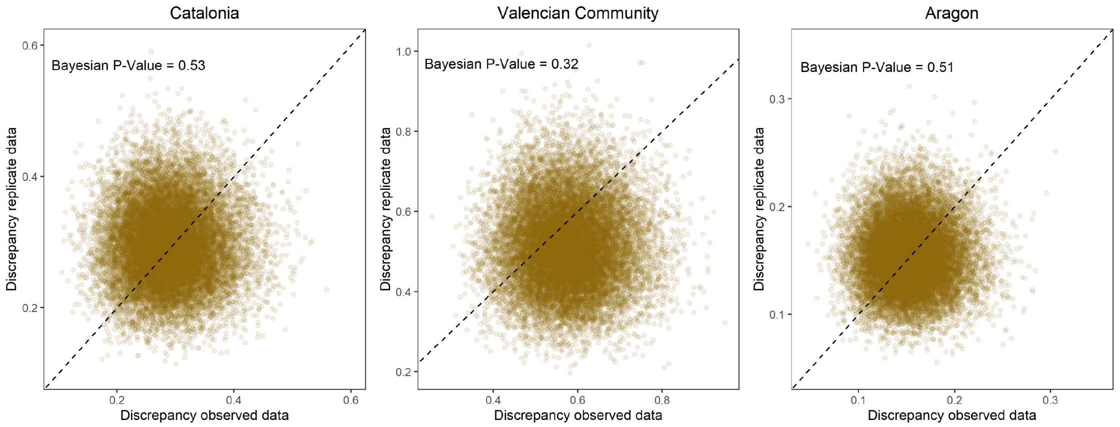

Figure S4. Posterior Predictive Checks for the state-space models (population dynamics model) of each griffon vulture population. Values close to 0 or 1 indicates lack of fit, while values close to 0.5 indicate a good fit.

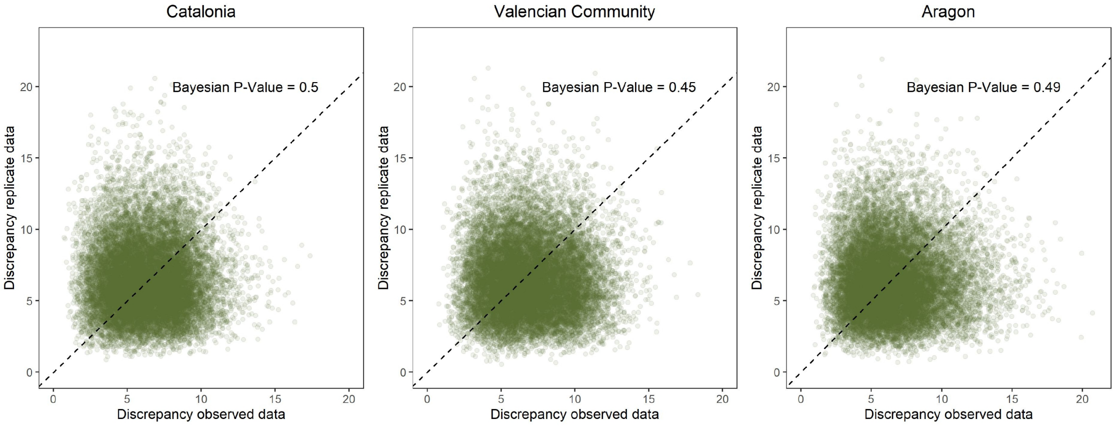

Figure S5. Posterior Predictive Checks for the Poisson models (productivity model) of each griffon vulture population. Values close to 0 or 1 indicates lack of fit, while values close to 0.5 indicate a good fit.

Appendix S3. Wind energy development and griffon vulture casualties in the three autonomous communities

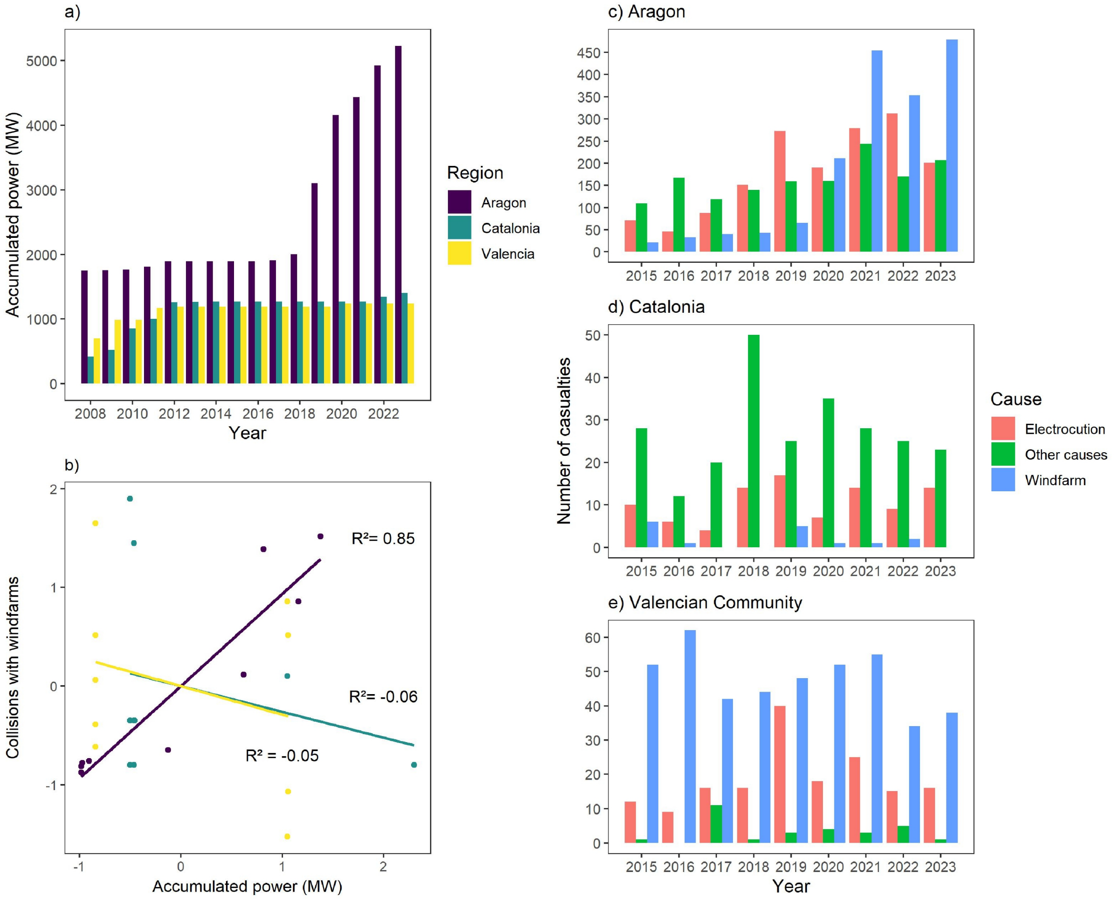

Figure S6. a) Accumulated power (Megawatts) of annual wind energy produced in each autonomous community from 2008 to 2023. In Catalonia and the Valencian Community, wind energy development has been limited compared to Aragon and has remained constant over time. In contrast, wind energy projects in Aragon have increased since 2019. b) Relationship between the (scaled) accumulated power and the (scaled) number of vultures collisions with windfarms from 2015 to 2023 in the three autonomous communities. Adjusted R^2 is shown for each smooth line, where Aragon shows the higher coefficient (0.85). From c) to e), the causes of admission of griffon vultures to wildlife recovery centres in each autonomous community from 2015 to 2023. Wind energy data is publicly available from Asociación Empresarial Eólica (https://aeeolica.org/).

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GENERAL DISCUSSION

Photography courtesy of Arnau Soler Costa

A BRIEF SUMMARY AND MAIN FINDINGS

Population and demographic models have been crucial for comprehending the population dynamics of plant and animal species, serving as the foundation for ecological and conservation studies since decades ago (Sæther et al. 1996, Coale and Trussell 1996, Mills 2012, Schaub and Kéry 2022). These models allow researchers to assess species' responses to environmental changes, identify critical factors influencing population stability (such as environmental or demographic influences), and develop strategies for their conservation. In this thesis, we aimed to explore the demographic response and population dynamics of the griffon vulture (*Gyps fulvus*) to a changing environment at local and regional scales, using capture-recapture methods and the novel integrated population models in both frequentist and Bayesian frameworks. At the local scale, our research focused on estimating the demographic response to food decline (i.e., organic matter) at a landfill in Catalonia, Spain, applying an extensive database of >3,000 banded individuals, collected through a systematic long-term ringing period (2012 to 2021). At the regional scale, we examined the population dynamics and the interdependence of three neighbouring populations in northeastern Spain—specifically in Catalonia, Aragon, and the Valencian Community. This analysis was based on a database of ca. 5,000 banded individuals with >48,000 recaptures/resightings and >150 dead recoveries in Europe, as well as breeding pairs count data and productivity at the autonomous community level in a long-term basis (2008 to 2021). We choose to study the griffon vulture due to the significant monitoring efforts across Spain, constituting an ideal study species and system to generate novel information on the population and demographic modelling, and applied conservation of long-lived animals. In addition, the griffon vulture is closely related to many endangered vulture species and shares key biological traits with them, this study species serves as an ideal example to provide useful insights on the dynamics of vulture populations. These insights can then be leveraged to improve conservation strategies for this seriously threatened guild of birds.

In Chapter 1, we investigated the demographic response of a local griffon vulture population by the reduced organic matter availability in an open landfill, a consequence of European sanitary measures aimed at landfill closures. By employing the Schwarz and Arnason formulation of the Jolly-Seber model, we found a significant decline in apparent survival due to reduced food availability. Nevertheless, local vulture abundance increased, likely due to the species' high dispersal capacity and increased regional population growth, respectively. In the Chapter 2 we focused on the age-specific demographic responses to food reduction at the landfill, utilizing a hierarchical Cormack-Jolly-Seber model. We observed an increase in transient individuals and changes in apparent survival rates across age classes, with heightened permanent emigration driven by intensified competition. Notably, immature residents demonstrated resilience, suggesting the persistence of high-quality individuals despite food scarcity as the apparent survival variances decreased with available organic matter. Finally, in Chapter 3, we developed a multi-site Integrated Population Model (ms-IPM) to analyse the griffon vulture population dynamics and their interdependence across three neighbouring populations—Catalonia, Aragon, and the Valencian Community. The ms-IPM provided the basis to identify distinct regional trends, with Catalonia's population growing, stabilization in the Valencian Community, and fluctuating trends in Aragon. Key demographic factors, including adult survival, floater-to-breeder ratios, and immigration, varied by region, with density dependence observed in certain parameters and at population levels unveiling the necessity of global conservation strategies consistent between regions able to implement specific conservation needs across populations in a cohesive manner.

THE DEMOGRAPHIC RESPONSES OF LONG-LIVED SPECIES TO FOOD SHORTAGE SCENARIOS

In this thesis, we determined how the griffon vulture responds to reduced food availability, particularly in predictable food sources like landfills. Landfills serve as important foraging resource for several populations, where in Spain the northern populations rely heavily in this feeding sites and other anthropogenic sources (Arrondo et al. 2023). By applying capture-recapture methods in a frequentist and Bayesian framework and accounting for heterogeneity in the data, we evaluated this response by estimating: 1) apparent survival for resident vultures of different age classes (Chapter 1 and 2), 2) the annual local abundance attending the landfill (Chapter 1), and 3) the age-specific probability of becoming transients after the first capture (Chapter 2).

Our findings revealed that the reduction in organic matter at the landfill in Central Catalonia led to a significant demographic shift: a decrease in apparent survival and a rise in transient individuals—i.e., those that opportunistically visit the landfill and do not return (Pradel et al. 1997, Genovart and Pradel 2019)—particularly among juveniles and adults. Nevertheless, abundance of vultures attending the landfill did not diminish, on the contrary, showed an increasing trend. Given that apparent survival is the product of true survival and site fidelity, we interpret the decline in apparent survival likely driven by vultures permanently emigrating from the area rather than increased mortality (Lebreton et al. 1992). Given the species' ability to adapt its foraging behaviour based on food availability, the reduced food at the landfill may prompted numbers of vultures to stop visiting the site regularly and feed in other sites, as it happened in consequence of the European Union sanitary legislation in response of the appearance of Transmissible Spongiform Encephalopathies (“mad cow disease”) that progressively limited the abandonment of dead livestock in the field (Donázar et al. 2010, Zuberogoitia et al. 2013). Therefore, the apparent survival probability we estimated on Chapter 1 and age-specific apparent survival and transient probability in Chapter 2 reflected primarily the probability of vultures visiting the landfill. Griffon vultures are known to forage large distances and very opportunistically (García-Ripollés et al. 2011, Monsarrat et al. 2013), concentrating near reliable food sources such as landfills and other predictable food sources (e.g., supplementary feeding stations for scavengers), where inexperienced young individuals learn to survive during periods of natural food scarcity by feeding on easily accessible waste (Dewey and Kennedy 2001, Garrido et al. 2002, Kennedy and Ward 2003, Oro et al. 2008, 2013, 2014). It is very likely that the reduction of food availability may have triggered density-dependent effects at the site, intensifying intraspecific competition and pushing individuals to disperse in search of alternative food sources (Bosè and Sarrazin, 2007). In this sense, we saw that juvenile apparent survival estimates, being the most mobile yet less competitive age group (Bosè et al. 2012, Cortés-Avizanda et al. 2012, Duriez et al. 2012), were particularly impacted, indicating higher rates of permanent emigration after food reduction. Interestingly, resident immature vultures did not show a decrease in apparent survival despite the food shortage, and we interpreted this behaviour likely due to the presence of high-quality individuals that preferred to return to the landfill and compete (Oro et al. 2014). In addition, it may be also explained by their lack of established territories, as their movements are primarily driven by conspecific attraction and the availability of feeding sites, leading them to remain and compete for the residual resources in the landfill (García-Ripollés et al. 2004, Duriez et al. 2012, Peshev et al. 2018). This demographic response has been showed in other long-lived species exposed to changes in food availability for the closure of a landfill (yellow-legged gulls, Delgado et al. 2021) and in another population of griffon vultures during the EU sanitary measures implemented during the mad cow disease period (Almaraz et al. 2022). The survival of resident adults, on the other hand, eventually declined, and may be attributed to insufficient food resources to meet their energy demands, therefore, pushing individuals to exploit other food resources. Additionally, while true mortality could contribute to this decrease, the lack of dead-recovery data in this study makes it difficult to confirm this hypothesis. Nevertheless, our findings are sound, and align with similar studies on other opportunistic species, such as spotted hyenas (Kolowski and Holekamp 2007), red foxes (Bino et al. 2010), and yellow-legged gulls (Payo-Payo et al. 2015, Zorrozua et al. 2020, Delgado et al. 2021), which also exhibited increased dispersion or home range sizes to find alternative food sources following reductions in landfills.

In this thesis, we also examined the impact of reduced food availability at the landfill on vulture abundance. Despite the organic matter decrease, we found that the local abundance of vultures visiting the site has not declined, but markedly increased. We believe that this trend is likely due to the ongoing increase in the breeding population of griffon vultures in Catalonia over the past four decades, as our abundance estimates highly correlated with these numbers, suggesting that enough food remains to attract these birds even with the presence of the waste treatment centre operating (Chapter 1). This result is significant because one expected benefit of reducing dumped organic matter is to decrease local populations of opportunistic species like vultures, which are often involved in wildlife-human conflicts (Margalida et al., 2014; Oliva-Vidal et al., 2022a). One possible explanation for this continued attraction is the inefficiency of waste triage at the waste treatment centre, where large pieces of organic matter are still being dumped (fragments >12 cm). Anecdotal evidence supports this, as large food residues were observed being deposited during marking campaigns. In addition, other vulture species such as the Egyptian vulture have not experienced a reduction in numbers (author’s personal observation). This suggests that the landfill continues to provide enough food to attract vultures and other species, as estimated numbers were around 450 metrics tons of organic matter poured during 2022 (see organic matter values in supplementary materials from Arévalo-Ayala et al., 2023a, 2023b). Previous research indicates that local vulture populations declined due to food shortages caused by regulations related to the BSE outbreak (Camiña and Montelío 2006, Donázar et al. 2009). These policies significantly reduced the overall food available for vultures across the country. Additionally, the closure of multiple landfills across a broader extension, also negatively affected population numbers in other long-lived species (Pinto et al. 2021, Delgado et al. 2023). However, in our study area, the food shortage was very localized (i.e., the studied landfill), and to our knowledge, other food sources like vulture feeding stations, wild ungulate herds, livestock, and other landfills close by may still support the local population.

Furthermore, it is important to highlight that the abundance estimates from the capture-recapture model include all individuals ever marked at the site, including those never recaptured, and account for a hypothetical super-population of unmarked individuals in the surrounding area that have an associated probability of entering to the study site (Schwarz and Arnason 1996, Cooch and White 2019). Given that griffon vultures can travel great distances daily to forage (120–300 km, García-Ripollés et al. 2011; Harel et al., 2016), it is likely that a portion of the regional population has visited the landfill at some point and at least one time. In fact, estimates of transient probability after first capture, as discussed in Chapter 2, revealed that this probability increased for immatures and adults as food availability decreased. This indicates that new individuals continue to arrive at the site, but the reduced food supply makes it less attractive for these birds to return as density dependence may arise as increased intraspecific competition.

Overall, our analytical approach has proven essential for unravelling the demographic response of a species adapted to feeding at a predictable food source under a scenario of drastic decline. This natural experiment provided a "before and after" perspective of such a trophic reduction, allowing for a comparative analysis of how the species responded demographically during periods of abundance and during severe food scarcity. We believe that the application of our method is important for understanding similar systems facing food reductions, particularly in predictable anthropogenic food sources. From a management view, this methodology is highly valuable for assessing the impacts of the circular economy, particularly policies aimed at closing landfills and the potential effects on species that rely on this resource. Monitoring these species around such infrastructures is therefore urgent, especially for highly mobile species like vultures, to better understand and mitigate their responses to these environmental changes.

A MULTISITE INTEGRATED POPULATION MODEL TO EVALUATE DEMOGRAPHIC PARAMETERS AND POPULATION DYNAMICS WITHIN A DECENTRALIZED CONSERVATION STRATEGY

In chapter 3 of this thesis, we focused on analysing the dynamics of griffon vulture populations across three neighbouring regions in the northeast Iberian Peninsula by implementing a multisite Integrated Population Model (ms-IPM). Using an IPM as analytical framework allowed us to integrate data from multiple sources, such as population counts, productivities and capture-recapture information (Besbeas et al. 2002, Schaub and Abadi 2010, Kéry and Schaub 2012, Schaub and Kéry, 2021). Using data of multiple sites, we were able to incorporate spatial structure and connectivity into our assessment, which is essential for understanding wide-ranging and highly mobile species like the griffon vulture. Briefly, this chapters' methodology benefited from the collaboration of autonomous administrations, researchers, volunteer networks, and ringing programs, which enabled large-scale multi-site monitoring despite challenges in data collection and temporal coverage. Utilizing the ms-IPM within a Bayesian framework allowed for the estimation of key vital rates, such as survival, productivity, emigration, immigration, and recruitment, quantification of breeder population sizes and productivity in years without data (since censuses are carried out every decade), different population fractions for which empirical data was not available (e.g., floaters), and assessments of their contributions on population growth and density dependence, while effectively accounting for uncertainty and heterogeneity in the data (Schaub and Kéry 2022). Although this approach is relatively underutilized (e.g., McCrea et al. 2010, Péron et al. 2010, Seward et al. 2019, Schaub and Kéry 2022), it offers significant insights, particularly in understanding how emigration and immigration between different sites contribute to local population changes (Schaub and Kéry 2022), ultimately offering robust insights into the conservation needs of different populations and species.

One of the main insights from the Chapter 3 is the significant role that floaters, or non-breeding individuals, play in the population dynamics of long-lived species (Penteriani et al. 2011). We found that the floater-to-breeder ratio was a key driver of population growth rate in the three populations, and more particularly in Catalonia and Valencian Community. Floaters are typically overlooked in many population studies because they are difficult to observe and monitor in the field (). However, they are crucial for maintaining population stability and resilience, particularly in species like the griffon vulture. Floaters act as a buffer against sudden declines in the breeding population, because they are a pool of individuals ready to replace dead breeders, but they are also responsible of colonizing new areas and expanding the distribution of the species (Hunt 1998, Penteriani et al. 2011, Robles and Ciudad 2017). In our research, estimating floaters in the Bayesian IPM framework is straightforward by using information of non-adult survival and productivity, which allowed us to quantify their numbers along with their uncertainties and assess their contributions to the overall population growth in each population (Schaub and Kéry 2022). By including floaters in our analyses, we gained a more complete understanding of the demographic processes shaping the griffon vulture population and for long-lived species in general. These findings underscore the importance of considering non-breeders in population models, especially for long-lived species, where the reproductive potential of the floater population can be pivotal in mitigating population declines and ensuring long-term stability (Penteriani et al. 2011, Robles and Ciudad 2017).

In this chapter, we also found that immigration plays an important role in population dynamics, with a particularly strong contribution estimated for the Valencian Community. However, low immigration rates across all populations indicate that these populations are largely self-sustaining, suggesting that local recruitment may play a primary role rather than relying heavily on immigration (Schaub et al. 2010, Millon et al. 2014). These findings were made possible through the Bayesian framework provided by the ms-IPM, which allowed us to work across multiple populations and account for individual exchanges. This is especially important because immigration is a vital rate that is difficult to measure in the field, as it is often challenging to distinguish between true immigrants and locally born individuals (Millon et al. 2019). In the context of IPMs, immigration can be estimated as a hidden parameter without direct empirical data, as information from other demographic sources and population sizes enables this estimation when we assume the population is open (i.e., immigration and emigration occur) (Abadi et al. 2010, Schaub et al. 2013, Schaub and Fletcher 2015). However, these estimates can be biased if the IPM is not correctly specified (Riecke et al. 2019, Paquet et al. 2021). The strength of using a multi-state capture-recapture model, which accounts for movements between sites, lies at the heart of the ms-IPM and provides the necessary information to estimate immigration volumes between populations effectively, which is relatively applicable in other study systems where capture-recapture methods have been carried out.

Our analysis revealed density dependence in the floater-to-breeder ratio and immigration rates in the Catalonia and Valencian Community populations. Interestingly, we also found a common effect of density dependence in dispersal rates (permanent emigration) across all three populations. We did not observe density-dependent effects on other vital rates as suggested in other study systems of long-lived species, such as survival or productivity (Payo-Payo et al. 2016, Margalida et al. 2020). This finding is particularly important because it suggests that dispersal may be a key mechanism through which some populations of long-lived species regulate itself in response to increasing densities (Matthysen 2005, Tavecchia et al. 2007, Bona et al. 2019). This same response occurs at small spatial scales where a common resource, like food, becomes insufficient to meet the needs of the population (Payo-Payo et al. 2015, Zorrozua et al. 2020, Delgado et al. 2021), increasing intraspecific competition through density-dependent mechanisms and finally increasing dispersal rates, as we identified in Chapter 1 and 2 (Arévalo-Ayala et al. 2023a, 2023b). The biology of long-lived species, characterized by slow life cycles and a strong emphasis on survival over reproduction (Sæther and Bakke 2000, Caswell 2001, Carrete et al. 2009, Genovart et al. 2013, Margalida et al. 2020), may explain why we did not observe density dependence in other vital rates. Given their high mobility (García-Ripollés et al. 2011, Monsarrat et al. 2013), griffon vultures may respond to local density pressures by moving to other regions rather than compromising their survival or reproductive outcome. This dispersal-driven response could be a less-studied but crucial aspect of population regulation in highly mobile, long-lived species (Matthysen 2005). Understanding how density dependence manifests in dispersal, could offer valuable insights into the population dynamics of other similar species facing habitat saturation or resource limitations.

The application of a discretely coded multisite IPM, where the sites were defined by political boundaries such as autonomous communities, may come with certain assumptions about each population extent, as may not always align with the natural distribution of the griffon vultures. For instance, in our study, the capture-recapture data of vultures marked in Valencian Community are from the north of Castellón province, which is near the border with Aragon and south of Catalonia. Nevertheless, Castellón province is home of the 86% of breeding pair vultures in the autonomous community according to 2018 census (Del Moral and Molina

2018), suggesting that our estimates represent the movement probabilities of a large proportion of the population in this region. In this sense, we believe that the assumption of administrative boundaries does not compromise the validity and robustness of our main findings, as the explicit treatment of movement between communities implicitly captures the spatial structure that governs the exchange of individuals. While it is clear that considering that individuals at a single site with a probability of dispersal or reproduction represents a summary (or an average) of the heterogeneity within this site, we can reasonably assume that the differences derived from this assumption are minimal. In other words, the assumption remains acceptable for capturing the overall dynamics without significantly distorting the reality of individual behaviours and movements within and between populations. In fact, the movement probabilities we estimated in Chapter 3 were extremely precise for almost all ages and sites, except for non-adults in the Valencian Community, suggesting that the discrete designation for each population effectively captured the overall site-specific movement probabilities. Examples of ms-IPMs using political boundaries as a spatial scale have shown this approach is reliable and effective to identify site-specific population dynamics while accounting the exchange of individuals (Morrison et al. 2016, Schaub and Kéry 2022). Finally, this scale is particularly relevant to local managers and policymakers, who are responsible for implementing conservation measures within their respective regions. Our study thus provides a robust framework for understanding population dynamics and guiding effective management strategies across these three important regions for griffon vultures and useful for other species and study systems.

LIMITATIONS OF THIS THESIS: A SELF-REVIEW OF METHODS

While our findings are robust and sound, there are several potential limitations we identified that should be addressed to refine future research. In Chapters 1 and 2, we used an extensive dataset of griffon vultures captured, marked, and recaptured using a walk-in trap at the Orís landfill in Central Catalonia (Spain), with systematic monthly ringing sessions since 2012. However, as food availability at the landfill decreases, the baited walk-in trap may be now functioning as a 'vulture restaurant', potentially biasing recapture probabilities. This shift could lead to a bias in survival estimates by making the traps more attractive than the increasingly scarce landfill resources. In our analyses, we detected this phenomenon known as 'trap-happiness', which means that there are certain vultures that are more likely to be repeatedly recaptured, suggesting a potential bias for this probability (Pradel 1993, Pradel and Sanz-Aguilar 2012). Particularly in chapter 2, we observed that recapture probabilities increased with time, which supports this hypothesis (Arévalo-Ayala et al. 2023b). To counteract this source of heterogeneity, we parameterized the recapture probability in our models by distinguishing between individuals previously recaptured and those that were not, using the PriorCapL function in program MARK within a frequentist framework for chapter 1 (Cooch and White 2019), and by the application of an individual categorical covariate in the hierarchical Cormack-Jolly-Seber model within a Bayesian framework using the state-space modelling for chapter 2 (Kéry and Schaub 2012). This strategy was also implemented in Chapter 3 (using an expanded dataset from vultures marked in Aragon and Valencian Community) in our ms-IPM, using the formulation of Pradel and Sanz-Aguilar (2012) for multistate models that allowed us to ultimately achieve more accurate survival estimates.

Trap-dependence is a common source of heterogeneity in capture-recapture methods when using baited traps or heavily sampling predictable feeding sites like landfills or other predictable food sources (Crespin et al. 2008, Pradel and Sanz-Aguilar 2012). For future research, we recommend increasing efforts to observe vultures at breeding sites, roosting areas, or in flight, if they have wing tags. Furthermore, during physical capture campaigns at sites like landfills, conducting thorough scans for marked individuals outside the traps and nearby could significantly reduce the impact of trap-dependence on survival analyses. Additionally, the use of GPS transmitters on individuals reduces the monitoring effort on field and would provide more accurate survival analyses (such as the known-fate model), as it would eliminate the problem of imperfect detection (Kéry and Schaub 2012).

Regarding Chapter 3, we encountered multiple limitations while implementing the ms-IPM. One of the primary challenges was the high heterogeneity of data collected across the three autonomous communities: Aragon, Catalonia, and the Valencian Community. These datasets varied significantly due to differences in the timing, continuity, and methods used in the capture-recapture campaigns. For instance, while Catalonia's marking efforts are still ongoing, those in the Valencian Community ceased in 2016 relying solely in resighting marked individuals, and Aragon's campaigns have been carried out systematically until 2014 and then in 2019 and 2021 (see Methods in chapter 3). The variation in marking methods also complicated our analysis; for example, Catalonia stopped marking vultures with wing tags in 2012, relying solely on plastic and metal rings, whereas the other regions continued to use all three types of marks. These discrepancies necessitated complex assumptions and structure for the multistate model, resulting in a final highly demanding computational process that took over 20 days to execute. This complex multistate model included 37 observed states such as age structure (four age classes), site (three locations), mark state (three states), and dead recovery, with other unobservable states to account for permanent emigration and trap-dependence, leading to an intricate 80 x 80 state transition matrix.

Moreover, given the varying timelines of the marking campaigns, strong assumptions were necessary, particularly concerning survival rates. Our ms-IPM spanned from 2008 to 2021, but marking in Catalonia only began in 2011. To address this gap, we modelled survival using random time effects, where estimates for years without data closely matched the hyper-mean estimated for the whole period (Kéry and

Schaub 2012). This approach, while assuming no significant fluctuations in survival during those years (which is something we would never know), was a statistically valid and honest method to use given the absence of data. If had we used fixed time effects (as is typical in capture-recapture studies and more common in frequentist approaches), we would have faced unidentifiable survival estimates for those years (basically, a flat distribution of posterior samples ranging from ~0 to ~1), leading to potentially biased and overly imprecise population size estimates for vultures in Catalonia (Schaub and Kéry 2022).

In addition to these challenges, inconsistencies in observation data posed a significant issue, especially regarding the retention of wing tags and plastic rings. Because accounting for tag loss was crucial to avoiding biases in survival estimates (Touzalin et al. 2023), we used informative priors for these probabilities based on studies of similar species (Santageli et al. 2020, *Torgos tracheliotos* and Rosteau et al. 2022, *Aegypius monachus*). This Bayesian approach allowed us to incorporate external information into our analysis, improving the accuracy of our estimates despite the limitations of our data (Lenk and Orme 2009, Morris et al. 2015, Banner et al. 2020, Schaub and Kéry 2022).

In this chapter 3, we encountered challenges when attempting to include environmental covariates in the model. For example, during the conceptualization of the study, we initially wanted to test if the temporal variability in survivals and productivities were partially explained by annual landfill waste. Nevertheless, reliable or complete data were often unavailable in the three regions. While high-quality data were accessible for Catalonia, similar data for Aragon and the Valencian Community were either incomplete or not publicly available. Despite efforts to obtain this information from regional administrations, we received partial responses. As a result, we decided to focus on a solely demographic assessment, applying demographic stochasticity in all population size estimates, and random time effects in survival and productivities to account for unmodeled variability (Kéry and Schaub 2012, Schaub and Kéry 2022).

This approach, we believe, resulted in robust and reliable estimates, although it does not allow us to infer the source of variability in our estimates from environmental covariates.

For population size estimates, we relied on national census data of the species, which are collected every 10 years. This provided only two data points (2008 and 2018) for Catalonia and Aragon (Del Moral 2009, Del Moral and Molina 2018), leading to high uncertainty in population sizes estimated from de ms-IPM in the years from 2009 to 2017, and 2019 to 2021, and more particularly for Aragon. In contrast, the Valencian Community have conducted annual monitoring since 1989, allowing for more precise population estimates for this population. In fact, allowing for the exchange of individuals between populations facilitated the sharing of trend information, which significantly improved the reliability of our results. In this sense, during the development of the IPM, we tested a model that assumed isolated populations (results not shown here), meaning no immigration or emigration occurring (i.e., closed populations). This model produced population size estimates with much greater uncertainty compared to the model that assumed an open population with individual movement between sites. The open population model, by contrast, provided more realistic and consistent estimates, reinforcing our confidence in the accuracy of our results.

We estimated ‘recruitment’ as a hidden parameter in our ms-IPM. Estimating a hidden parameter is a common practice in IPMs because the joint likelihood from various data sources enables the estimation of parameters without direct empirical data (Tavecchia et al. 2009, Schaub and Kéry 2022). For our study, estimating recruitment was essential due to the lack of prior information on recruitment probability for this species in the literature. The estimation of this parameter was crucial in our ms-IPM to link the non-breeding and breeding populations. However, the relatively low estimates we obtained for each population and age class (non-adults and adults) likely reflect the recruitment proportion from the non-breeding segment and not a recruitment probability *per se*, suggesting that our estimate may be treated as a 'correction factor' as it might be confounded with other related parameters, such as breeding propensity (Robinson et al. 2014, Schaub and Kéry 2022).

Lastly, we included an estimate of immigrant individuals from outside our study system (i.e., outside of the three autonomous communities), making strong yet biologically plausible assumptions about their numbers (see Appendix S2.1 of Chapter 3). This was vital to avoid underestimating non-breeder populations, especially in Aragon. Multi-site IPMs relies on the assumption that the exchange of individuals occurs solely between the populations incorporated in the multi-state model, making the system closed from immigration from elsewhere. By assuming a closed system limited to the three regions, we risked to negatively bias the population size estimates, particularly during years of low adult survival between 2009 and 2013 in Aragon where we detected a decrease in vulture numbers. Aragon, being the largest population in our study system with over 5,000 breeders in 2008, would have shown unrealistic population declines without accounting for immigration from elsewhere (e.g., a drop of hundreds of individuals from one year to the next), since the model would only allow immigrants volumes from Catalonia and Valencian Community which numbers were very low. By allowing for the entry of immigrants from other parts of Spain, we produced more realistic population estimates for Aragon, with the cost of greater uncertainty around estimates of years without data. Briefly, we assumed that immigrants came from neighbouring provinces like Guadalajara, Cuenca, Soria, La Rioja, and Navarra, as these are the closest populations to Aragon (see Appendix S2.1 of Chapter 3 for calculation). We assumed that individuals from these areas are more likely to emigrate to Aragon, while those from more distant locations would be less likely. To illustrate this assumption, GPS-tagged individuals from Segovia (n=15), west of Guadalajara and Soria, moved exclusively to Andalucía, while those from Andalucía (n=42) showed minimal movement to the south of Aragon (Morant et al. 2023). Similarly, vultures tagged in

Andalucía (n=48) demonstrated almost no movement to the Valencian Community or Aragon (Delgado-González et al. 2022), making our assumption of a higher probability of emigration from western provinces to Aragon highly plausible. We believe that our application of demographic stochasticity and a variable ratio of immigrant proportions yielded honest and low biased estimates on population sizes. However, future research could benefit from incorporating, for example, GPS data from tracked individuals to estimate dispersion rates, which can provide further insights into the dynamics of these populations (Schaub and Kéry 2022). Recent development of IPMs merged with individual-based models using data from GPS-tagged individuals provide great promise to incorporate movement behaviour and dispersal in analyses of population dynamics (Petracca et al. 2024).

CONSERVATION IMPLICATIONS

This thesis highlights the critical intersection between the goals of the 2030 Agenda for Sustainable Development and the need to safeguard biodiversity. While the agenda's objectives are vital for sustainability, it is essential to ensure that these efforts do not inadvertently negatively affects wildlife. As this thesis pinpoint, the closure of open landfills, aligned with the circular economy framework (Directive 2008/98/EC and Directive (EU) 2018/850), is a key sustainability goal to reduce waste production and the negative environmental impacts it generates. One of the aims is preventing the access of opportunistic species that may be involved in human-wildlife conflicts (Plaza and Lambertucci 2017). However, this action poses significant challenges for species such as vultures that have been able to rely on these predictable food sources (Tauler-Ametller et al. 2017, Arrondo et al. 2023, Cerecedo-Iglesias 2023). In Chapters 1 and 2, we revealed that the abrupt reduction in organic waste availability in landfills leads to increased permanent emigration and lower apparent survival rates among griffon vultures, predominantly affecting juveniles and adults. This is particularly concerning in regions like Catalonia, where the reduction of organic matter in landfills are being implemented (see Appendix D in Arévalo-Ayala 2023b). Although other food sources such as supplementary feeding sites (both legal and illegal), livestock and game carcasses may still provide food for these scavengers, the possible demographic shifts underline the necessity of mitigating the impacts of landfill closures in the near future, particularly for the north griffon vulture population that have adapted to this non-natural food source (Arrondo et al. 2023). For example, recent spatial-use network simulations have shown that regional landfill closures could shift trophic resource selection in Egyptian vultures to extensive livestock (Cerecedo-Iglesias et al. 2023). In this sense, one effective strategy would be to expand the underrepresented Protected Areas for Feeding of Necrophagous Species (ZPAEN zones in Spain) in some regions (e.g., Catalonia where only 13% of its territory is a ZPAEN zone), ensuring that vultures have access to natural food sources from extensive livestock which could help stabilize vulture populations during this transition. Encompassed with this measure, promoting extensive livestock farming in rural areas (i.e., reverting rural abandonment), could provide natural foraging opportunities for vultures. However, this practice must be carefully managed, including banning the use of toxic drugs like diclofenac, which remains legal in Spain and poses a serious threat to vulture populations (Green et al. 2004, Margalida et al. 2021, Cook et al. 2024). In addition, the implementation of a randomly network of light supplementary feeding stations could help in this transition. Finally, it is crucial to monitor obligate and facultative scavenger species across multiple landfills at a regional scale. This would allow investigating the impact of reduced organic matter or landfill closures on demographic parameters and, ultimately, population dynamics (see Pinto et al. 2021, Delgado et al. 2023), which would help refining appropriate conservation measures.

Chapter 3 delved deeper into the need for interregional coordination in conservation efforts for highly mobile and distributed species. Our study revealed distinct regional trends and dependencies across neighbouring populations of griffon vultures in Catalonia, Aragon, and the Valencian Community. The use of multisite integrated population models, which included explicit data on individual exchange between regions, is a very useful tool to identify varying conservation needs in terms of key vital rates and their interdependence (e.g., Péron et al. 2010, Seward et al. 2019). For instance, while the griffon vulture population in Catalonia is growing, the population in Aragon shows fluctuating trends. In contrast, the population in the Valencian Community exhibited density dependence, suggesting it may be stabilizing and functioning as a source of individuals for other areas as productivities show no signs of being affected by population density. The main contributions of vital rates also differed between the studied local population dynamics, for example, Aragon population was driven by adult survival, while Catalonia from floaters, immigrants and adult survival, and Valencian Community from immigrants and floaters only. This highlights the importance of considering regional dynamics to ensure effective global conservation strategies with enough flexibility for the application of specific local measures. Moreover, although we could not relate any demographic parameter with environmental covariates in this study given the gaps in covariate information, it is important to highlight that the expansion of wind energy, one of the most promoted SDG of the 2030 Agenda, poses a significant threat to vulture populations, particularly in regions like Aragon, where wind farm development is highly advanced and where survival levels are the lowest. Our research has shown that adult survival is a key driver of population dynamics. Data we gathered on griffon vulture casualties in rehabilitation centres in Aragon indicate that wind turbines have become a leading cause of mortality for vultures in these areas, threatening local populations (see Appendix S3 of Chapter 3). To reconcile the goals of sustainable energy development with biodiversity conservation, it is essential to take selective mitigation measures on windfarms to avoid the negative effects on biodiversity. As not a single formula exists, some strategies rely on carefully select sites for windfarms, turbine shutdown on demand or when birds are present or in periods with high collision risk (e.g., migratory periods), among others (see review in Marques et al. 2014). Finally, we believe that the demographic monitoring of populations that cross political and administrative borders, such as vultures, requires the standardization of methodologies, particularly those based on capture, marking, and recapture of individuals. These efforts should be coordinated in terms of timing, coverage area, and specific capture sites and ideally supported by administrations as it was the case in Aragon and Valencian Communities. Additionally, important environmental covariates that enable broad temporal and spatial analyses should be made available, centralized, and standardized to improve the quality and comparability of these analyses across regions.

In conclusion, the findings of this thesis offer valuable insights that extend beyond our study species, the griffon vulture, and are relevant for the conservation of other threatened vultures and long-lived birds in general. By using advanced models like ms-IPM, we were able to estimate critical demographic parameters such as immigration, emigration, and the role of non-breeders. These results are essential for designing effective conservation strategies for highly mobile species that cross human borders, highlighting the need to account for both regional and local dynamics.

CONCLUSIONS

1. Current European Union directives under the Circular Economy framework seek to decrease organic matter dumped in landfills and close these facilities, thereby reducing a key food source for vulture species habituated to this predictable anthropogenic source. Our findings indicate that the reduction of organic waste led to a significant decline in the apparent survival of resident griffon vultures, primarily due to increased permanent emigration. This indicates that vultures are less likely to remain or return to landfills when the availability of organic waste is reduced.

2. Despite the observed decline in apparent survival of resident griffon vultures following the reduction of organic waste at the landfill, the local population abundance did not decrease, but increased. This suggests that local waste management measures are not effective enough to significantly prevent scavengers from using these facilities, as population dynamics at a regional scale appear to be more influential than local waste management practices. The vultures habituated to foraging at the landfill seem to have adjusted their foraging behaviour to cope with the diminished availability of landfill waste by finding alternative nearby food sources, such as other predictable and unpredictable food sources. Nonetheless, the availability of organic matter is still sufficient to attract vultures, including those individuals that visit the facility only sporadically.

3. Vultures are affected differently according to age by the reduction of organic matter in a landfill. Juvenile and adult vultures, who seemed to be more dependent on landfill food sources, showed higher sensitivity to the reduction in organic waste. Interestingly, resident immatures displayed the opposite trend, suggesting the persistence of high-quality individuals despite the food scarcity as has been shown in other

sites and species. This suggests that immatures are highly competitive, outperforming juvenile age classes under such conditions. Additionally, the very low availability of organic matter may not be sufficient to sustain the requirements of adult individuals, prompting them to seek alternative food sources.

4. We demonstrated that the probability of becoming a transient after initial capture increased in both immature and adult vultures following the reduction in organic matter availability in the landfill. Notably, adults exhibited a higher probability compared to immatures, and may be attributable to the diminished attractiveness of the landfill as a secure food source, persuading adults to rely more heavily on other sites. Conversely, immatures exhibited a lower probability of becoming transient and this may be explained by their lack of established territories, as their movements are primarily driven by conspecific attraction and the availability of feeding sites, leading them to remain and compete for the residual resources in the landfill.

5. The multisite integrated population model revealed significant regional differences in demographic parameters and population dynamics of griffon vultures across Aragon, Valencian Community, and Catalonia. These differences underscore the necessity for tailored global conservation strategy that permit flexibility to address specific needs and challenges of each region. We examined how different vital rates—such as survival, productivity, and immigration—contribute to population growth rates across the regions. For example, we found that in Aragon, adult survival rates were lower compared to the other two populations, when population growth in this autonomous community is dependent on this parameter. This suggests that improving adult survival in Aragon could have a significant positive impact on the overall population dynamics. We also highlighted the critical role of movements between sites in maintaining vulture populations.

Catalonia, and more particularly Valencian Community, relied heavily on immigration from other regions to sustain its population dynamics.

6. This thesis underscores the need for integrated waste management policies that consider the ecological impacts on scavenger species. It advocates for conservation measures such as expanding ZPAEN (Protection Zones for the Feeding of Necrophagous Species of Community Interest) areas, promoting extensive livestock farming, and establishing a network of small, randomized supplementary feeding stations. These strategies can help mitigate the potential negative effects of reduced food availability from landfills while supporting the natural foraging behaviours and essential ecological services provided by vultures. Implementing these measures can ensure stable food sources, reduce mortality risks, and prevent dispersal linked to food scarcity, thereby securing local vulture populations.

7. The application of multisite integrated population models offers a comprehensive understanding of the interconnectedness of vulture populations across regions governed by different conservation administrations. This approach highlights the crucial roles of immigration and emigration in population dynamics, emphasizing their importance in effective conservation planning at regional scales. Conservation strategies must be account for tailored actions to address regional differences in population dynamics and local ecological needs.

8. Finally, our findings stress the importance of effectively integrating environmental policies across sectors such as renewable energy, waste management, livestock practices, and current conservation measures such as supplementary feeding stations into interregional coordinated conservation efforts. These strategies should account for the interdependence of vulture populations across regions. Specific conservation actions include managing mortality risks, particularly in areas prone to infrastructure-related dangers like wind farms, and

ensuring the availability of stable, toxin-free food sources. Moreover, protecting key habitats and establishing safe movement corridors (i.e., areas free of dangerous infrastructures) between regions are essential for maintaining population connectivity and long-term stability of the species.

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