Ecosystem drivers of breeding and foraging in an endangered scavenger

PROGRAMA DE DOCTORADO EN MEDIO AMBIENTE Y SOSTENIBILIDAD

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Elche, 2025

Ecosystem drivers of breeding and foraging in an endangered scavenger.

Factores ecosistémicos que influyen en la reproducción y la alimentación de un carroñero amenazado.

Lola Fernández Gómez

PhD Thesis

Elche, 2025

Programa de Doctorado en Medio Ambiente y Sostenibilidad

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Tesis doctoral presentada por María Dolores Fernández Gómez en la Universidad Miguel Hernández de Elche para la obtención del título de Doctora en el Programa de Doctorado en Medio Ambiente y Sostenibilidad.

Elche, 2025

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La presente Tesis Doctoral, titulada "Ecosystem drivers of breeding and foraging in an endangered scavenger", se presenta bajo la modalidad de **tesis por compendio** de las siguientes **publicaciones:**

Chapter I

Fernández-Gómez, L., Sánchez-Zapata, J. A., Donázar, J. A., Barber, X., & Barbosa, J. M. (2023). Ecosystem productivity drives the breeding success of an endangered top avian scavenger in a changing grazing pressure context. Science of The Total Environment, 168553. https://doi.org/10.1016/j.scitotenv.2023.168553

Chapter II

Fernández-Gómez, L., Sánchez-Zapata, J. A., Donázar, J. A., de la Riva, M., & Barbosa, J. M. (2025). Overgrazing triggers cascading effects on a top avian scavenger: long-term changes in diet and breeding success. European Journal of Wildlife Research, 71(2). https://doi.org/10.1007/s10344-025-01896-6

OTRAS PUBLICACIONES INCLUIDAS EN ESTA TESIS DOCTORAL

La presente Tesis Doctoral, titulada "Ecosystem drivers of breeding and foraging in an endangered scavenger", incluye trabajos cuya publicación se encuentra en preparación:

Chapter III

Fernández-Gómez, L., Sánchez-Zapata, J. A., Juan M. Pérez-García, Donázar, J. A., García-Alfonso, M., Montoya-Bernabeu, P., Barbosa, J. M., Riders on the storm? Saharan dust disrupts movement patterns of an endangered top scavenger.

Chapter IV

Fernández-Gómez, L., Börger, L., Sánchez-Zapata, J. A., Donázar, J. A., Barbosa, J. M. Foraging strategies of a top avian scavenger across breeding phases.

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INFORMA:

Que Dña. María Dolores Fernández Gómez ha realizado bajo la supervisión de nuestro Programa de Doctorado el trabajo titulado "Ecosystem drivers of breeding and foraging in an endangered scavenger" conforme a los términos y condiciones definidos en su Plan de Investigación y de acuerdo al Código de Buenas Prácticas de la Universidad Miguel Hernández de Elche, cumpliendo los objetivos previstos de forma satisfactoria para su defensa pública como tesis doctoral, en la modalidad de compendio de publicaciones.

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This thesis has been supported by a pre-doctoral grant (PRE2019-089199) from the Spanish Ministry of Science and Innovation, the European Social Fund (ESF), and the Spanish State Research Agency (AEI), as the intermediate body responsible for managing the funding, within the framework of project RTI2018-099609-B-C21.

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"In nature, nothing exists alone"

Rachel Carson

"To do science is to search for repeated patterns, not simply to accumulate facts."

Robert MacArthur

A mi familia, por ser mi pilar.

A mi abuela Aure, por ser mi ejemplo.

CONTENT

ABBREVIATIONS AND ACRONYMS

CAP – Common Agricultural Policy

ECE – Extreme Climatic Event

GAM – Generalized Additive Model

GAMM – Generalized Additive Mixed Model

GLM – Generalized Linear Model

GLMM – Generalized Linear Mixed Model

HPFP – Highly Predictable Feeding Places

LM – Linear Model

NDVI – Normalized Difference Vegetation Index

NSD – Net Squared Displacement

SFS – Supplementary Feeding Station

SUMMARY

This thesis investigates the complex interplay between environmental conditions, food resource availability, and human-induced pressures in shaping the breeding success, the foraging behavior and therefore conservation outlook of the endangered Canary Egyptian vulture (*Neophron percnopterus majorensis*). Across four complementary chapters, long-term data reveal that both natural and anthropogenic factors such as ecosystem productivity, livestock density, extreme climate events, and food predictability, interact to influence key aspects of vulture ecology, including breeding success (Chapter I and II), movement patterns (Chapter III and IV), foraging behavior (Chapter IV), and dietary composition (Chapter II). The findings collectively emphasize the importance of ecosystem integrity and adaptive conservation strategies that incorporate spatiotemporal variability and the effects of human activity.

In Chapter I, we discover that ecosystem-level processes, including primary productivity, livestock abundance, and density-dependent dynamics, significantly influence the breeding success of the endangered Canary Egyptian vulture (*Neophron percnopterus majorensis*). Over 22 years of population monitoring on Fuerteventura Island revealed that top-down pressures from livestock lead to vegetation degradation through overgrazing, which in turn imposes bottom-up limitations on vulture reproduction. These findings underscore the cascading effects of climate, land use, and policy decisions, highlighting how even species relying on anthropogenic subsidies remain sensitive to broader ecological conditions.

In Chapter II, we explore the relationship between food availability, dietary diversity, and reproductive success, demonstrating that while livestock carcasses represent the most abundant food resource, wild prey diversity plays a crucial role in sustaining breeding success. Based on 20 years of dietary data, we show that wild prey availability and reduced grazing pressure enhance diet diversity and reproductive output. This reveals a conservation paradox: although livestock subsidies stabilize food resources, they simultaneously disrupt ecosystems by suppressing wild prey populations, thus negatively affecting the vultures' long-term viability.

In Chapter III, we examine how Canarian Egyptian vultures respond behaviorally to recurrent Saharan dust storms, a poorly studied yet increasingly relevant extreme climatic event. By analyzing GPS data from 70 individuals over 2,555 tracking days, we find that vulture mobility significantly declines during dust

storm events, particularly among males and subadults. This behavioral adaptation likely serves to minimize exposure to adverse conditions such as low visibility and dehydration risk. Our results contribute to a growing body of literature emphasizing the need to integrate extreme weather events into conservation planning, particularly as such phenomena are expected to intensify under climate change.

In Chapter IV, we assess how Egyptian vultures modify their foraging strategies in response to environmental conditions and food predictability throughout the breeding season. Tracking 49 individuals across five breeding cycles, we find that vultures limit their foraging range and rely more on natural food sources during chick-rearing, but expand their movements when ecosystem productivity is low. These patterns suggest that conservation strategies must account for the spatial and temporal variability of both natural and anthropogenic resources. The study emphasizes the importance of maintaining natural habitat quality and ecosystem functionality to support vulture populations amid environmental change.

RESUMEN

Esta tesis investiga la compleja interacción entre las condiciones ambientales, la disponibilidad de recursos alimenticios y las presiones inducidas por el ser humano en la determinación del éxito reproductivo, el comportamiento de forrajeo y, en consecuencia, la perspectiva de conservación del alimoche canario en peligro de extinción (*Neophron percnopterus majorensis*). A lo largo de cuatro capítulos complementarios, los datos a largo plazo revelan que tanto los factores naturales como los antropogénicos, como la productividad del ecosistema, la densidad ganadera, los eventos climáticos extremos y la predictibilidad de los recursos alimenticios, interactúan para influir en aspectos clave de la ecología del alimoche, incluyendo el éxito reproductivo (Capítulos I y II), los patrones de movimiento (Capítulos III y IV), el comportamiento de forrajeo (Capítulo IV) y la composición dietética (Capítulo II). En conjunto, los hallazgos destacan la importancia de la integridad ecosistémica y de estrategias de conservación adaptativas que integren la variabilidad espacio-temporal y los efectos de la actividad humana.

En el Capítulo I, descubrimos que los procesos ecosistémicos, como la productividad primaria, la abundancia de ganado y las dinámicas dependientes de la densidad, influyen significativamente en el éxito reproductor del alimoche canario. A lo largo de 22 años de monitoreo en Fuerteventura, se observó que el sobrepastoreo reduce la cobertura vegetal, lo que limita indirectamente el éxito reproductivo de la especie. Esta cascada de efectos descendentes y ascendentes pone de relieve la importancia de considerar los impactos ecosistémicos indirectos en la conservación.

En el Capítulo II, exploramos cómo la disponibilidad de alimento y la composición de la dieta afectan los resultados reproductivos. Aunque los cadáveres de ganado dominan la dieta del alimoche, la presencia de presas silvestres y la menor presión de pastoreo aumentan la diversidad dietética y el éxito reproductivo. Estos hallazgos evidencian una paradoja conservacionista: el ganado aporta estabilidad alimentaria, pero su exceso altera la red trófica que sustenta a la población.

En el Capítulo III, examinamos las respuestas conductuales frente a tormentas de polvo sahariano. A partir de datos GPS de 70 individuos, mostramos que los alimoches reducen su movimiento durante estos eventos, probablemente para evitar condiciones adversas como la baja visibilidad y la deshidratación. Este estudio resalta cómo fenómenos climáticos extremos, aunque poco estudiados, pueden alterar el comportamiento animal y deben integrarse en la planificación de la conservación, especialmente en un contexto de cambio climático.

En el Capítulo IV, evaluamos los cambios estacionales en las estrategias de búsqueda de alimento en función de la variabilidad ambiental y la predictibilidad de los recursos. Durante la crianza de pollos, los alimoches priorizan fuentes naturales de alimento y reducen su rango de forrajeo, mientras que en períodos de baja productividad aumentan sus desplazamientos. Estos resultados subrayan la necesidad de estrategias conservacionistas dinámicas que se ajusten a las necesidades ecológicas a lo largo del ciclo vital de la especie.

INTRODUCTION

Ecosystem functioning and community structure.

All living organisms rely on energy, which, as Antoine Lavoisier stated in the XVIII century, is neither created nor destroyed but transformed. In ecosystems, this energy flows through structured systems such as food chains and food webs, transferring from one trophic level to another. At the foundation of this flow is primary productivity, which is the process by which plants, algae, and other autotrophs convert solar energy into biomass. This biomass becomes the starting point for the transference of energy, supporting herbivores (primary consumers) and the sub-sequential levels (secondary and tertiary consumers, carnivores and omnivores). However, the transfer of energy across trophic levels is highly inefficient; only about 10% of the energy at one level is passed to the next, with the rest lost to metabolic processes, heat, and waste. This inefficiency limits the amount of energy available to higher trophic levels, shaping the structure and complexity of food webs. Ecosystems with high primary productivity can sustain larger populations and more diverse communities, while those with lower productivity support simpler and smaller communities (Begon et al., 2006).

Within these structured communities, organisms interact to regulate the flow of energy and biomass. Consumption is one of the most critical interactions, where energy stored in organic matter is transferred between organisms. Primary consumers graze on autotrophs, transforming stored solar energy into forms usable by higher trophic levels. Similarly, secondary and tertiary consumers depend on this energy flow to meet their metabolic needs. The efficiency of consumption controls energy transfer and the biomass distribution across trophic levels, influencing the population sizes of organisms and the ecosystem structure overall. Additionally, depredation facilitates nutrient cycling by breaking down and redistributing nutrients stored in biomass, making them accessible to other components of the ecosystem. For example, when herbivores feed on plants, they contribute to the movement of nutrients through the food web, ensuring that essential elements remain available for ecosystem functioning (Forbes et al., 2019).

Ecosystems also operate under various control mechanisms that dictate population dynamics and energy flow. These mechanisms can be broadly categorized into top-down and bottom-up processes (**Figure 1**). Top-down control involves the influence of higher trophic levels, on lower levels, such as herbivores and primary producers. Conversely, bottom-up control describes how the availability of resources at the base of the food web, such as nutrients and primary productivity, shapes the dynamics of higher trophic levels. While traditional ecological perspectives emphasized the dominance of bottom-up processes, recent research highlights that ecosystems often exhibit a combination of both controls, functioning in tandem to shape community structure (Baum & Worm, 2009; Ripple et al., 2024).

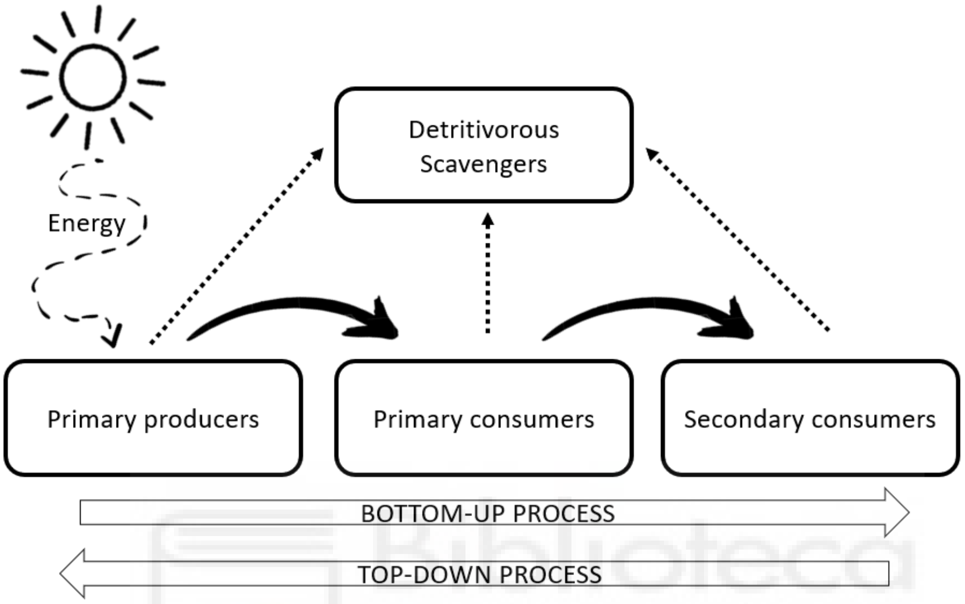

Figure 1: Diagram linking the functioning of a trophic cascade among the different parts of the trophic chains (rectangular blocks), and the energy fluxes among them (black arrows). In the bottom, the direction of the trophic cascades, from left to right, bottom-up and from right to left, top-down.

A closely related concept is that of indirect effects, which have been studied extensively under the framework of trophic cascades. Coined by Robert T. Paine in 1980, trophic cascades describe the ripple effects initiated by changes in one trophic level that indirectly impact non-adjacent levels. These effects are often observed when alterations in consumer population influence producers, but the phenomenon is not restricted to top-down cascades. Historical descriptions of such dynamics can even be traced back to Darwin's *The Origin of Species* (1859), where he noted the interconnected relationships between cats, mice, bees, and plants, although he did not use the term "trophic cascade." Modern ecology recognizes trophic cascades as bidirectional, encompassing both bottom-up and top-down interactions, and playing a critical role in the structure and function of ecosystems (Ripple et al., 2016). While much of the literature on food webs focuses on direct interactions between consecutive trophic levels (e.g., vegetation-herbivore or predator-prey relationships), there is growing interest in understanding the indirect effects that shape ecosystem dynamics. These indirect relationships, particularly trophic cascades, reveal how disturbances in one part of the food web can propagate across the system, influencing community composition and energy flow in complex and sometimes unexpected ways.

Understanding these cascading effects provides a valuable framework for exploring broader ecological patterns, including population dynamics. Population dynamics are further shaped by both environmental conditions and resource availability through direct and indirect effects of climate, biological interactions, and human modification of landscapes (Coulson et al., 2011; SÆther et al., 2004; Simard et al., 2010). Even in the current scenario where species are becoming more reliant of anthropogenic-based resources, ecosystem-level primary productivity remains determinant of vertebrate life-history parameters (Pettorelli et al., 2005, 2011). Breeding success, a critical demographic parameter, is similarly influenced by these dynamics, though the link between primary productivity and reproductive outcomes remains poorly understood (although see Marcelino et al., 2020). Breeding success is conditioned by multiple factors, including climate, habitat quality, individual fitness, and resource availability, but can also be disrupted by intra-regulatory mechanisms like density-dependent competition for food or mates (Chambert et al., 2020). During breeding seasons, many species shift their diets to exploit transient resources or mitigate the stress of offspring rearing (Dhondt & Hochachka, 2001; Jiguet, 2002; Montague et al., 1986), illustrating how both climate-driven natural and anthropogenic factors interact to shape reproductive outcomes.

Climate as modulator of ecosystem functioning

Climate, through its seasonal changes on temperature, precipitation, and environmental conditions, serves as a fundamental driver of ecosystem structure and function (Doney et al., 2012; Grimm et al., 2013; Xie et al., 2023). It directly regulates primary productivity, as climate determines the rates of photosynthesis, nutrient uptake and overall plant growth, forming the foundation of energy transfer throughout ecosystems (Cleveland et al., 2011; Yan et al., 2023). This dynamic is critical because the amount of energy available in an ecosystem—determined by climate—sets the limits for the number and complexity of trophic levels the ecosystem can sustain. Warm and humid systems, such as tropical rainforests, support vast amounts of life due to the abundance of energy and resources (Alamgir et al., 2018; Gibson et al., 2011). In contrast, arid systems, such as deserts, while warm, lack sufficient moisture to sustain comparable energy levels, leading to much lower levels of productivity overall (McNeely, 2003).

Beyond regulating productivity, climate also influences the resilience of ecosystems, or their ability to recover from disturbances. For instance, ecosystems in stable climates with consistent rainfall and temperature patterns tend to develop complex food webs and rich biodiversity, which enhance their resilience (De Boeck et al., 2018; García-Palacios et al., 2018). On the other hand, ecosystems in regions with highly variable or extreme climates (such as arid ecosystems) may struggle to maintain stable populations or recover from disturbances. This can both direct and indirectly influence ecosystems, since it can compromise species distribution and abundance.

Climate change and extreme climatic events

Climate change is an established global phenomenon (Cook et al., 2016). Much of the attention has been directed toward factors such as rising global temperatures and sea levels (Hansen et al., 2006; Runting et al., 2013). In fact, most of the literature has been focused on long-time scale changes in means of environmental variables and their direct impacts on the biota (Chapman et al., 2014; Jones et al., 2016). These studies have allowed us to form an overall picture of how climate change has shaped the environment (Scheffers et al., 2016). However, ongoing evidence sustains that those changes in the extreme weather, or in the increased frequency of extreme weather events can have more serious environmental consequences than changes in climate averages (Harris et al., 2018; Vasseur et al., 2014).

Extreme weather and climatic events—defined as weather or climatic conditions that are statistically rare for a particular location—such as cyclones, hurricanes, floods, heatwaves, and dust storms have become more frequent and intense in many regions of the world due to anthropogenic climate change (Stott, 2016; Ummenhofer & Meehl, 2017). There are multiple definitions of Extreme Climatic Events (hereafter, ECEs), depending on the perspective from which they are defined—whether climatological or impact-related in the biological sense (Van de Pol et al., 2017). One of the most widely used definitions comes from the Intergovernmental Panel on Climate Change (IPCC), which defines an ECE as the occurrence of a weather or climate variable exceeding a threshold near the upper or lower ends of the observed range, typically the top or bottom 5% to 10% (IPCC, 2012). However, this definition is purely climatological and mathematical, without accounting for the biological effects of such events. Some studies argue that classifying an event as an ECE solely based on climatological thresholds is insufficient if there is no demonstrated biological impact on fauna (Van de Pol et al., 2017).

Therefore, research must consider the effects on wildlife before categorizing an extreme weather episode as an ECE. A greater synthesis of research on ECEs is needed, as their anecdotal and descriptive nature makes it difficult to assess their long-term ecological consequences (Smith, 2011). On top of that, there is a significant knowledge gap regarding how long-term trends in ECEs affect vertebrates and how these events can impact their life and behavior, as most existing literature focuses on plant species (Maxwell et al., 2019).

Movement ecology as approach to behaviour

Movement ecology offers a transformative lens through which to study animal behavior, foraging patterns and efficiency in the energy use, emphasizing the importance of spatial and temporal patterns in understanding ecological interactions. By integrating tracking technologies, spatial analysis, and ecological modeling, movement ecology helps uncover how animals navigate their environments, locate resources, and respond to environmental changes. This emerging scientific discipline aims to establish the theoretical basis for why and how animals move (Holden, 2006), with potential to disentangle how species interact under different environmental conditions.

Various factors shape animal movement, but they can generally be categorized as biotic and abiotic factors (**Figure 2**, Nathan et al 2008). The resources required for an organism to survive, and function are distributed heterogeneously across space and time. Consequently, the relationship between the space that an organism occupies within a landscape influences its survival and reproduction, thereby affecting population dynamics (Hawkes, 2009; Morales et al., 2010). Based on these principles, movement ecology seeks to answer fundamental questions such as why animals move, where they move, and how they move within a new conceptual framework. This approach considers not only internal and individual factors but also how the environment shapes movement (**Figure 2**). As mentioned earlier, abiotic (environmental) factors influence the spatial and temporal distribution of resources, which, in turn, determine how mobile organisms exploit them. Therefore, knowing the relationship between environmental factors and movement is key to assess life-history patterns of organisms and to understand how ecosystems function.

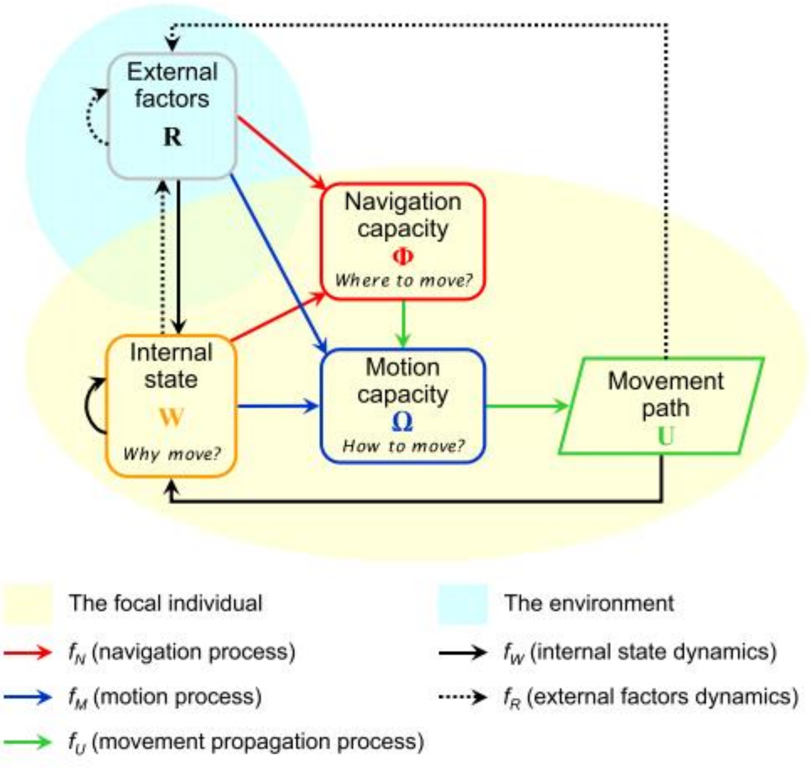

Figure 2: A general conceptual framework for movement ecology, composed of three basic components related to the individual and the environment and the interplay of processes among them. Nathan et al 2008 in PNAS.

Scavengers as study model

Scavengers provide a unique perspective for studying ecosystem dynamics, as they link trophic levels through the consumption of carrion (see **Figure 1**). Carrion is considered a high-quality form of detritus that is composed of dead animal matter (Wilson & Wolkovich, 2011). The role of scavengers on ecosystem functioning has been historically underestimated, but recently its key role has been acknowledged (Sebastián-González et al., 2019, 2020). They play a vital role in nutrient recycling (Beasley et al., 2015), disease regulation (Ogada et al., 2012), and energy transfer within food webs (DeVault et al., 2003). Within them, vultures are considered the only obligate scavengers. From the 23 species of vultures worldwide, 14 of them are threatened (Ogada et al., 2012). Vultures are an excellent example of "landscape species", which are characterized by their important regulatory role within ecosystems and their use of ecologically diverse areas (Redford et al 2000). These species also act as mobile links connecting patches of different habitats, or similar habitats separated by barriers, therefore helping to maintain the general resilience of ecosystems (Lundberg and Moberg 2003).

This is particularly relevant in the context of current climate change, as other authors have explored the relationship between scavenger communities, ecosystem function, and climate. Temperature and precipitation are known to influence the richness and diversity of scavenger assemblages (Gomo et al., 2020; Marneweck et al., 2021), and under the current climate change scenario, a significant reduction in scavenger species richness has been predicted. Such a decline could have cascading effects on ecosystem functioning and resilience, as scavengers play a crucial role in nutrient cycling and disease regulation (Marneweck et al., 2021). Among scavengers, vultures are considered one of the most important providers of ecosystem services due to their specialized carrion consumption behavior (Moleón et al., 2014). Any alterations in their abundance or distribution could significantly affect ecological processes, particularly in regions where they are the dominant scavengers. Their role in removing organic waste helps reduce disease transmission by limiting the spread of pathogens found in decomposing carcasses (O'Bryan et al., 2018). Additionally, in the face of climate-driven mass mortality events, vultures contribute to the rapid recycling of nutrients, preventing prolonged carcass accumulation that could disrupt ecosystem balance (Barton et al., 2023). Given these critical contributions, understanding the factors that influence vulture populations—including their reliance on human-related resources and their vulnerability to environmental changes—is essential for ensuring the stability of scavenger-mediated ecosystem services.

One of the most common tools to palliate the decrease in vulture populations worldwide has been the installation of supplementary feeding stations (SFS). These facilities provide predictable food (i.e., carrion) to mitigate anthropogenic impacts that otherwise cannot be eliminated (at least in the long-term) and that may affect the conservation status of a species (Moreno-Opo, Trujillano, & Margalida, 2015; Oro et al., 2008; Robb et al., 2008). Supplementary feeding stations have proved to increase preadult survival, breeding productivity and settlement of new breeding pairs (Margalida et al., 2014), but conversely it has also been proved that can distort the natural feeding behavior, and the large aggregations of individuals can also have negative consequences for less competitive vultures' species (Cortés-Avizanda et al., 2010; Moreno-Opo, Trujillano, & Margalida, 2015).

The reliance of vultures on anthropogenic resources has been extensively explored in scientific literature. Most studies highlight the importance of the stable food supply that domestic livestock provides to vulture populations. For example, Cabrera-García et al., (2020) found that livestock played a major role in the diet of a population of Egyptian vultures (*Neophron percnopterus*) in northern Spain. Similarly, Olea & Mateo-Tomás, (2009) described the close relationship between transhumant livestock and griffon vultures (*Gyps fulvus*), noting how the movement of these birds to feed on livestock carcasses can contribute to species conservation.

However, while livestock can support vulture populations by providing a predictable food source, the high pressure exerted by livestock on the environment can have detrimental effects on the ecosystem (Wolf et al., 2021). Overgrazing can impact both biotic and abiotic factors (Cingolani et al., 2014; Neilly et al., 2016), affecting plant communities and altering soil conditions (Capó et al., 2022; Van De Koppel et al., 1997), which in turn has cascading effects on other taxa (Barzan et al., 2021a; Davidson et al., 2017). These ecological disruptions may not only influence the availability of carrion but also shape scavenger community structures and interspecific interactions. Therefore, studying how vultures, as primary carrion consumers, utilize these human-related feeding resources is crucial for understanding their feeding behavior and developing effective conservation strategies.

As ecosystems become increasingly disconnected from their biotic processes due to anthropogenic intensification (Newbold et al., 2016), conservation strategies must adopt multidisciplinary approaches to effectively target species and restore functional integrity. This disconnection—where key ecological interactions, such as nutrient cycling and trophic dynamics, are disrupted—undermines ecosystem resilience. Political decisions often exacerbate this uncoupling, as seen in the case of Bovine Spongiform Encephalopathy (BSE) regulations in Spain, where mandating carcass incineration instead of natural abandonment severed a critical resource for scavengers. This policy divergence with Portugal altered vulture foraging behavior, effectively creating an ecological barrier at the border (Arrondo et al., 2019). Similarly, the Common Agricultural Policy (CAP) has historically accelerated ecosystem-process decoupling by incentivizing agricultural intensification, which drives habitat fragmentation, biodiversity loss, and the decline of ecosystem services (Assandri et al., 2019; Simoncini et al., 2019). Despite reforms, CAP remains inadequately integrated with conservation goals, failing to monitor or mitigate the disruption of biotic processes (Concepción & Díaz, 2019; Simoncini et al., 2019). Effective conservation must prioritize reconnecting ecosystems to their foundational processes, ensuring that policy and management address both species and the functional networks they sustain.

Aims and objectives of this thesis

The general aim of this thesis was to unravel the importance of the ecosystem function in several life parameters of an endangered endemic vulture, the Egyptian vulture (*Neophron percnopterus*). Particularly, we aimed to:

1) Determine how the primary productivity contributed to the breeding success of this species in an arid ecosystem, with the particularity of having heavy grazing pressure from domestic livestock (**Chapter I**).
2) Understand the effects of the source of the food (wild or domestic) in relation to the number of chicks reared to assess the impact on breeding of anthropogenic resources (**Chapter II**).
3) Describe and assess the effects of extreme climatic events that have the ability of disrupt the ecosystem natural processes (**Chapter III**).
4) Describe the movement patterns during one of the most stressful periods, breeding, and how they use the feeding resources available (**Chapter IV**).

MATERIALS AND METHODS

Study area

The present thesis was carried out entirely in Fuerteventura Island (28◦25′57″N 14◦00′11″O) which has an extension of 1660 km^2 (**Figure 3**). Fuerteventura is one of the easternmost islands from the Canary archipelago. It is situated in the north-east Atlantic Ocean, being Fuerteventura located at 97 km from Morocco coast and 1400 km from the Iberian Peninsula. In contrast to the other islands of the archipelago, the mean altitude is low with 54% of the land below 200 m a.s.l., and 87% below 400 m a.s.l. (Donázar, Palacios, et al., 2002). Some mountain ridges have sheer hillsides and cliffs. The climate is very dry with a mean annual temperature of 21.1ºC and 98 mm of annual rainfall (AEMET 2015). It is an arid landscape, composed mainly of grasslands and shrublands, where woodland is almost completely absent. The annual rainfall on this island is 105 mm, with a mean temperature of 19 ◦C, reached in summer, and autumn daily temperatures of over 40 ◦C (Rodríguez Delgado, O., García Gallo & Reyes Betancort, 2000a; Zazo et al., 2002). In addition, aridness is increased by strong northerly winds, the so-called "alisios" (with an average speed of 20 km/h) that are particularly strong during spring and summer (Johnson & Stevens, 2000). This area is widely known for recurring dust storms that mostly occur during winter months, when they are more intense (Suárez-Molina et al., 2024). These storms imply low visibility during the duration of the event, and an impoverishment of the air quality, with health consequences for the islander population (Dominguez-Rodriguez et al., 2020). On this island, crops are extremely scarce, with potential arable lands covering only 16.75% of the territory (Molina, 2002), of which only 0.77% are cultivated (ISTAC, 2023). The resident human population in 2024 was almost 128.744 people (INE 2025), mostly living in the town of Puerto del Rosario (35%).

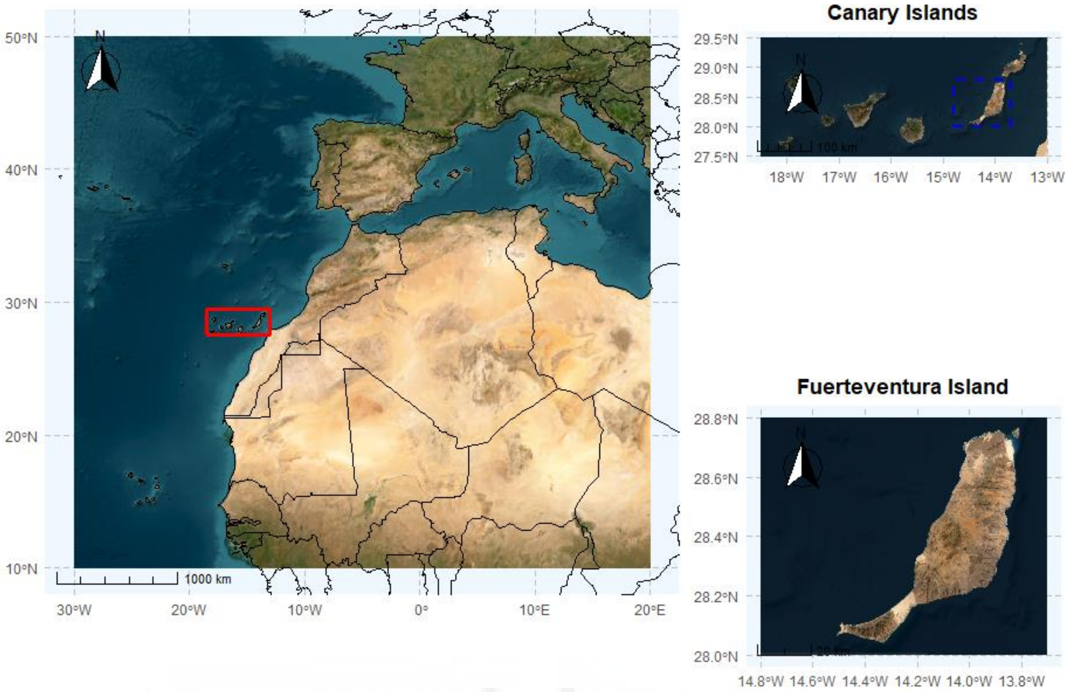

Figure 3: Map locating the Canarian archipelago (red rectangle) and the Fuerteventura Island within the archipelago (blue rectangle).

Livestock farming in fuerteventura

Pre-European colonisers introduced goats (*Capra hircus*) at around 500 BC (Cabrera, 1996). When the Europeans arrived, the number of goats was estimated at around 30,000–60,000 (18–36 goats per km^2). It is also believed that Europeans maintained stable numbers (around 30,000) until the 20th century. The first accurate census (1970) estimated around 12,000 goats, and numbers steeply increased after this date (Gangoso et al., 2006a).

Nowadays, livestock farming is shifting to semi-intensive and intensive practices, and the number of small traditional farms is declining. In fact, the Canarian Institute of Statistics (ISTAC) has reported in 2020 that the Canarian archipelago has lost over 40% of the entire livestock population in the last two decades. In Fuerteventura, where most of the domestic livestock is mainly composed of goats and some sheep, this decline is coupled with the shift towards more intensive practices, where costs are reduced therefore affording farmers to keep their livestock. However, intensive practices involve high concentrations of confined livestock and a more intensive use of antimicrobials (Blanco et al., 2019), which in turn can have detrimental consequences on those species feeding on domestic livestock carcasses. Additionally, in the Canary Islands the abandonment of livestock remains near farms is illegal. However, carcass abandonment frequently occurs, especially at farms located in remote areas (García-Alfonso et al., 2019). Thus, the farms in Fuerteventura Island act as stable feeding resource that vultures visit (García-Alfonso et al., 2020).

Biodiversity of Fuerteventura

Fuerteventura Island exhibits high biodiversity despite its arid conditions. The island supports over 500 vascular plants, being over 60 endemic to the archipelago and 15 are exclusive to Fuerteventura Island (Reyes-Betancort et al., 2008). Faunal endemism is significant, particularly among invertebrates, with over 3,000 endemic arthropods to the Canary Islands and ~100 exclusive to Fuerteventura. Vertebrate endemics include the Fuerteventura stonechat (*Saxicola dacotiae*) (Illera et al., 2006), the Canarian houbara (*Chlamydotis undulata fuertaventurae*), a subspecies adapted to arid zones (Alonso et al., 2024), and the Canarian Egyptian vulture (*Neophron percnopterus majorensis*), being the latter the only obligate scavenger on the island. Facultative scavengers include the Canarian raven (*Corvus corax canariensis*), seagulls (*Larus michahellis atlantis*) and the Canarian buzzard (*Buteo buteo insularum*).

Marine ecosystems feature seagrass meadows (*Cymodocea nodosa*) and critical habitats for loggerhead turtles (*Caretta caretta*) and angel sharks (*Squatina squatina*) (Brito et al., 2002). Current threats include invasive species, such as the California kingsnake (*Lampropeltis californiae*), cats (*Felis catus*) and habitat degradation (Nogales et al., 2006). Protected areas, such as Corralejo and Betancuria Rural Park, or Cuchillos de Vigán Natural Monument, aim to mitigate these pressures.

Focal species

The present thesis uses the Egyptian vulture (*Neophron percnopterus*) as focal species. The Egyptian vulture is a globally endangered long-lived scavenger (BirdLife International, 2022). It is a medium-sized (2–3 kg) monogamous species that generally breeds in holes in cliffs on open landscapes in semi-arid areas, and its clutch size is up to two eggs. They have delayed maturity, with the first breeding attempt at around 7 years. Although they are territorial, during the long pre-adult stage individuals tend to congregate in large numbers in feeding location and communal roosts, a behaviour exhibited mainly by non-adult individuals (del Hoyo et al., 1994). Both parents lay eggs for approximately 42 days and chicks spend 70–90 days in nests before fledging (Cramp & Simmons, 1980; Kumar et al., 2020). Both sexes invest an equitative parental effort in food provisioning and nestling feeding (Morant Etxebarria et al., 2019). This species is widely distributed across South Europe and North Africa, the Middle East, Central Asia and India, and has numerous island populations (e.g., Balearic archipelago, Socotra and Masira in the Arabian Sea, Cape Verde and the Canary Islands in the East-Atlantic). The Canarian Egyptian vulture (*Neophron percnopterus majorensis*) is an endemic subspecies to the Canarian archipelago, where its distribution was formerly wide (Donázar, Palacios, et al., 2002). Currently, the population is restricted to the Fuerteventura and Lanzarote islands, where the stronghold is on the Fuerteventura Island (over 90% of the population). The main causes of non-natural mortality that have contributed to its population decline are electrocutions or collisions with power lines, shooting and poisoning (Donázar, Palacios, et al., 2002; Gangoso et al., 2009).

To mitigate non-natural mortality in this population, a LIFE-Nature Project was implemented between 2004 and 2008 (LIFE04NAT/E/000067). Specifically, LIFE management actions were focused on the modification of power lines with anti-collision and anti-entanglement systems (performed during 2005) and the implementation of awareness-raising and environmental education campaigns to educate the public about the negative effects of illegal poisoning. The island currently holds two supplementary feeding stations with the goal to provide supplementary feeding for this Egyptian vulture population. The first was opened in 1998 (Tiscamanita) and is mainly supplied by slaughterhouse pig remains (heads, viscera, lungs, hearts, etc). In 2008, as an additional LIFE measure, a second supplementary feeding station was opened in northern Fuerteventura (Villaverde). This station is mainly supplied with goats from the surrounding farms that the farmers deposit inside the facility. This site, however, present a much less degree of use (van Overveld et al., 2018). Additionally, vultures are also known to gather on the Urban Waste Dump located in the vicinity of the capital of the island, Puerto del Rosario (**Figure 4**).

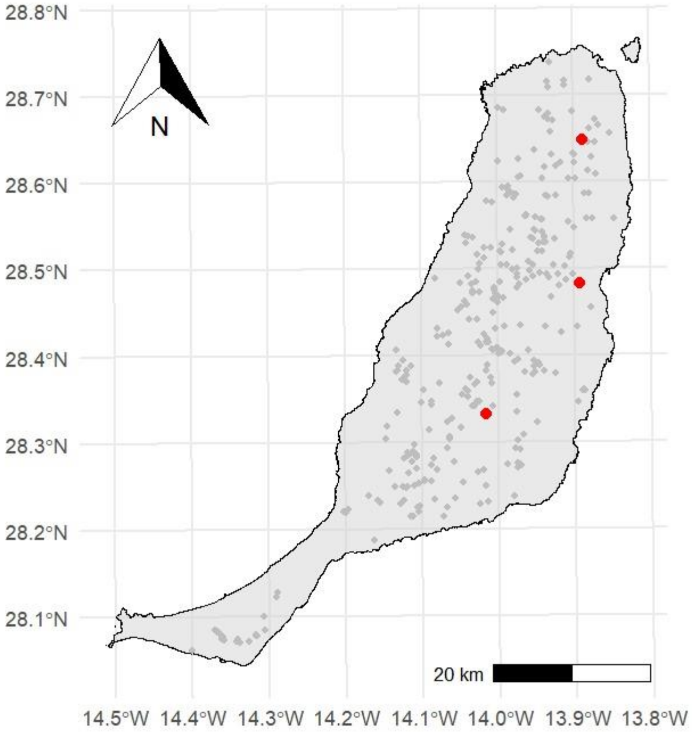

Figure 4: The predictable feeding sites in Fuerteventura Island. The northern point is Villaverde feeding station, the middle red point is the Urban Waste Dump, and the southern red point belongs to Tiscamanita feeding station. Grey points represent the 291 livestock farms up to 2017 (García-Alfonso et al, 2020) in Fuerteventura Island.

Population monitoring

Population monitoring of this subspecies of Egyptian vulture (*Neophron percnopterus majorensis*) has been carried out consistently since 1998. As part of the monitoring, individuals are tagged, currently having over 90% of the population individually identifiable (Badía-Boher et al 2019). Individuals were tagged with a plastic PVC ring in one tarsus, and with a metallic ring in the other, with a unique number. With this, all the individuals tagged are identifiable with binoculars. The effort of the monitoring was mainly towards the breeding season. Every year, nests were followed weekly from distance by using telescopes (20-60x) or binoculars (8-10 × 42) to identify breeding activity, such as mating, incubation and, ultimately, chick rearing. When the behaviour of a couple indicated incubation, the date was collected, and the nest was surveyed to determine the hatching date. Nests with successful hatching were accessed to mark chicks with plastic and metallic rings when chicks were around 50–60 days old. During that visit to the nest, other additional information was gathered, such as diet information by counting and identifying the prey remains in the nests, blood samples, feather samples, collect any non-hatched eggs, etc. The adults were trapped during the years of the monitoring using canon net traps. All the individuals marked were genetically sexed, and the age was estimated based on moulting in the case of the adults. Additionally, roosting sites, electric line pylons used for resting and sleeping were regularly surveyed to account for all the individuals tagged to determine the survival of each individual. This was particularly important during the breeding season when one of the breeding parents was missing, to detect abandonment of the nest or the death of an individual.

GPS tracking information

As part from the monitoring, 70 adults (30 males, 40 females) were trapped with cannon nets and tagged with solar-powered GPS transmitters throughout the study period. Individuals were genetically sexed, and their age was known because they were either individually tagged in nests when they were chicks or were dated when trapped for moult characteristics (Forsman, 1998). Two types of devices were used: 29 individuals were equipped with UvA-BiTS (https://www.uva-bits.nl/ Amsterdam, the Netherlands), 40 with E-obs (GmbH, https://e-obs.de/, Munich, Germany), and one individual was tagged with both devices during the study period. Both device brands have multiple sensors to measure altitude, speed and geographical coordinates according to a defined time interval (see below). Devices were attached as backpacks using a 0.84- and 1.12-cm wide Teflon harness. The total harnessing system weighed between 31 g (UvA-BiTS) and 54 g (E-obs), constituting 1.4-2.4% of the mean body mass of this species (Sergio et al., 2015). We used GPS data from 1 January 2015 onwards because the GPS settings for the individuals tagged in 2013 to 2015 were programmed to collect data over much wider time intervals, hindering comparability between the first period (2013-2015) and the second (2015-2024). All the devices applied during our study period (2015-2024) were programmed with time intervals lasting between 1 and 5 min.

UvABiTS devices (**Figure 5**) operate using a Bluetooth-based network to transfer collected data. This process requires a base station, which consists of an antenna and a laptop. Data transmission occurs when birds enter the reception zone, which can be expanded with the use of a relay. However, these devices do not support individual localization through radiotracking. They do allow for the configuration of two distinct time blocks, enabling high-frequency data collection during the day and lower-frequency collection at night. Additionally, a designated area can be programmed with specific settings.

Figure 5: UvABiTS device on the left picture, and a Canarian Egyptian vulture tagged with an UvABiTS device on the right. Photography © M. García-Alfonso.

E-obs devices (**Figure 6**), in contrast, rely on GSM-GPRS signals, the same technology used in mobile phones. Unlike UvABiTS, they do not require a base station. However, to facilitate data retrieval in areas without signal coverage, they include a high-speed radio link for wireless on-site downloads. Typically, data is transferred daily, and if a connection is temporarily unavailable, the data remains stored until the next successful transmission. E-obs devices support radiotracking, making it easier to locate deceased individuals compared to UvABiTS. However, they lack the ability to configure two separate time blocks or define a specific area with custom settings.

Figure 6: Details of an e-obs device on the left and a Canarian Egyptian vulture being equipped with an e-obs device on the right. Photography © J. A. Donázar (left) and M. García-Alfonso (right).

For both types of devices, once data is downloaded, it is removed from the transmitter's memory, ensuring continuous storage availability. Data collection settings can be modified at any time, with changes applied during the next connection.

Due to the operational requirements of UvABiTS devices, two base stations and three relays have been installed (**Figure 7**). Relay batteries must be replaced every three months, and the entire system requires regular monitoring and occasional maintenance. Additionally, device batteries must be periodically checked to adjust settings when voltage is low, preventing interruptions in data collection.

Figure 7. Details of the required system for the proper functioning of UvABiTS devices. (A) Laptop installed close to the main supplementary feeding station serving as base station number 1. (B) Antenna connected to laptop 1. (C) Relay used during the installation of a supporting relay for the base station 1. (D) Laptop installed close to the garbage dump serving as base station number 2. (E) Antenna connected to laptop 2. (F) Relay installed inside the garbage dump supporting base station 2. (G) Another relay installed inside the garbage dump supporting the base station 2. Photography © M. de la Riva (top) and L. Gangoso (bottom).

Environmental and climatic data used per chapter

For the present thesis, we have used different sources of climate, environmental and weather data regarding the spatial and temporal resolution needed to answer the research questions.

For the first chapter (**Chapter I**), we used remote sensing information combining the satellite data from LANDSAT 5, 7, 8 and MODIS to compute the NDVI (Normalized Differenced Vegetation Index) over 22 years (1998-2020). This index has the following formula:

$$NDVI = \frac{NIR - RED}{NIR + RED}$$

The NDVI has been widely acknowledged as proxy for ecosystem-level primary productivity. We filtered satellite images and discarded those with clouds or shadows by means of the per-pixel Quality Assessment metadata. Then we used the CORINE Land Cover 2018 map to identify and mask the satellite pixels with natural vegetation. We averaged the mean and standard deviation of NDVI for several time-period combinations. For temperature data, we used the NOAA layer, and for precipitation the CHIRPS layer. All the information was processed in Google Earth Engine.

For the second chapter (**Chapter II**), as the whole study period was comprised by MODIS satellite, and also that the spatial resolution was a buffer of 4 km of extension, we used a single satellite for calculating the NDVI, which can be used as proxy for ecosystem-level primary productivity. We also used the Corine Land Use Cover 2018 for calculating the NDVI only in natural areas. For temperature, we used again the NOAA layer and for precipitation the CHIRPS layer.

For the third chapter (**Chapter III**), we extracted the dust data from the WMO - Barcelona Dust Regional Centre (WMO SDS-WAS Regional Centre for Northern Africa, Middle East and Europe, https://dust.aemet.es/). We used the information derived from the MULTI-MODEL corresponding with the surface level dust concentration (kg/m^3). Local daily information of wind conditions precipitation and temperature was extracted from the meteorological station of Puerto del Rosario, Fuerteventura.

The last chapter (**Chapter IV**) combined information from two different sources. For those analyses with daily temporal resolution, we used also the data from the meteorological station from Puerto del Rosario for temperature, precipitation and wind data. For those analyses comprising different temporal and spatial scales, we extracted the satellite information from MODIS satellite for NDVI, CHIRPS for precipitation and NOAA for temperature. For dust, we extracted the dust data from the WMO - Barcelona Dust Regional Centre (WMO SDS-WAS Regional Centre for Northern Africa, Middle East and Europe, https://dust.aemet.es/) corresponding with the surface level dust concentration from the MULTI-MODEL.

Response variables used per chapter

Each of the chapters of this thesis benefits from different parts of the long-term monitoring and GPS tracking history of this endemic subspecies in Fuerteventura Island. To comply with the objectives and aims proposed, the data used per each chapter was as follows.

For the first chapter (**Chapter I**), we utilized extensive population monitoring to calculate breeding success, measured as the number of chicks successfully reared divided by the number of breeding territories per year over a 22-year period (2000–2021).

For the second chapter (**Chapter II**), we used the monitoring data differently by selecting breeding territories that had been active for at least 10 years since the start of the study. For those territories, we recorded the number of chicks reared (or none) during the study period and compared their diet. Additionally, as part of the standardized ringing procedure for chicks, field technicians counted and identified each prey item present in the nest whenever they accessed it. This information served as a proxy for estimating the diet of the chicks reared in each territory.

For the third chapter (**Chapter III**), we use the GPS tracking information for calculating the daily distance accumulated, by summing all the displacements made per each individual and day (in m). We also included in the analysis the age and the sex of the individuals.

For the fourth chapter (**Chapter IV**), we firstly took advantage of the long-term monitoring data for splitting the breeding season into phases: i) pre-breeding, ii) incubating, iii) chick rearing, iv) post-breeding and v) non-breeders, which included those who either did not attempt to breed or failed at any stage of breeding. This information was gathered by field technicians who surveyed nests and recorded egg-laying and hatching dates. We then analysed whether movement patterns differed among these phases by calculating net squared displacement using GPS tracking data. Second, we quantified the time spent at predictable feeding sites, such as supplementary feeding stations and farms. Lastly, we analysed the home range and core areas of individuals that successfully raised a chick, using GPS tracking data along with hatching and independence dates obtained from monitoring records.

CHAPTER I

Ecosystem productivity drives the breeding success of an endangered top avian scavenger in a changing grazing pressure context.

Lola Fernández-Gómez, José A. Sánchez-Zapata, José A. Donázar, Xavier Barber, Jomar M. Barbosa.

This chapter corresponds to the following published article: Fernández-Gómez, L., Sánchez-Zapata, J. A., Donázar, J. A., Barber, X., & Barbosa, J. M. (2023). Ecosystem productivity drives the breeding success of an endangered top avian scavenger in a changing grazing pressure context. *Science of The Total Environment*, 168553. https://doi.org/10.1016/j.scitotenv.2023.168553

Abstract

Environmental conditions and resource availability shape population dynamics through direct and indirect effects of climate, biological interactions and the human modification of landscape. Even when a species seems dependent on predictable anthropogenic food resources or subsidies, ecosystem-level factors can still determine population dynamics across taxa. However, there is still a knowledge gap about the cascade effects driven by climate, vegetation functioning, resource availability and governmental policies on key aspects of species reproduction for top scavengers. Here we put to good use 22 years (2000-2021) of extensive population monitoring from the endemic Canary Egyptian vulture (*Neophron percnopterus majorensis*) on the Fuerteventura Island (Canary Islands, Spain) to study the relative importance of demographic factors, ecosystem conditions and availability of anthropogenic food sources on breeding success. Our results suggest that ecosystem-level primary productivity, the number of livestock animals present on the island and Density-dependent processes determine the temporal changes in the breeding success of this species. We firstly accounted for a top-down effect of livestock on island vegetation, where overgrazing directly reduces landscape-level vegetation biomass. We, consequently, found a bottom-up effect between vegetation and the Egyptian vulture's breeding success. In this context, minimal changes in ecological conditions can impact the species inhabiting these ecosystems, with direct consequences on a key population stage, such as breeding season, when energy requirements are higher. These results are especially relevant because cascading and indirect effects of ecosystem processes and governmental policies are often overlooked when pursuing conservation goals of endangered species.

Keywords: agricultural policies; anthropogenic resources; carrion; demography; regime shift; trophic cascade

1. Introduction

Natural- or human-driven ecosystem changes have a key influence on species survival and reproduction at different trophic levels, and from plants to vertebrates. Some cascading effects of ecosystem changes on species become extremely important in arid environments because the biota is driven by variable and ephemeral ecosystem conditions (Beever et al., 2017). Therefore, subtle changes in environmental and ecological conditions may have direct consequences for the species inhabiting harsh ecosystems, especially during critical periods like breeding season, when energy requirements are higher (Salamolard & Weimerskirch, 1993). Additionally, perturbations, such as droughts or overgrazing, can catastrophically disturb ecosystem functioning (Van De Koppel & Rietkerk, 2004), which results in potential shifts in species demographic tendencies.

Population dynamics are shaped by both environmental conditions and resource availability through direct and indirect effects of climate, biological interactions and the human modification of landscapes (Coulson et al., 2001; SÆther et al., 2004; Simard et al., 2010). Even when species seem largely dependent on predictable anthropogenic food resources or subsidies (Oro et al., 2013), ecosystem-level primary productivity can still determine changes in the life parameters of vertebrates (Donázar et al., 2020), in addition to habitat selection and movement ecology (general review, (Pettorelli et al., 2011). Recent studies have demonstrated the key role that ecosystem productivity plays in species demographical parameters through trophic cascading effects on primary, and even on secondary, consumers (Barbosa et al., 2020; Donázar et al., 2020). The relation between primary productivity and breeding success, however, remains largely unknown (but see (Marcelino et al., 2020)). Breeding success is conditioned by numerous factors, e.g. favourable weather conditions, habitat availability and condition, individual-level fitness and life-stage and resource availability. Intraregulatory mechanisms, such as Density-dependence effects, can also interfere negatively with raptors' breeding success (Chambert et al., 2020), with direct competence for resources (i.e. lack of feeding resources or mating partners). In fact, there is compelling evidence that during the breeding season, the diet of many species changes to either exploit transient food resources or overcome the stress of raising offspring (Dhondt & Hochachka, 2001; Jiguet, 2002; Montague et al., 1986). Indeed we expect these natural ecosystem processes to interact with anthropic factors to determine breeding success.

Livestock farming has been identified as one of the main feeding resources for scavengers (O´Neal, 2016). However, it is also highlighted as a major ecosystem disruptor that affects ecosystem structure, functioning and stability (Li et al., 2018). Several studies have suggested that man-introduced herbivores can perturb the whole ecosystem through processes, such as overgrazing, nitrification, or even the alteration of moisture retention and soil fertility (Campbell & Donlan, 2005; Coblentz, 1978). These processes may aggravate insular ecosystems, where the evolutionary context of plant-herbivore interactions differ from the mainland, and are characterised by the presence of a high rate of endemism. Insular vegetation is usually well-adapted to local climatic conditions, and has evolved without vertebrate herbivores being present (Bowen & Vuren, 2018), which allow them to allocate resources and energy that would otherwise be used to defend other destinations (Moreira et al., 2021). This, in turn, favours greater palatability, which triggers a higher rate of predation from herbivores (Cubas et al., 2019).

The Egyptian vulture (*Neophron percnopterus*) is a medium-sized (2-3 kg), globally endangered obligate scavenger that lives in a variety of habitats, mainly open landscapes in arid ecosystems (BirdLife International, 2022). It is widely distributed across South Europe and North Africa, the Middle East, Central Asia and India, but there are numerous island populations (Donázar et al., 2005). Egyptian vultures have the particularity of exploiting a wide prey range, from livestock carcasses on which they very much depend (Cabrera-García et al., 2020; Milchev et al., 2012) to carcasses of wild prey, such as small mammals, birds and reptiles, which has been positively related to breeding success (Margalida et al., 2012).

In the presnt work, we put to good use the 22 years (2000-2021) of extensive population monitoring of the Canary Egyptian vulture (*Neophron percnopterus majorensis*) on the Fuerteventura Island (Canary Islands, Spain) to study the relative importance of climate, primary productivity, livestock and intraspecific competition on breeding success. On Fuerteventura, goats were introduced by pre-European colonisers in 500 BC. Indigenous people maintained a farming subsistence system on the island, which implied that the goat population was limited by environmental conditions and extreme events, such as droughts. According to (Cabrera, 1996), Europeans kept the Density of the goats on the island stable (approximately 30,000) in the 18th century, until 1970 when the number of domestic cattle started to sharply rise. Past and future livestock farming changes may, therefore, produce cascading effects on different trophic levels, even on top obligate scavengers. One important question to be addressed is whether these human-induced changes on ecosystem processes are persistent or reversible over time. Our main hypothesis is that breeding success depends on food availability (both livestock and wild prey carcasses). Livestock carcasses largely depend on agricultural policies and external sources of feed inputs (Schillhorn Van Veen, 1999). Therefore, contrasting changes in agricultural policies may lead to disruptive patterns in Canary Egyptian vulture reproductive traits. Wild prey carcasses might be related mostly to ecosystem primary productivity (Grande et al., 2009). Consequently, we expect higher ecosystem-level primary productivity to enhance the breeding success of the Egyptian vulture population through trophic cascading effects between primary productivity and primary consumers. Finally, in a scenario of increasing vulture population growth favoured by EU LIFE funds, we expect intraspecific competition might also negatively influence breeding success.

2. Methods

2.1 Study area and target population:

The Canary Islands are situated in the north-east Atlantic Ocean, 97 km from Morocco and 1,400 km from the Iberian Peninsula. This study was located on Fuerteventura (1,660 km^2), the south-eastern island of the Canary archipelago, which is located at 28°25′57″N 14°00′11″O. It is an arid landscape, composed mainly of grasslands and shrublands, where woodland is almost completely absent. The annual rainfall on this island is 105 mm, with a mean temperature of 19ºC, reached in summer, and autumn daily temperatures of over 40ºC (Rodríguez Delgado, O., García Gallo & Reyes Betancort, 2000a; Zazo et al., 2002).

The endemic subspecies of Egyptian vulture *Neophron percnopterus majorensis*. inhabits the Canary Islands. This subspecies was once abundant across the entire archipelago early the 20th century, but in the last few decades its populations has steeply declined due to heavy unnatural mortality linked with power lines and illegal poisoning, as well as shootings and lead intoxication through bullet ingestion (Donázar, Palacios, et al., 2002; Gangoso et al., 2009; Gangoso & Palacios, 2002). Nowadays, it is only present on the Lanzarote and Fuerteventura Islands, with the bulk (> 90% of the total population) on the latter (Donázar, Palacios, et al., 2002; Gangoso et al., 2009). Since 2006, its population has grown owing to conservation measures funded by EU LIFE projects (Badia-Boher et al., 2019a).

2.2 Field procedures: Vultures' breeding success and Density

Breeding success was calculated for the whole study area as the number of chicks per number of territories occupied every year for our study period (2000-2021). All the known territories were monitored and other areas were surveyed for new territories from February to the end of April. Then those territories with a pair displaying breeding behavior, i.e. copulation, nest building, common roost etc., were monitored at least 3 times a week for egg laying. Then if laying behavior was detected, the nest was monitored twice a week until the egg hatched, and the nest was closely monitored thereafter. When chicks were 50-60 days old, they are ringed with both metal and PVC rings. This good capture effort allowed over 90% of the population to be individually identified in 2022 (Badia-Boher et al., 2019a). The average breeding success was 0.49 for our study period, with a maximum of 0.63 in 2002 and of 0.2 in 2012. After reaching this minimum in 2012, breeding success presented a highly fluctuating pattern (Supplementary Material, **Figure S1 - A**).

The *Density* of breeding territories was measured as the number of breeding territories occupied every year. This parameter showed a steady increase throughout the study period. The maximum number of occupied territories was reached in 2021 with 81 territories (Supplementary Material, **Figure S1 - D**).

2.3 Environmental variables

The NDVI (Normalised Difference Vegetation Index) has been pointed out as a good proxy for monitoring vegetation response to climate and to estimate ecosystem-level productivity (Pettorelli et al., 2005; Schloss et al., 1999). For this study, we calculated the NDVI by combining the satellite data from LANDSAT 5, 7, 8 and MODIS. We filtered satellite images and discarded those with clouds or shadows by means of the per-pixel Quality Assessment metadata. Then we used the CORINE Land Cover 2018 map (https://land.copernicus.eu/pan-european/corine-land-cover) to identify and mask the satellite pixels with natural vegetation (i.e., natural grasslands, mixed forest, sparsely vegetated areas and sclerophyllous vegetation). We then fitted a Multivariate Autoregression State-Space model (MARSS) to fill any missing data in the satellite temporal series (see Barbosa et al. 2020 for details on this procedure). We averaged a single NDVI value per month for our entire study area, i.e. the Fuerteventura Island. By proceeding in this way, we avoided any discrepancy in the spatial resolution that could result from combining different satellites.

All the environmental variables are detailed in **Table 1**. We took the precipitation data from the CHIRPS dataset (https://www.chc.ucsb.edu/data/chirps) by first summing accumulated precipitation per month. The temperature data were extracted from the NOAA (https://www.ncei.noaa.gov/) by averaging the monthly values.

Table 1: Environmental variables fitted in the MARSS models. For analytical purposes, we split the natural year into two 6-month periods: (1) from January to June, which comprises most of this species' breeding season (copulation, nest building, common roost, chicks' firsts months of life, when they rely more on parental care); (2) from July to December, which corresponds to non-breeding season. The response variable was the breeding success (number of chicks per number of occupied territories) per year for our study period (2000-2021). For all the variables, we calculated the mean and standard deviation. For visual support and guidance, please check **Figure 1**.

Family	**Variable**	**Nomenclature**	**Description**
NDVI	NDVI current breeding season	*NDVI breeding season*	Corresponding to the first 6 months of the year (January to June, first period of the year) of the current breeding season.
	NDVI 6 months before the breeding season	*NDVI 6 months bbs*	Corresponding to the 6 months before the start of the breeding season (previous year).
	NDVI 12 months	*NDVI 12 months*	Corresponding to the 6 months before the breeding season and the current breeding season, i.e. the second period from the previous year and the first period of the corresponding year.
	NDVI 1 year before the breeding season	*NDVI 1-year bbs*	Corresponding to the 6 months before the breeding season and the breeding season from the previous year, i.e. is period 1 and period 2 from the previous year.
	NDVI previous breeding season	*NDVI previous breeding season*	Corresponding to the previous breeding season, i.e. period 1 from the previous year.
Precipitation	Precipitation current breeding season	*Precipitation breeding season*	Corresponding to the first period of the year.
	Precipitation 6 months before the breeding season	*Precipitation 6 months bbs*	Corresponding to the second period of the previous year, i.e. 6 months before the start of the breeding season.
	Precipitation 12 months	*Precipitation 12 months*	Corresponding to the 6 months before the breeding season and the current breeding season, i.e. the second period from the previous year and the first period of the corresponding year.

	Precipitation 1 year before the breeding season	*Precipitation 1-year bbs*	Corresponding to period 2 of the previous year (6 months before the breeding season) and the breeding season from the previous year, i.e. period 1 and period 2 from the previous year.
	Precipitation previous breeding season	*Precipitation previous breeding season*	Corresponding to the previous breeding season, i.e. period 1 from the previous year.
Temperature	Temperature current breeding season	*Temperature breeding season*	Corresponding to the first period of the year.
	Temperature 6 months before the breeding season	*Temperature 6 months bbs*	Corresponding to the second period of the previous year, i.e. 6 months before the start of the breeding season.
	Temperature 12 months	*Temperature 12 months*	Corresponding to the 6 months before the breeding season and the current breeding season, i.e. the second period from the previous year and the first period of the corresponding year.
	Temperature 1 year before the breeding season	*Temperature 1-year bbs*	Corresponding to period 2 of the previous year (6 months before the breeding season) and the breeding season from the previous year, i.e. period 1 and period 2 from the previous year.
	Temperature previous breeding season	*Temperature previous breeding season*	Corresponding to the previous breeding season, i.e. period 1 from the previous year.

2.4 Livestock

The annual numbers of goats (the main livestock species on the island) and sheep were extracted from the annual livestock censuses from the Canarian Institute of Statistics (ISTAC, http://www.gobiernodecanarias.org/istac/estadisticas/sectorprimario/agricultura/ganaderia/C00013A_1.html.) We observed that the numbers of livestock fluctuated during the study period, with the minimum in 2020 with 80,228 goats and sheep (48.2 animals per km^2), and a maximum of 155,311 in 2006 (93.56 animals per km^2). Interestingly, we identified a drastic drop in the number of livestock from 149, 161 livestock animals in 2012 to 99,126 in 2013, which entails a decrease of 50,035 individuals in a single year (33.5% reduction). This livestock heard reduction period matches the year when financial subsidies from the European Common Agricultural Policy were drastically cut (https://www.fega.gob.es/es/datos-abiertos/informes/ayudas-directas), which heavily funded sheep and goat farming on the island. From 2010 to 2011, there was a 78.63% decrease in financial aid (Supplementary Material **Figure S2**).

2.5 Model fitting

We ran several MARSS models (Multivariate Autoregressive State-Space models) to test whether the environmental conditions, anthropogenic resources and population size shaped the breeding success of our target population of Egyptian vultures on the Fuerteventura Island. We selected MARSS models because they are designed for considering the linear stochastic dynamical system within a time-series framework, which perfectly fits long-term climatic data (Holmes et al., 2012; Hsieh et al., 2022; Walsh et al., 2016). The model was fitted with the MARSS package in R (Holmes, 2013) and it is formulated as follows:

$$\boldsymbol{x_t} = \boldsymbol{B}\boldsymbol{x_{t-1}} + \boldsymbol{u_t} + \boldsymbol{C_{tc_t}} + \boldsymbol{w_t};\quad \text{where } \boldsymbol{w_t} \sim \text{MVN}(\boldsymbol{0}, \boldsymbol{Q_t}) \qquad \text{Eq. (1)}$$

$$\boldsymbol{y_t} = \boldsymbol{x_t} + \boldsymbol{v_t};\quad \text{where } \boldsymbol{v_t} \sim \text{MVN}(\boldsymbol{0}, \boldsymbol{R_t}) \qquad \text{Eq. (2)}$$

The MARSS models are composed of two models: a process model (Eq. 1) and an observation model (Eq.2). The process model comprises a state process, whose parameters are **B**, **u** and **Q**. In the first equation (process model), x_t refers to the data observed at time t. In our scenario, it refers to the observed breeding success (x) per year (t). This model is the sum of the mathematical parameters of the state process (**B**, u, **Q** and **C**), plus the biologically-related variables (x_t, c_t). Matrix **B** allows the interaction between state processes. In our scenario, this parameter (**B**) accounted for a Density-dependent effect between the current breeding season and the previous one ($\mathbf{Bx_{t-1}}$). Vector u describes the mean trend of the state process. In our scenario, we did not fit any biological variable attached to this parameter because it is often used for auto-regressive trend processes (stochastic level models) and was, hence, set to the default setting (see below). **C** is the matrix whose elements describe the effect of each covariate (ct, environmental variables, such as the NDVI, precipitation or temperature, for each fitted time period, plus Density and Livestock) on breeding success, and w is a matrix of the process error per year (t), with process errors (those intrinsic errors associated with the observation process) at time t being distributed as a multivariate normal with mean **0** and covariance matrix **Q.**

The observation model (y_t) aims for "true" values for breeding success with the sum of the observed values (xt) and the error associated with those observations (v_t). This error has a multivariate normal distribution, with mean **0** and covariance matrix **R**. The particular settings for all the parameters are detailed in Supplementary Material – Appendix 1. We set 10,000 iterations using the *kem* method, which is based on the EM algorithm (expectation-maximisation) with a Kalman filter. This approach is both faster and robuster for reaching the vicinity of maximum likelihood (Holmes, 2013).

We ran a MARSS model for each fitted time period (as defined in **Table 1** and **Figure. 1**) to test the effect of the different environmental variables (NDVI, precipitation and temperature), Density and Livestock variables on breeding success. We subsequently used the same time period per environmental variable (i.e. NDVI, precipitation and temperature) so that all the environmental variables that were inputted in each MARSS model occurred during the same time period. We did not fit two different time periods in the same model because environmental variables across periods had a Spearman's correlation of over |0.5| ((Graham, 2003), see **Figure. 1** for further details). Model selection was done by relying on the model with the lowest AICc (Akaike Information Criterion corrected for small samples, Sugiura, 1978).

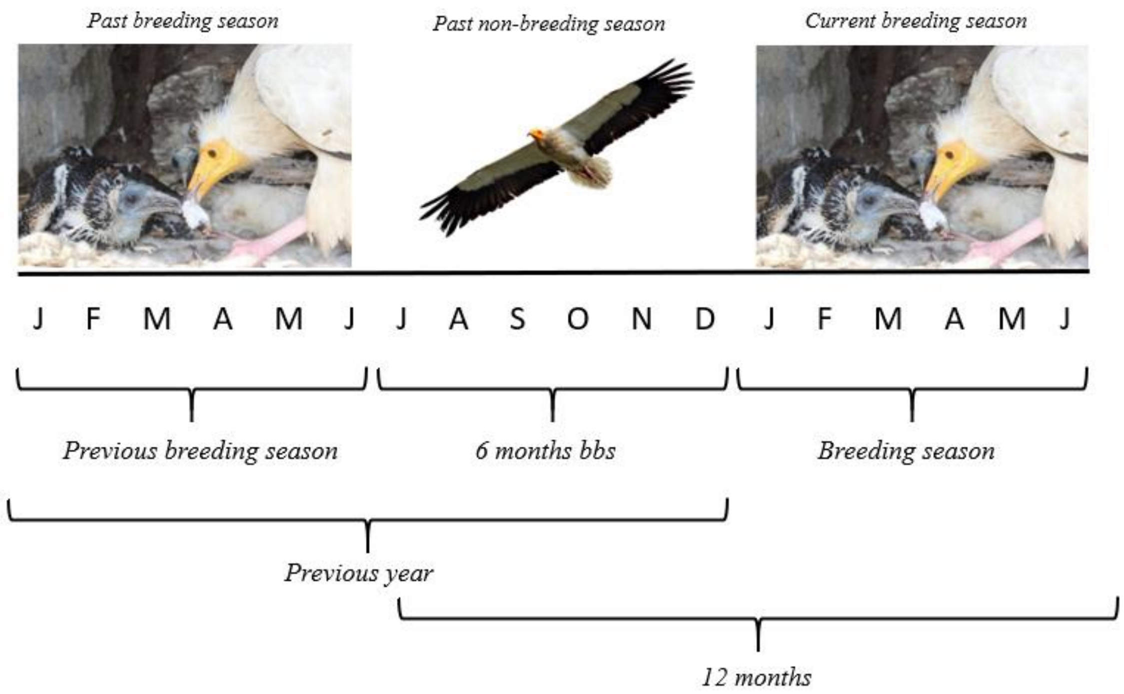

Figure 1: Time periods used in the explanatory variables fitted in each MARSS model (see Table 1 for details). Bbs stands for before the breeding season.

3. Results

All the MARSS models reached convergence in less than 15 iterations (**Table 2**). The model with the lower AICc value indicates that the mean NDVI for the 6 months before breeding season (*NDVI 6 months bbs*) positively affected breeding success (**Table 3**). Besides, both *Livestock* and *Density* showed negative effects on reproductive success because the credibility intervals remained above zero in 88% of the cases for *Livestock* and 77% for *Density* (**Table 3**).

Table 2: All the possible combinations of variables per considered time period. MARSS models are ranked by AICc. The response variable was breeding success (number of chicks per number of occupied territories) per year for our study period (2000-2021). We fitted only one time period per model due to correlation issues among the environmental variables across time periods.

Order	Variables	LogLike	AICc	ΔAICc
1	Mean NDVI 6 months bbs + Livestock + Density	-25.568	68.736	0
2	Mean NDVI 12 months + Livestock + Density	-25.992	69.584	0.848
3	Mean NDVI 12 months + Mean Precipitation 12 months + Mean Temperature 12 months	-26.236	70.071	1.335
4	Mean NDVI 6 months bbs + Mean Precipitation 6 months bbs + Mean Temperature 6 months bbs	-26.287	70.175	1.439
5	Mean NDVI previous year + Livestock + Density	-26.658	70.917	2.181
8	Mean NDVI previous year + Mean Precipitation previous year + Mean Temperature previous year	-27.34	72.28	3.544
10	SD NDVI 12 months + Livestock + Density	-27.723	73.046	4.31
11	Mean NDVI previous bs + Livestock + Density	-27.761	73.123	4.387
12	Mean NDVI breeding season + Livestock + Density	-27.778	73.156	4.42
13	SD NDVI previous year + Livestock + Density	-27.827	73.254	4.518
15	Mean NDVI breeding season + Mean Precipitation breeding season + Mean Temperature breeding season	-29.079	75.757	7.021
6	Mean NDVI 6 months bbs + Livestock + Density + Mean Precipitation 6 months bbs + Mean Temperature 6 months bbs	-24.691	76.459	7.723
18	Mean NDVI previous bs + Mean Precipitation previous bs + Mean Temperature previous bs	-29.597	76.794	8.058
7	Mean NDVI 12 months + Livestock + Density + Mean Precipitation 12 months + Mean Temperature 12 months	-25.053	77.183	8.447
20	SD NDVI 12 months + SD Precipitation 12 months + SD Temperature 12 months	-30.137	77.874	9.138
9	Mean NDVI previous year + Livestock + Density + Mean Precipitation previous year + Mean Temperature previous year	-25.549	78.175	9.439
21	SD NDVI previous year + SD Precipitation previous year + SD Temperature previous year	-30.404	78.408	9.672
14	SD NDVI 12 months + Livestock + Density + SD Precipitation 12 months + SD Temperature 12 months	-26.992	81.061	12.325
16	SD NDVI previous year + Livestock + Density + SD Precipitation previous year + SD Temperature previous year	-27.297	81.67	12.934
17	Mean NDVI previous bs + Livestock + Density + Mean Precipitation previous bs + Mean Temperature previous bs	-27.33	81.737	13.001
19	Mean NDVI breeding season + Livestock + Density + Mean Precipitation breeding season + Mean Temperature breeding season	-27.617	82.311	13.575

These results indicate that ecosystem-level primary productivity, the amount of livestock and density-dependence processes collectively determine this species' breeding success (**Figure 2**). Interestingly, primary productivity played a key role within the 6 months prior to the start of the breeding season. The output from the MARSS models within ΔAICc<2 is detailed in Table S1 (Supplementary Material). Although precipitation and temperature were not included in the best model (**Table 2**), mean precipitation and temperature prior to the breeding season were included in two models with ΔAICc < 2. Both climatic variables are widely pointed out as being closely related to primary productivity.

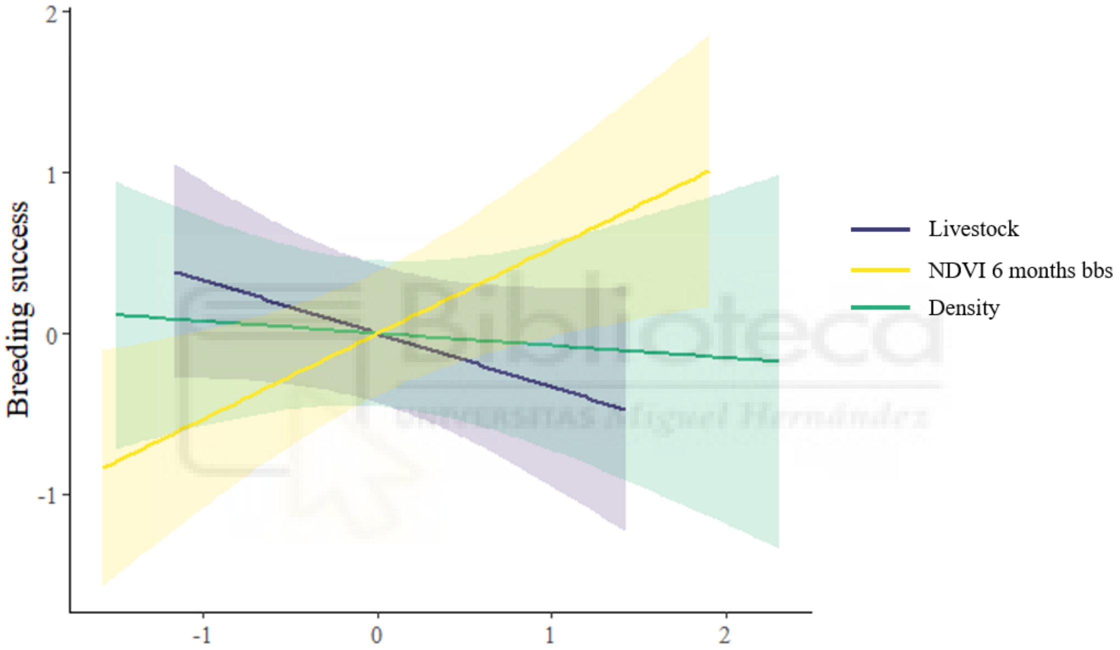

Figure 2: Linear relation among the three fitted variables from the best model selected by AICc and the response variable "breeding success". Together, these variables drive the breeding success of the Egyptian vulture. The effect of *Livestock* on breeding success is represented on the black line; the NDVI from the 6 months before the breeding season (*NDVI 6 months bbs*) on the yellow line; and *Density* of conspecifics (number of territories occupied every year on the island) on the green line.

We found differences in the temporal tendencies of breeding success before and after 2012 when comparing the averages and slopes from the raw data (**Figure 3**). During the first period (2000-2012), when the island presented high livestock density, primary productivity and breeding success drastically declined. During the second period (2013-2021), when livestock density dropped, primary productivity and breeding success stabilised. For both period, *Density* significantly increased and had doubled for the second period.

Table 3: Output for the best model selected by AICc. The response variable was breeding success (number of chicks per number of occupied territories) per year for our study period (2000-2021). ML estimate is "Maximum Likelihood algorithm", Std Error is Standard Error, CI is for Credibility Interval (95%). For further details about the mathematical parameters (B, u and Q), please see the Methods section, subsection "Model fitting".

Type of parameter	Parameters	ML estimate	Std Error	Low CI	Up CI
State process	B	-0.191	0.177	-0.538	0.157
	U	-0.007	0.165	-0.331	0.316
	Q	0.598	0.180	0.245	0.952
Covariates	NDVI 6 months bbs	0.443	0.189	0.072	0.952
	Livestock	-0.331	0.223	-0.767	0.105
	Density	-0.247	0.211	-0.661	0.165

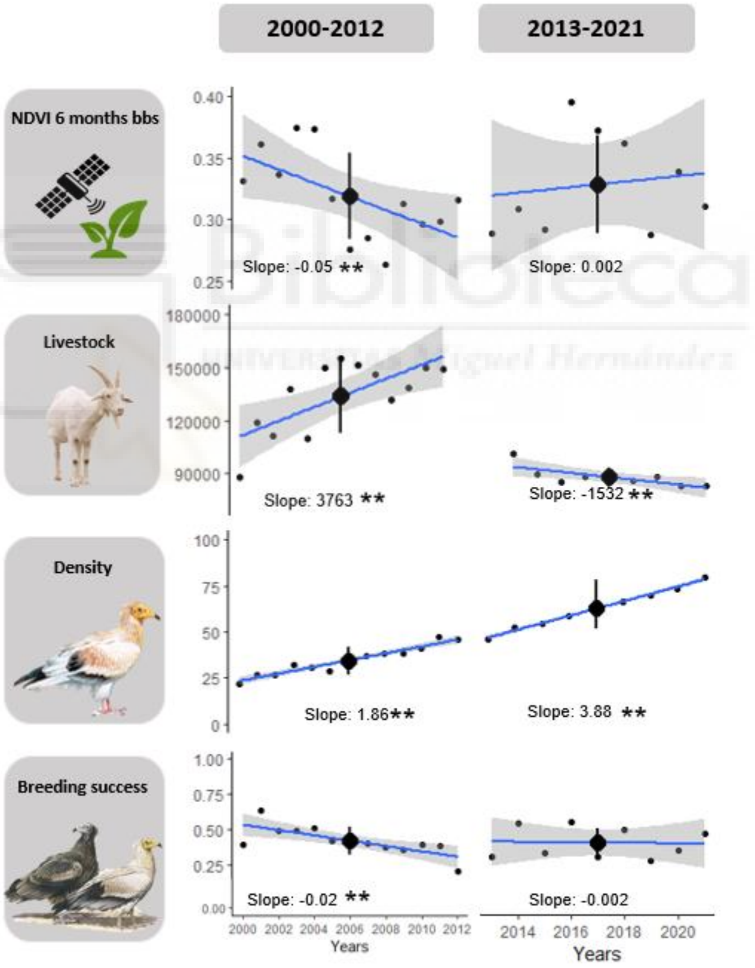

Figure 3: Temporal tendencies before and after 2012 for NDVI 6 months before the breeding season (*NDVI 6 months bbs*), *Livestock*, *Density* and *Breeding success*. Black dots represent the raw data. The blue line denotes the long-term trend for each period (A, C, E and G for 2000-2012; B, D, F, H for 2013-2021). The grey-shaded area depicts the associated 95% confidence interval of each linear trend. The central black dots represent the average of each variable per period. The vertical black lines refer to the associated standard deviation. Asterisks represent statistical significance of the corresponding slope (** for p-values < 0.03).

4. Discussion

Using a two-decade long dataset, we found that the top-down and bottom-up processes modulated the breeding success of a top obligated scavenger. We firstly accounted indirectly for a top-down effect of livestock on island vegetation, i.e. overgrazing directly affects the ecosystem-level primary productivity. Secondly, we also accounted for a bottom-up effect between the vegetation and breeding success of the Egyptian vulture. This is especially relevant because bottom-up and top-down processes usually relate two consecutive trophic levels (e.g. plant-herbivores, primary consumers-secondary consumers, e.g. (Hunter & Price, 2008), but very few studies have linked these types of ecosystem processes with the population dynamics of top scavengers (Coulson et al., 2011; Donázar et al., 2020).

Previous studies have highlighted that long-term monitoring is needed to fully understand population dynamics because it particularly underlines the fact that extrapolation from short-term surveys may indeed mislead subjacent population trends (Collins, 2001; Gagnon et al., 2011; Gosz, 1999). This is especially true for ecosystem-level processes, where longer study periods are required to obtain robust results. Within the time range of our study, we also observed a coincident shift in temporal tendencies of ecosystem-level primary productivity, the Egyptian vulture's breeding success, the number of breeding territories occupied every year (*Density*), livestock production and governmental subsides for agricultural production. Together, these results support the potential occurrence of a regime shift between 2012 and 2013, which was triggered by declining livestock production.

The most striking finding was a significant declining trend in primary productivity and breeding success during the period of high livestock abundance. These tendencies shifted in 2013 (after a drastic reduction in goat numbers) to wide interannual variability with a constant trend of ecosystem productivity and vulture breeding success. In addition, the increase in the rate of the number of breeding territories occupied every year (*Density*) after 2013 was twice rate that during the period before that year. This might be related to the fact that population dynamics of long-lived birds, such as vultures, are more sensitive to survival than to breeding success (Sæther & Bakke, 2000a). Overall, our results suggest that long-term overgrazing may have shifted island ecosystem functioning, which merits further research to understand how reversible these shifts are and whether the relative importance of both top-down and bottom-up play a role in these processes. Ecological regime shifts are marked changes in ecological processes that are profound enough to reconfigure the ecosystem, which affects several trophic levels (Lees et al., 2006). Although identifying regimen shifts and thresholds is challenging, it is a subject of recent interest shown in ecology, which might be particularly relevant to address science-based conservation strategies for long-lived species (Andersen et al., 2009).

Unexpectedly, livestock negatively affected the breeding success of the studied population. Livestock presence has been acknowledged as being key for sustaining vulture populations (Dobrev et al., 2016; Olea & Mateo-Tomás, 2009). Some studies have highlighted the close relation between Egyptian vulture and livestock carcasses (Cabrera-García et al., 2020; Mateo-Tomás & Olea, 2010). Hence we expected the relation between the livestock and breeding success of the Egyptian vulture to be positive. However, other studies have noted the overlooked importance of wild prey in this species' diet (Donázar et al., 2020; Margalida et al., 2012). Interestingly, our results suggest that the high grazing pressure (overgrazing) as a consequence of greater governmental subsidies and livestock production may have triggered unexpected cascading effects on ecosystem functioning, which impact several trophic levels. In our study area, Fuerteventura, there have been wide fluctuations in livestock abundance before and after 2012, which temporally overlap with CAP subsidies. Changes in CAP subsidies are known to have a profound impact on the ecosystem, by ranging from determining or changing livestock composition or stocking rates (Ramos et al., 2021), to impacting the ecosystem through land-use changes (Chiron et al., 2013).

Livestock overgrazing may disrupt the presence and abundance of small herbivores (Filazzola et al., 2020) and, consequently, provoke a shortness in the availability of the wild preys of Egyptian vultures, which would comprise several taxa (e.g. reptiles, small mammals like rodents, rabbits, birds (Milchev et al., 2012; Oro, 1992)). This entails a disruption in the bottom-up processes that regulate the vegetation-primary consumers interaction and would, therefore, affect the next trophic levels, i.e., the primary consumers-scavenger relation. As we found positive effects of primary productivity and negative effects of livestock on breeding success, our results suggest that this scavenger species very much relies on natural ecosystem dynamics and is not as dependent on livestock carrion as suggested for other populations (Cabrera-García et al., 2020; Tauler-Ametller et al., 2018). Interestingly, we also found that the mean precipitation and temperature prior to breeding season affected breeding success. Although these climatic variables were not included in the best selected model, they were present in two of the four models (Table S1, Supplementary Material). Both precipitation and temperature are closely related to primary productivity (Schloss et al., 1999).

Lastly, it is important to note that we found a negative relation between the breeding success and density of conspecifics, measured as the number of occupied territories per year. Following (O. Krüger et al., 2012), a reduction in fecundity, coupled with an increase in population, is usually caused by a decline in the quality of available resources due to increasing intraspecific competition for mates, nesting sites or food. With fewer resources, and given an increase in energy expenditure due to increased antagonistic encounters, vital rates might also be negatively affected (Fernández-Bellon et al., 2016).

4.1 Management implications.

Long-term overgrazing has been identified as one of the greatest threats to biodiversity and ecosystem functioning in grasslands worldwide, especially for arid and semi-arid ecosystems (Filazzola et al., 2020; Li et al., 2018). This process tends to aggravate insular ecosystems, where goats are one of the most widely-spread species of all introduced vertebrates on islands. In addition, goat is the second species in number of eradication attempts on Mediterranean islands (Capizzi, 2020). The negative pressures and effects they have on soil and vegetation properties have also been widely described (Capó et al., 2022). However, livestock carcasses that derive from human activities are also the main feeding resource for avian scavengers, and some of these species are endangered (Cortés-Avizanda et al., 2016). This entails a contradiction in conservation programmes for scavengers because, on the one hand, livestock carcasses provide feeding resources and determine the assemblages between the scavenger's guild (Cortés-Avizanda et al., 2010) but, on the other hand, it deeply disturbs the ecosystem through changes in primary productivity (Milchunas et al., 1988) by threatening the survival of highly endangered endemic plant species (Gangoso et al., 2006b). This study provides scientific evidence for the cascading effects of these perturbances at several trophic levels, which interfere with top-down and bottom-up processes. These indirect effects are often overlooked in pursuit of direct straightforward effects and are not, therefore, considered in conservation strategies and guidelines. Here we have disentangled how political changes in European funding can impact an ecosystem at several trophic levels by contributing to unforeseen impacts on an endangered species. Our results may help to inform European policies that account for ecosystem functioning and biodiversity conservation.

Acknowledgments:

Population monitoring was done by J. Roldan, J.A. Sarrion, W. Moreno, J. Ramírez, S. Sierra, C. Díez, M. Mallo, R. Agudo, A. Trujillano, and C. J. Palacios. O. Ceballos, F. Hiraldo, A. Sanz-Aguilar, A. Cortés-Avizanda, V. Saravia, K.

Heissenberger, M.-S. García- Heras, M. A. Cabrera and F. Rodríguez also helped with the fieldwork. The Consejería de Agricultura, Ganadería, Pesca y Aguas del Gobierno de Canarias provided data on livestock numbers. Monitoring was funded by the Cabildo Insular de Fuerteventura, Viceconsejería de Medio Ambiente del Gobierno de Canarias, Research Projects REN 2000- 1556 GLO, CGL2004-00270, CGL2012-40013-C02-01, CGL2015- 66966-C2-1-2-R and RTI2018-099609-B-C21 (Spanish Ministry of Economy and Competitiveness and EU/FEDER), and the Severo Ochoa Excellence Award from the Spanish Ministry of Economy and Competitiveness (SEV-2012-0262). T.Sánchez-Zapata and L. Fernández-Gómez were supported by the TRASCAR project (RTI2018-099609-B-C21) from the Spanish Ministry of Science and Innovation, the European Regional Development Fund and DIGITALPAST (TED2021-130005B-C21) from the Spanish Ministry of Science and Innovation, NextGeneration EU. This study also forms part of the AGROALNEXT (2022/038) programme. It was supported by MCIN with funding from European Union NextGenerationEU (PRTR-C17.I1) and by the Generalitat Valenciana. J. M. Barbosa was supported by the Generalitat Valenciana (CIDEGENT/2020/030). X.B. was supported by the the Spanish Ministry of Science and Innovation-State Research Agency for grant PID2019-106341GB-I00 (jointly financed by the European Regional Development Fund, FEDER).

CHAPTER II

Overgrazing triggers cascading effects on a top avian scavenger: long-term changes in diet and breeding success.

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This chapter corresponds to the following published article: Fernández Gómez, Fernández-Gómez, L., Sánchez-Zapata, J. A., Donázar, J. A., de la Riva, M., & Barbosa, J. M. (2025). Overgrazing triggers cascading effects on a top avian scavenger: long-term changes in diet and breeding success. *European Journal of Wildlife Research*, *71*(2). https://doi.org/10.1007/s10344-025-01896-6

Abstract

Wildlife feeding and nutrition are key drivers of several demographic parameters, such as breeding success and survival, influencing long-term population viability. To comply with the diet requirements that ensure offspring survival, parents adapt their forage strategies to the environmental conditions and resource availability. This is especially important for central-place foragers like raptors, where prey availability in the surroundings of nest and livestock carcasses significantly impact both foraging efforts and breeding success. Here we take advantage of 20 years extensive monitoring (2001-2020) of the Canarian Egyptian vulture (*Neophron percnopterus majorensis*) on the Fuerteventura Island (Canary Islands, Spain) to assess (1) what factors drive vulture diet diversity and, (2) how the number of livestock and diet diversity coupled together with environmental conditions affect breeding success and, ultimately, the conservation of vulture populations. We identified 3,787 prey items belonging to 37 different species. Diet diversity was positively related to the number of wild prey and to low livestock grazing pressure periods. Breeding success was positively related to the number of wild prey, low herbivory pressure and, to a lesser extent, to diet diversity. These results demonstrate the importance of wild prey on Canarian Egyptian vulture's diet, albeit livestock carcasses are the most abundant feeding resource. We argue that livestock have controversial conservation implications for this species because it provides a stable feeding resource, but, in turn, is one of the major ecosystem disruptors. Overgrazing by livestock can negatively affect wild primary consumers, which are essential for this endemic vulture population.

Keywords: ecosystem dynamics; scavenger; species fitness; temporal series; trophic cascade

1. Introduction

The combined effect of environmental conditions, species abundance, animal behaviour and human management decisions can have cascading effects on different trophic levels (Teichman et al., 2013; Terborgh et al., 2001). For instance, livestock production may result in landscape overgrazing, which can lead to cascade changes on ecosystem-level primary productivity, primary consumers, prey availability and, consequently, on foraging patterns of secondary consumers (e.g. Fernández-Gómez et al., 2023). These top-down and bottom-up processes are usually associated with directional effects between two consecutive trophic levels. However, only a few studies have explored the network of cascading effects across multiple trophic levels (but see Coulson et al., 2011; Donázar et al., 2020), including a top avian scavenger. Bottom-up cascading effects have unexpectedly proved to be important to top scavengers (Fernández-Gómez et al., 2023), as perturbation at the lower trophic level (primary productivity) by livestock overgrazing propagates to a higher trophic level with alternating positive and negative effects on population fitness. However, the mechanisms behind these regulatory population processes from top-down or bottom-up forces are still uncertain for top scavengers. For instance, seasonal changes in environmental conditions and wild prey availability in overgrazed ecosystems could collectively lead to changes in top scavengers' diet.

Livestock farming constitutes one of the most widespread human activities worldwide (Herrero et al., 2009; Reid et al., 2008). More importantly for our study context, the availability of livestock carcasses is a well-known source of food for avian top scavengers (Cabrera-García et al., 2020; Olea & Mateo-Tomás, 2009). As a side effect, livestock grazing can be detrimental to the ecosystem (Wolf et al., 2021) because very high grazing pressure (overgrazing) can negatively affect both biotic and abiotic factors (Cingolani et al., 2014; Neilly et al., 2016). The negative pressure exerted by domestic livestock on soil and vegetation has been widely acknowledged (Capó et al., 2022; Van De Koppel et al., 1997), as has the multitrophic effects that the presence of livestock entails (e.g. in birds, Barzan et al., 2021; in invertebrates, Davidson et al., 2017; Filazzola et al., 2020). Thus, livestock production with high herbivory pressure generates cascading effects on wild primary consumers, where loss of food resources and shelter can severely impact their populations (Cingolani et al., 2014). Consequently, a reduction in wild food availability would impact demographic parameters such as survival or the breeding success.

Breeding success is a key parameter to assess species fitness and population growth. This parameter is extremely important for endangered species because they usually have small population sizes and are confined to restricted areas (Lanfear et al 2014). Understanding the extrinsic and intrinsic factors that impact breeding success is crucial for species conservation. Among the intrinsic factors, age, sex and experience play a significant role in breeding success because these individual-level factors influence the effectiveness of parental care and, in turn, offspring survival (Klug & Bonsall, 2014). To comply with energy requirements, parents either forage to meet all the important elements for adequate growth or produce food (e.g., lactation in mammals) which is, in turn, also conditioned by foraging capacity. However, not every food resource is suitable or has the necessary nutritional values to ensure offspring survival (Jodice et al., 2006). Sometimes offspring need other nutrients that are not present in proper quantities in parents' usual diet (Catry et al., 2016; Margalida et al., 2009). Consequently, species often change or extend their diet during the breeding season (Salamolard & Weimerskirch, 1993) to either overcome the stress for parents to raise offspring or to feed their offspring with all the necessary nutrients (Catry et al., 2016; Saraux et al., 2011).

Climate is a key extrinsic factor that can negatively impact breeding success (Descamps et al. 2015; Halupka et al. 2023). It is well established that the synchronisation between species food requirements and food availability depends on climate conditions and seasonality (McKinnon et al., 2012). Any mismatch in these factors can disrupt breeding success because the temporal alignment between offspring food requirements and prey availability is lacking (Durant et al., 2007). In particular, climate can affect the density and distribution of prey species, which has implications for not only breeding success, but also for a population's survival and long-term viability (Muller et al., 2022). To overcome potential climate constrains to breeding success, a species' diet may present high plasticity. This allows switching to alternative prey when the preferred ones are scarce and, thus, allows parents to meet the feeding requirements of their offspring. Widening the dietary niche (i.e., increasing the diet diversity) is a well-described strategy for generalists' predators (Dell'Arte et al., 2007 and references therein). By increasing prey diversity in diet, they can buffer the negative consequences of poor preferred prey availability, hence, improving reproductive performance (Whitfield et al., 2009). For central-place foragers like seabirds and raptors, the ability to switch prey can be determinant for their reproductive performance. As they go back and forth to their nests to feed offspring, the availability of prey in the foraging area is decisive in terms of effort and energy (Boyd et al., 2014; Mills et al., 2020; Whitfield et al., 2009).

In recent years, wildlife's use of human food subsidies has been highlighted as a major threat to biodiversity (Newsome et al., 2015; Oro et al., 2013). Although there are many examples of successful populations that use human food subsidies from places like urban waste dumps (Evans & Gawlik, 2020; Kristan et al., 2004), evidence for detrimental consequences for wildlife is also ample (see a general review, Newsome et al., 2015; Rodewald et al., 2011). These resources are often predictable in both space and time, and of poorer quality, which makes them an ecological trap for those species that rely on them (Cortés-Avizanda et al., 2012). This is a particular concern for vulture populations because they are the most threatened functional guild in the world (Buechley & Şekercioğlu, 2016), and have greatly suffered those impacts and potential risks associated with feeding in inadequate places (McGrady et al., 2018; Plaza & Lambertucci, 2017) or on contaminated carcasses (Blanco et al., 2017, 2023). An example of this vulnerability is the "diclofenac crisis" (Green et al., 2004; Oaks et al., 2004), which resulted in the catastrophic death of over 95% of the vulture populations in Asia, caused by feeding on contaminated livestock treated with veterinary pharmaceuticals.

Here we apply long-term monitoring (2001-2020) of the endangered Canary Egyptian vulture (*Neophron percnopterus majorensis*) on the Fuerteventura Island (Canary Islands, Spain) to study the relative importance of ecosystem conditions and diet to breeding success (defined as the number of chicks reared per territory/year) in a context of changing livestock stocking rates over time. On Fuerteventura, goats were introduced around 500 BC (Cabrera, 1996). Numbers remained stable until the late 20th century, since they sharply rose until 2012 when cuts in Common Agricultural Policy (CAP) funds led the number of livestock to decline (see methods). The negative effects of livestock overgrazing on bird populations from the island have been related to habitat modification and the spread of diseases (Carrete et al., 2009; Illera, 2001). In a previous study (Fernández-Gómez et al., 2023), we accounted for a top-down effect of livestock on island vegetation (primary productivity) that influenced breeding success at the population level. In the present study, we downscaled to the territory level, i.e. the breeding success and diet of several reproductive pairs to bridge the knowledge gap about what environmental and dietary factors compromise the local-level number of chicks reared by the Canarian Egyptian vulture subspecies. Our main hypothesis was that breeding success would be positively related to the consumption of wild prey as tentatively suggested in previous studies (Fernández-Gómez et al., 2023; Margalida et al., 2012), albeit large availability of livestock carcasses. We also expected climate to indirectly affect breeding success by a cascading trophic effect on the vegetation, primary consumers and prey diversity found in nests. The large number of livestock for several years of our study period would negatively affect vegetation and have a negative effect on the primary consumers that depend on vegetation. Consequently, the diversity found in nests over the years with smaller amounts of livestock would be higher. Lastly, a positive relation between prey diversity and breeding success was expected.

2. Methods

2.1 Study area and field procedures:

This study was conducted on Fuerteventura (1,660 km^2), the south-eastern island of the Canary archipelago, located at 28°25′57″N 14°00′11″O. It is considered an arid landscape with annual mean precipitation of 105 mm. Its landscape is dominated mainly by bared soil, grasslands and scrubs, and woodland is practically absent (Rodríguez Delgado et al. 2000).

The Egyptian vulture (*Neophron percnopterus*) is a globally endangered long-lived scavenger (BirdLife International, 2022). It is a medium-sized (2-3 kg) monogamous species that generally breeds in holes in cliffs on open landscapes in semi-arid areas, and its clutch size is up to two eggs. Both parents lay eggs for approximately 42 days and chicks spend 70-90 days in nests before fledging (Cramp & Simmons, 1980; Kumar et al., 2020). Both sexes invest an equitative parental effort in food provisioning and nestling feeding (Morant Etxebarria et al., 2019). This species is widely distributed across South Europe and North Africa, the Middle East, Central Asia and India, and has numerous island populations (e.g., Balearic archipelago, Socotra and Masira in the Arabian Sea, Cape Verde and the Canarian archipelago in the East-Atlantic). The Canarian Egyptian vulture is an endemic subspecies to the Canarian archipelago, where its distribution was formerly wide. Currently, the population is restricted to the Fuerteventura and Lanzarote islands (Canary Islands), where the stronghold is on the Fuerteventura Island (over 90% of the population). The main causes of non-natural mortality that have contributed to its population decline are electrocutions or collisions with power lines, shooting and poisoning (Donázar, Palacios, et al., 2002; Gangoso et al., 2009). In order to palliate the decline of the species, two supplementary feeding stations were located in Fuerteventura Island (**Fig. 1**). The main supplementary feeding station located in the centre of the island is operative since 1998 and is mainly supplied by slaughterhouse remains (pigs) although sometimes some goats are dumped there. This supplementary feeding station has been provided with similar amounts of food during the study period (Badia-Boher et al. 2019). The most recent one is the northern one, that was created as an additional European-LIFE project measure in 2008 (Badia-Boher et al. 2019). This feeding station shows a much lower degree of use (van Overveld et al. 2018). Additionally, the island also has an Urban Waste Dump which is also rarely used (van Overveld et al. 2018).

The monitoring of this population has been carried out since 1998. Individuals have been marked with both plastic and metallic rings, with over 90% of the population being individually identifiable (Badia-Boher et al., 2019). We selected territories with at least 10 years of both breeding and diet data for our study period (from 2001-2020, n=20 years), which resulted in 15 territories (**Fig. 1**).

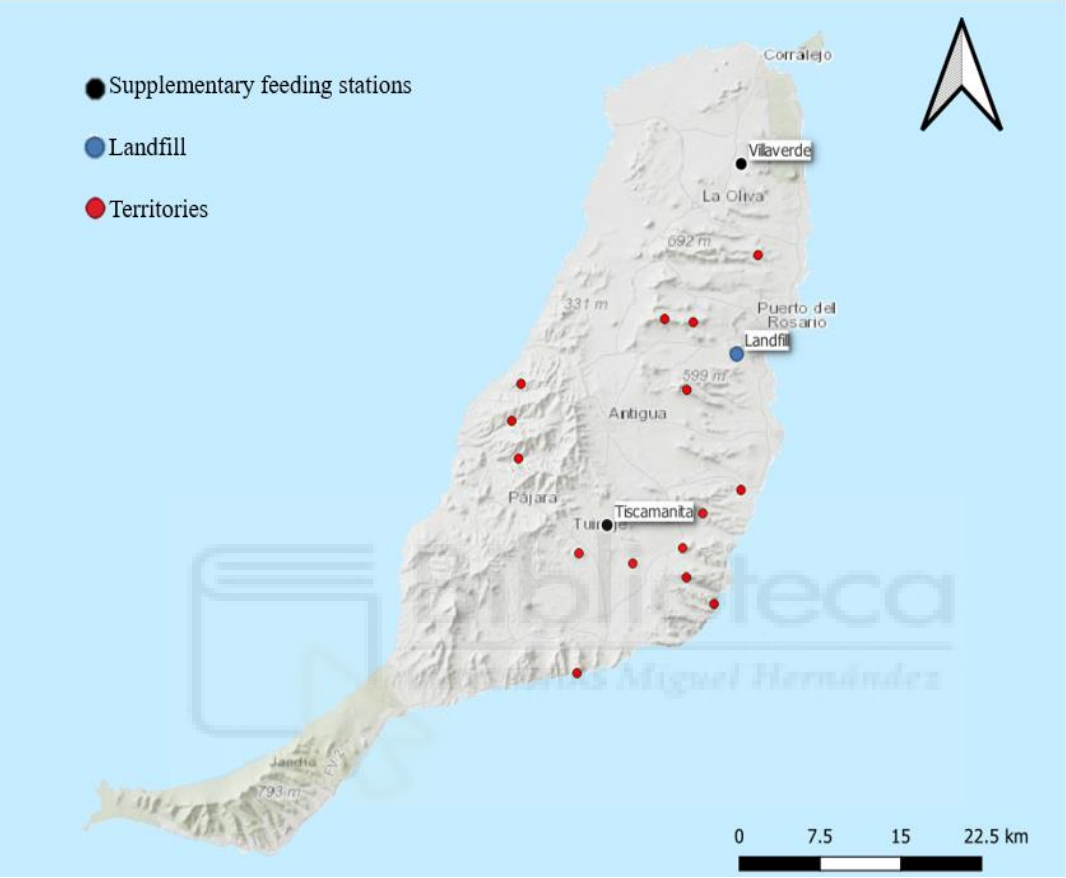

Fig. 1 Spatial distribution of the sampled territories of the Egyptian vulture located on the Fuerteventura Island. In black, the two supplementary feeding stations: Tiscamanita and Villaverde. Red dots represent the breeding territories (n=15). Blue dot represents the location of the landfill. The background map shows the digital elevation model.

Every year, nests were followed weekly from distance by using telescopes (20-60x) or binoculars (8-10x42) to identify breeding activity, such as mating, incubation and, ultimately, chick rearing. Nests were accessed to either mark chicks with plastic and metallic rings when chicks were around 50-60 days old. Prey remains were collected and identified in the nests during the ringing. In most cases, remains were identified to species level. The analysis of prey remains is a valid and widely used methodology to establish the relationship between diet and reproductive success, as has already been proven for this species (Cabrera-García et al., 2020; Hidalgo et al., 2005; Margalida et al., 2012). The remains corresponding to small and medium-sized vertebrates (excluding livestock) were counted to determine the minimum number of individuals (Hidalgo et al., 2005; Hoy et al., 2017; Lourenço et al., 2015). The number of recognisable pieces (bones, feathers, or skulls) was counted, and it was estimated whether they belonged to the same individual or not. For example, if we found two set of left dove wings and also other bones that indicate that could be three (such as 5 dove legs), then we would consider that at least three different doves were brought to the nest. The quantification for large prey remains (sheep and goats), differed. Each piece found was counted independently, i.e. if 5 pieces of goats were found in the nest, they were counted as 5 goats when calculating diversity. This does not imply that Egyptian vultures consumed 5 goats, but rather that when weighing their use of available food resources, 5 times they chose to consume goats, versus the rest of the smaller species on which they feed. This quantification method represents the selection of the food resource available at the moment of searching for it and carrying to the nest (Garcia-Heras et al., 2017). The Egyptian vulture feeds their chicks by carrying small pieces in the beak. While the small and medium-sized prey are usually brought to the nest entirely due to their small size, remains of larger prey such as livestock are taken piece by piece. Thus, as the large prey are carried in smaller pieces, the remains may or may not have attached bone to the muscle or skin. When consumed, these pieces may not leave any trace behind, thereby underestimating the contribution of large mammals to the diet (Donázar & Ceballos, 1988; Sánchez-Zapata et al., 2010). This potential bias, however, is the same for all the nests examined, so we did not expect any significant negative consequence in our analysis because we were still able to evaluate the relative importance of each remain category among nests.

2.2 Goat population trends:

Pre-European colonisers introduced goats (*Capra hircus*) at around 500 BC (Cabrera, 1996). Before that, it is believed that Canarian Egyptian vultures fed on seabirds and marine mammal carcasses (Gangoso et al., 2006a), which is a well-described food source for some coastal populations of New World vultures in South America (Lambertucci et al., 2018; Wallace & Temple, 1988). When the Europeans arrived, the number of goats was estimated at around 30,000-60,000 (18-36 goats per km^2, Cabrera 1996). It is also believed that Europeans maintained stable numbers (around 30,000) until the 20th century. The first accurate census (1970) estimated around 12,000 goats, and numbers steeply increased after this date (Gangoso et al., 2006a). In the past two decades, the number of goats has fluctuated (Fernández-Gómez et al., 2023, also see **Figure. 2**), with a special emphasis placed on the change noted between 2012 and 2013, when the number of goats dropped by over 50,000 heads.

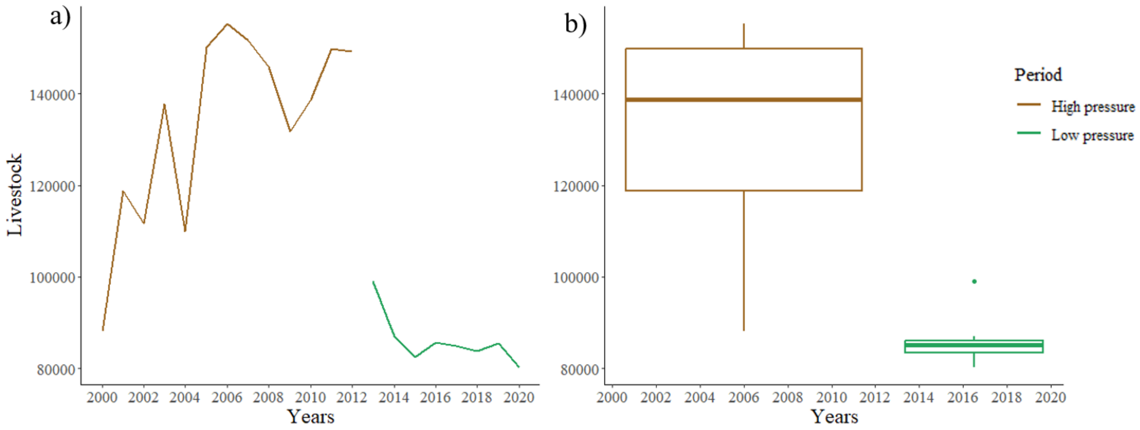

Fig. 2 a) Number of livestock (mainly goat) estimated for the Fuerteventura island during different time periods of herbivory pressure: "high pressure" represents the amount of livestock present during the period (2001-2012) and the "low pressure" period (2013-2021). b) Boxplot representing the median number of livestock per each time period, high and low pressure. Upper line from the box represent the third quartile and the bottom line of the box represents the first quartile. Vertical bars refer to the 95% CI interval, and the single dot on top the low pressure boxplot represent an outlier.

This change was attributed mainly to funding cuts from the CAP. Today the number of goats is around 85,000 heads (over 50 goats per km^2), but during the period with large numbers, there were up to 155,000 heads (100 heads per km^2). Many are kept on farms with variable degrees of freedom, but around 20,000 heads are not subject to economic exploitation, and live completely free in mountains areas with difficult access (Gangoso et al., 2006a). The negative effects from livestock to bird populations from the island have been previously described because livestock overgrazing has modified the habitat and promoted the spread of diseases (Carrete et al., 2009; Illera, 2001).

2.3 Statistical analyses:

To evaluate what factors drive vulture diet diversity and how their diet and environmental conditions affect breeding success, we used two sets of response variables: "*Diet diversity*" and "*Breeding success*". The "*Diet diversity*" response variable was calculated as the Shannon Index per territory and year (Spellerberg and Fellor, 2003), and was modelled as Linear Mixed-Effect model (LME). The "*Breeding success*" response variable was calculated as number of chicks reared per territory and year and was modelled as Generalised Linear Model (GLM) with Poisson error distribution and logit link function.

The explanatory variables are detailed in **Table 1**. The environmental variables were calculated each year based on a buffer of 4 km, which overlaps over 85% of the core area of the breeding individuals tagged on the island (Kernel Utilization Distribution, KUD50%, reference bandwidth =1500, the author´s unpublished data). We extracted the average *Temperature*, *NDVI* (Normalized Difference Vegetation Index) and the accumulation of *Precipitation* within the 4 km buffer for the semester corresponding to the breeding season (January to June). Shannon and Evenness Indices were calculated as detailed in Spelleberg and Fedor (2003). Livestock pressure data were collected from the Canary Institute of Statistics (ISTAC, 2024). In Fernández-Gómez et al (2023), we determined the period ranging from 2000 to 2012 as the *high-pressure* of *Herbivory* period, and the period from 2013 to 2021 as the *low-pressure* period. The *Number of Wild* and *Marine* prey were calculated by adding the amount of prey remains corresponding to wild species for the former, and from marine species for the latter. To establish the contribution of diet diversity and composition in the number of chicks reared for 15 territories of Egyptian vultures over 20 monitoring years, we separately analysed the diet and breeding data. These two analyses allowed us to firstly disentangle which factors drove the diet diversity found in nests, and then in a second step, to introduce diet diversity as an explanatory variable in the second set of models corresponding to breeding success.

Variables were checked to avoid collinearity, excluding those with a Spearman correlation coefficient > |0.5|. No correlations exceeding |0.5| were identified among the groups of variables. The *dredge* function was used for model building. Model ranking was based on AICc criteria (Akaike´s Information Criterion corrected for small sample sizes, (Sugiura, 1978), and averaging was done with those top-ranked models within ΔAICc < 2 (Symonds & Moussalli, 2011). The R statistical software, version 3.4.0, with the stats package was used for estimating confidence intervals, lme4 (Bates et al., 2015) for LME analyses, AICcmodavg for model ranking and averaging (Mazerolle, 2013), and the MuMIn package (K. Barton, 2019) for GLM modelling.

Table 1: Explanatory variables used to describe those factors that drive the diet diversity and breeding success of Canary Egyptian vultures.

Category	Variable	Nomenclature	Description	References/ Source
Dietary	H Shannon – Wiener Index	*Diversity* $^{a, b}$	It quantifies specific diversity by considering not only the number of different species, but also how many prey items per species are found.	(Spellerberg & Fedor, 2003)
	J Evenness from the Shannon – Wiener Index	*Evenness* ^{b}	A homogeneity index associated with the H Shannon - Wiener Index, with 1 if all the species have an equal probability of appearing in the territory.	(Spellerberg & Fedor, 2003)
	Number of wild prey	*Wild* $^{a, b}$	Number of wild species found per year and territory.	(Margalida et al., 2012)
	Number of marine prey	*Marine* ^{b}	Number of marine species found per year and territory.	(Gangoso et al., 2006a)
	Livestock pressure	*Pressure* $^{a, b}$	Before and after the drastic decline in livestock numbers, corresponding to a first period (2001-2012) with high grazing pressure, and second period from	Source: https://www.gobiernodecanarias.org/istac/, (Fernández-Gómez et al., 2023), see **Figure 1**.

			2013 to 2020, with low grazing pressure.	
Environmental	Temperature	*Temperature* [a, b]	The mean temperature corresponding to the breeding season (January to June, n=6 months).	Data source: NOAA (National Oceanic and Atmospheric Administration, https://www.ncei.noaa.gov/)
	Precipitation	*Precipitation* [a, b]	The mean precipitation corresponding to the breeding season (January to June, n=6 months).	Data source: CHIRPS (Climate Hazard group InfraRed Precipitation with Station data, https://www.chc.ucsb.edu/data/chirps)
	Normalised Difference Vegetation Index	*NDVI* [a, b]	The mean NDVI (Normalised Difference Vegetation Index), corresponding to the breeding season (January to June, n=6 months).	Data source: MODIS satellite data (Moderate-Resolution Imaging Spectroradiometer, https://modis.gsfc.nasa.gov/data/dataprod/mod13.php)

a) Diet diversity response variable b) Breeding success response variable

3. Results

Between 2001 and 2020 (n=20 years), the 15 monitored pairs bred 182 chicks. During this study period, 3,787 prey items were identified in the nests belonging to at least 37 different species (30 identified at the species level, plus seven at the genre level), and probably more because 5.25% were impossible to determine (**Table 2**). The average amount of prey per territory was 18.84 prey items (sd ± 19.32). Of the total amount of identified prey, the dominant prey species were doves (*Columba livia,* 25.14%), followed by goat (24.72%) and rabbit (*Oryctolagus cuniculus,* 19.59%) remains, which accounted for 69.45% of the total amount of the found prey remains. Overall, prey was wild (61.5%), terrestrial (96.2%) and exotic (90%) as opposed to domestic, marine and native. Interestingly, over the years the percentage of diet corresponding to the classification of being either wild and native has increased, especially during the low herbivory pressure period (2013-2020) (Supplementary Material, **Fig. S1.1** and **S1.2**).

Table 2: Prey items found per groups and the percentage of each species per total amount of items counted during our study period for the 15 sampled territories.

Groups	Species	Remains (%)	Number of prey
Mammalia	*Capra hircus*	24.72	940
	Oryctolagus cuniculus	19.59	745
	Sus scrofa domestica	3.68	140
	Atelerix algirus	2.32	89
	Felis catus	1.71	65
	Atlantoxerus getulus	1.37	52
	Viscera	1.26	48
	Ovis orientalis aries	1	38
	Canis familiaris	0.63	24
	Rattus sp	0.26	10
	Undetermined mammals	0.32	12
Aves	*Columba livia*	25.14	956
	Gallus gallus domesticus	7.02	267
	Undetermined avian	2.37	90
	Upupa epops	1.13	43
	Larus sp	0.82	32
	Streptopelia sp	0.74	28
	Corvux corax	0.45	17
	Burhinus oedicnemus	0.42	16
	Procellariidae	0.37	14
	Lanius excubitor	0.34	13
	Alectoris rufa	0.26	10
	Pterocles orientalis	0.19	7
	Anas platyrhynchos domesticus	0.13	5
	Falco tinnunculus	0.11	4
	Apus apus	0.08	3
	Passer domesticus	0.05	2
	Coturnix coturnix	0.05	2
	Alectoris barbara	0.05	2
	Cursorius cursor	0.03	1
	Hydrobatidae	0.03	1
	Tyto alba	0.03	1
	Neophron percnopterus	0.03	1
	Apus unicolor	0.03	1
Fishes	Undetermined species	1.71	65
	Muraena augusti	0.42	16
	Stephanolepis hispidus	0.08	3
Mollusca	*Sepia sp*	0.13	5
	Octopus vulgaris	0.05	2
	Teuthida sp	0.05	2
Reptiles	*Gallotia stehlini*	0.16	6
Others	Human food	0.24	9
	Undetermined feces	0.19	7
	Canis familiaris feces	0.16	6
	Capra hircus feces	0.08	3

The averaged model for the "*Diet diversity*" response variable resulted in a positive relation between the *Diversity* of the diet measured as the Shannon Index and the *Number of wild prey* in nests, as well as with the period with *Low pressure* of grazing, i.e., those years with a smaller amount of livestock present (**Table 3**).

Table 3: Results of the model averaged to disentangle the factors that shape diet diversity in the 15 territories of Egyptian vulture. *Low pressure* refers to the period with a few livestock present on the island. *Wild* is the number of wild prey found in nests. *Precipitation* refers to the cumulative precipitation for the breeding season. Std. Error stands for Standard Error, CI for Confidence Interval. See Table 1 for a complete description of the explanatory variables. In bold, those parameters that do not overlap zero.

Parameters	Estimate	Std. Error	2.5%CI-	97.5%CI
Intercept	**1.379**	**0.035**	**1.311**	**1.447**
Low pressure	**0.271**	**0.063**	**0.147**	**0.395**
Wild	**0.092**	**0.029**	**0.034**	**0.149**
Low pressure:Wild	**0.289**	**0.103**	**0.085**	**0.492**
Precipitation	-0.016	0.028	-0.071	0.038

This indicates that during those years with fewer livestock present on the island, the diet diversity found in nests was higher for the years with more wild prey (**Fig. 3**).

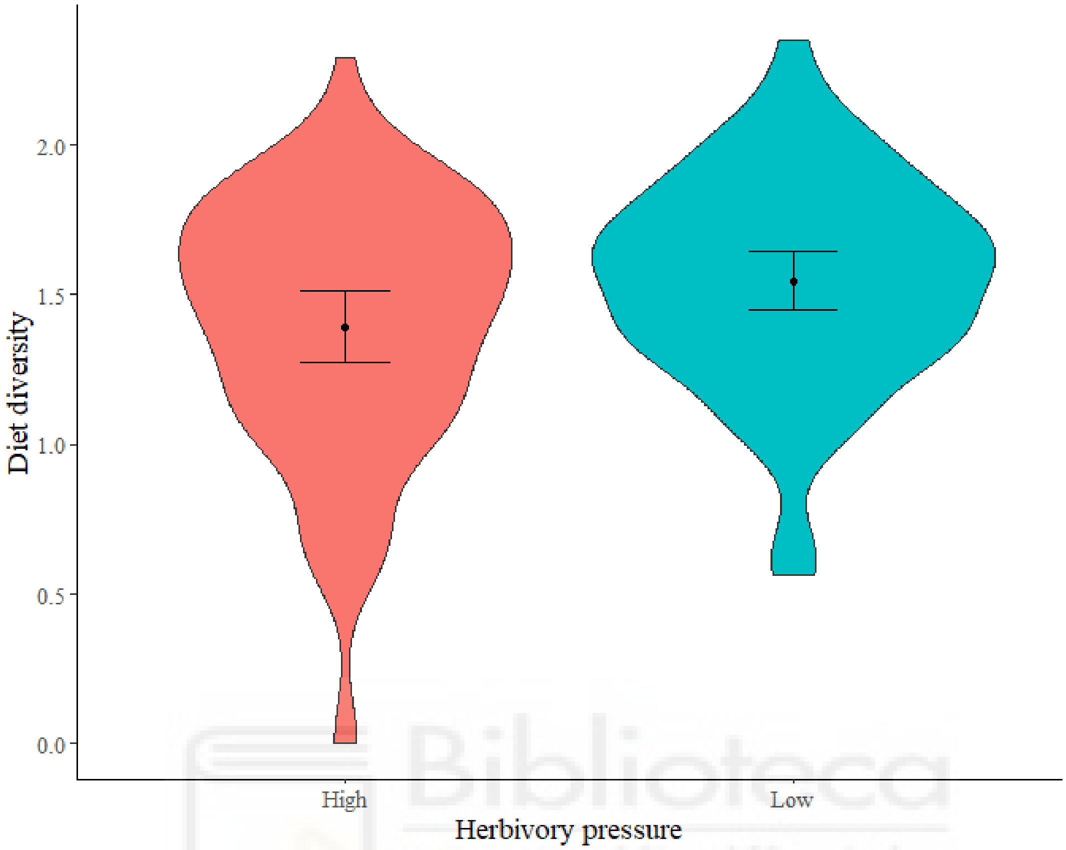

Fig. 3 Average and standard deviation of the diet diversity of the sampled 15 territories of Egyptian vulture across the different studied herbivory pressures. The "High herbivory pressure" period corresponds to 2001-2012 and the "Low herbivory pressure" period to 2013-2021. Black dots represent the average diet diversity measured as the Shannon index per periods. Bars depict the standard deviation.

The *Number of wild prey* and *Low pressure* interaction was also significant, which indicated that for those years with a small amount of livestock, diversity would be higher if there were a larger number of wild prey present in nests. None of the climate variables explained temporal changes in diet diversity.

The averaged model for the "*Breeding success*" response variable resulted in a single model (**Table 4**), which indicates that *Number of wild prey* and the period with *Low pressure* for grazing had a positive relation with the number of raised chicks, with a slight positive relation with weak statistical support between diet diversity and breeding success.

Table 4: Results of the model averaged to disentangle the factors that shape the breeding success of the Egyptian vulture. *Low pressure* refers to the period with a few livestock present on the island. *Wild* is the number of wild prey found in nests. *Precipitation* refers to the cumulative precipitation for the breeding season. *NDVI* is the average of the Normalised Difference Vegetation Index for the breeding season. *Marine* is the number of marine prey

found in nests. *Diversity* is diet diversity, calculated as Shannon Index. Std. Error stands for Standard Error, CI for Confidence Interval. See Table 1 for a complete description of explanatory variables. In bold, those parameters that do not overlap zero.

Parameters	**Estimate**	**Std. Error**	**2.5%CI**	**97.5%CI**
Intercept	**-0.273**	**0.105**	**-0.480**	**-0.065**
Low pressure	**0.372**	**0.164**	**0.048**	**0.695**
Diversity	0.156	0.086	-0.013	0.325
Wild	**0.144**	**0.070**	**0.007**	**0.282**
Marine	-0.052	0.074	-0.199	0.094
Precipitation	0.053	0.075	-0.095	0.201
NDVI	0.033	0.073	-0.111	0.176

This indicates that breeding success was higher for those years with fewer livestock present on the island. Additionally, those nests with a larger amount of wild prey had higher breeding success (**Fig. 4**).

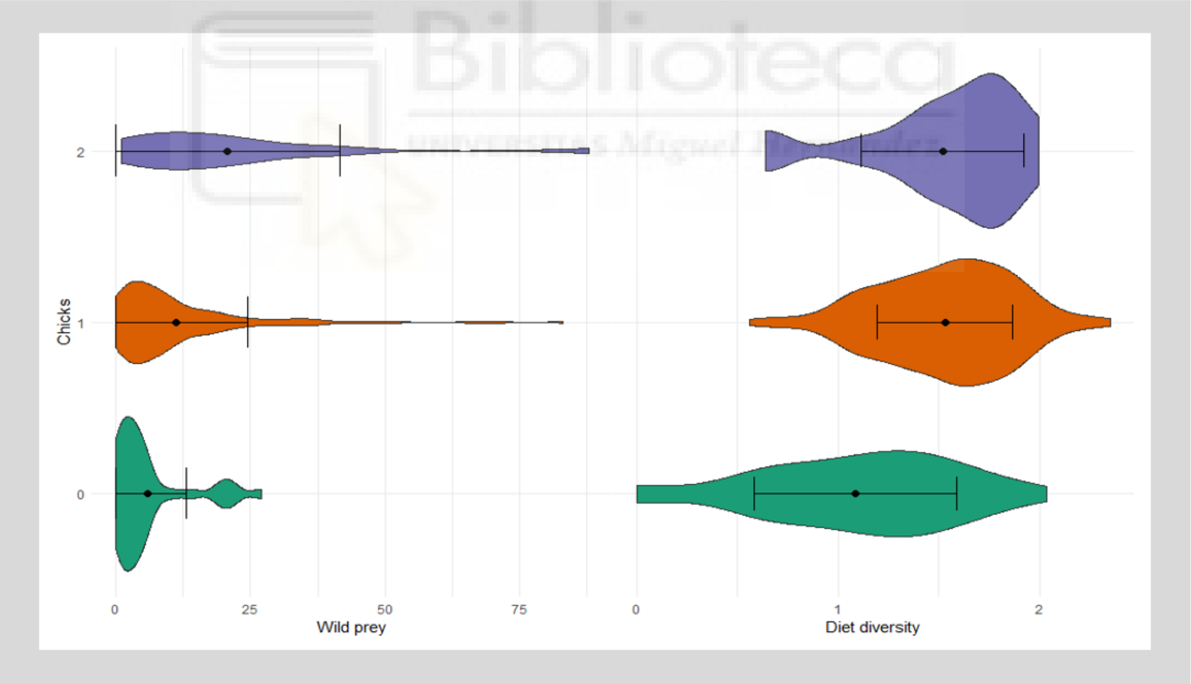

Fig. 4 Average and standard deviation of wild prey and diet diversity per number of chicks present in nests for the 15 sampled territories of Egyptian vulture**.** Black dots represent the average wild prey and diet diversity per each number of chicks in the nests. Error bars depict the standard deviation.

4. Discussion

Our study reveals cascading effects of livestock production on the diet and fitness (breeding success) of the Egyptian vulture. In particular, we first described how overgrazing affected diet diversity, which consequently conditioned breeding success at a local-level scale; i.e. territories. Together, these results suggest a cascading effect from livestock, vegetation and primary consumers to a top avian scavenger, with controversial consequences of livestock production to the conservation of avian scavengers. This is a significant finding because, typically, processes like top-down and bottom-up are usually associated with interactions between two consecutive trophic levels and rarely are used to indicate conservation strategies. However, very few studies (but see Coulson et al., 2011; Donázar et al., 2020) have explored the network of cascading effects across multiple trophic levels, including a top avian scavenger, which makes the present research particularly relevant.

We found a positive correlation between breeding success and the amount of wild prey found in nests. This association aligns with prior research reported by several authors, who have suggested the significance of wild prey for this species' diet, linked with body mass fluctuations of individuals (both adults and immatures) (Donázar et al., 2020), and breeding performance (Margalida et al., 2012). Other studies have highlighted the qualitative importance of food remains for breeding success (productivity) (Margalida et al., 2009).This study contributes further evidence that this species' breeding success is linked with the consumption of wild prey. The qualitative importance of wild prey is underscored by the fact that small-sized animal remains supply essential micronutrients that are present to a much lesser extent in the soft tissues of domestic ungulates (Houston, 1978; Reynolds & Perrins, 2010). Additionally, small animals are usually consumed whole, which provides certain elements like calcium, which is necessary for the bone mineralisation of chicks (Houston, 1978). Consequently, a decline in wild prey species availability would not only decrease this species' diet diversity, but could also have adverse repercussions on its reproductive outcome.

Declining grazing pressure also enhances breeding success. The relation between livestock and the Egyptian vulture has been addressed by several studies. For some populations, the tight positive relation between this species and the presence of livestock has been described because it provides a stable food resource (Cabrera-García, 2020). However, for other populations (e.g., the Balkans), the livestock carrion placed at supplementary feeding stations has proved inefficient to increase productivity and survival (Oppel et al., 2016). Furthermore, the number of livestock negatively affects the body mass of the study population through negative cascading effects between vegetation and primary consumers. Donázar et al. 2020 described how increases in annual oscillations of primary productivity (i.e. high coefficient of variation of annual values of NDVI) were associated with higher body mass of this population of Egyptian vulture. The authors hypothesize that high annual oscillation in primary productivity, driven by grazing and climate, would increase the mortality of wild primary consumers and consequently provide higher carrion availability in the ecosystem. As the vulture's body mass was negatively correlated with the amount of livestock, that would indicate that livestock affects the primary productivity and therefore the vulture's body mass acquisition

On the Fuerteventura Island, farming is currently shifting from a mainly extensive regime to semi-intensive and intensive facilities (García-Alfonso et al., 2020). Goats represent one of the most man-introduced species on the island, mostly because of their resistance and adaptability to thrive in harsh environments (Silanikove, 2000). The negative consequences that this species exerts on vegetation, especially on insular ecosystems, have been widely described (Campbell & Donlan, 2005; Coblentz, 1978). Another of the main negative impacts of man-introduced species is alterations of trophic chains. The impacts of introduced species on raptors' diet and its repercussions on trophic chains are a subject of recent interest in ecology (Speziale & Lambertucci, 2013). Although our study population presented a wide diet spectrum that comprised at least 37 species, the main prey species were domestic dove, goat and rabbit, which accounted for 69.45% of diet none of which are native to the Canary Islands. Doves were the most common prey (25.14%), followed by goat (24.7%). Doves are abundant on the Island of Fuerteventura. Consequently, the Egyptian Vulture would be taking advantage of a resource that is widely spread across the island.

Our results suggest that diet diversity is positively related to the amount of wild prey remains found in nests, especially during periods with low herbivory pressure. Also, the territories with more wild prey remains bred more chicks. However, a possible bias towards territories with zero chicks must be considered. If territory failure occurs in an early stage, parents stop feeding. Hence there is a possibility of those territories having intrinsically fewer prey than those with one chick or two. However, as shown in **Fig. 4**, for those territories with zero raised chicks, the distribution of diet diversity occupies the whole range of the X axis, which proves that failures also occur in late breeding season stages.

The fact that diet was more diverse when the number of livestock was lower can be a response to higher prey availability in the surroundings of nests. When prey abundance and availability data are lacking, this can be quantified by assessing the remains collected in nests (Amar et al., 2003; Garcia-Heras et al., 2017; Leckie et al., 2008). Also, it can be argued that the increased presence of wild species remains in nests is an adaptive response to reduced livestock availability. If livestock were the preferred prey and the consumption of wild prey were a compensative measure, breeding success would be lower for those years with lower livestock numbers. Our present scenario is the opposite: breeding success was higher during the period with lower grazing pressure, i.e., when the number of livestock decreased. When grazing pressure dropped (from 100 to 50 goats/km^2), vegetation partially recovered (indicated by an increase in the NDVI, Fernández-Gómez et al., 2023), as presumably did the primary consumers population, which relies on this vegetation either for shelter or consuming. Livestock overgrazing is known to compromise the presence and abundance of wild herbivores (Filazzola et al., 2020; Marino & Rodríguez, 2022) in a series of consecutive cascading trophic processes.

Other time-related effects that may cause higher breeding success during the low-pressure period must also be considered. Following Badia-Boher et al. (2019), adult survival has improved since the implementation of the LIFE European project (2004-2008, LIFE04NAT/E/000067). For long-lived species, adult mortality is one of the most sensitive parameters, determining population trends as well as reproductive performance (Sæther & Bakke, 2000b). In the present scenario, it could be argued that the improvement in survival affected positively to the breeding success, since parental loss is known to impact negatively the breeding success (Kokko, 1999).

4.1 Conservation implications:

Our study has proved that scavengers heavily rely on natural ecosystem dynamics because both the diet and breeding success of this population of Egyptian vultures were conditioned by cascading trophic processes linking livestock, vegetation and primary consumers. These cascading effects are often overlooked in conservation programmes, which can ultimately have negative implications for the conservation of endangered species if they are not accounted for. This is especially relevant for scavengers because providing livestock carcasses at supplementary feeding stations is a common tool to palliate the decline of their populations (Cortés-Avizanda et al., 2010; Moreno-Opo, Trujillano, Arredondo, et al., 2015). Thus, it is easy to misinterpret that increased livestock presence is always beneficial for vulture populations.

The challenging relationship between this Egyptian vulture population and livestock production has been previously discussed by other authors (Gangoso et al., 2006). Livestock overgrazing has strong negative effects on the plant community, soil and primary consumers that ultimately, as this study reveals, compromises this population’s breeding success. But livestock remains account for almost 25% of the vulture´s diet and are also a key food resource for not only this species, but also for other Canarian subspecies of facultative scavengers such as the raven (*Corvus corax canariensis*) and the buzzard (*Buteo buteo insularum*) (Gangoso et al., 2006a). Therefore, although livestock must be managed to avoid reaching high densities because of the negative effects described in this study, it must be done carefully. At present, livestock farming constitutes the livelihood of a large fraction of the islanders (Castro et al., 2018), so considering livestock reductions in stocking rates can be difficult to achieve. This subject needs further research to fully disentangle how to proceed with livestock management on the island because livestock is currently producing contradictory outcomes for this species. On one hand, the livestock is affecting the vegetation and the primary consumers, therefore affecting the reproductive outcome of an endangered species, but in the other hand, livestock constitutes a large fraction of the diet of this and other species, in addition to support economically to many people in the island. Overall, future conservation programmes of scavengers must take into account these indirect cascading relations, especially in fragile insular ecosystems.

5. Statements and declarations

5.1 Funding

J.A. Donázar, T. Sánchez-Zapata and L. Fernández-Gómez were supported by the TRASCAR project (RTI2018-099609-B-C21) from the Spanish Ministry of Science and Innovation. T. Sánchez-Zapata and L. Fernández-Gómez by the European Regional Development Fund and DIGITALPAST (TED2021-130005B-C21) from the Spanish Ministry of Science and Innovation, NextGeneration EU. This study also forms part of the AGROALNEXT (2022/038) programme. It was supported by MCIN with funding from European Union NextGenerationEU (PRTR-C17.I1) and by the Generalitat Valenciana. J. M. Barbosa was supported by the Generalitat Valenciana (CIDEGENT/ 2020/030).

5.2 Competing interests

The authors have no relevant financial or non-financial interest to disclose.

6. Acknowledgements

Population monitoring was done by J. Roldan, J.A. Sarrion, W. Moreno, J. Ramírez, S. Sierra, C. Díez, M. Mallo, R. Agudo, A. Trujillano, and C. J. Palacios. O. Ceballos, F. Hiraldo, A. Sanz-Aguilar, A. Cortés- Avizanda, V. Saravia, K. Heissenberger, M.-S. García- Heras, M. A. Cabrera and F. Rodríguez also helped with the fieldwork. The Consejería de Agricultura, Ganadería, Pesca y Aguas del Gobierno de Canarias provided data on livestock numbers. J.A. Donázar, T. Sánchez-Zapata, J. M. Barbosa and L. Fernández-Gómez were supported by the TRASCAR project (RTI2018-099609-B-C21 from the Spanish Ministry of Science and Innovation and the European Regional Development Fund) and DIGITALPAST project (TED2021-130005B-C21 from the Spanish Ministry of Science and Innovation and NextGeneration EU). This study also forms part of the AGROALNEXT (2022/038) programme with founds from European Union NextGenerationEU (PRTR-C17.I1) and Generalitat Valenciana. J. M. Barbosa was supported by the Generalitat Valenciana (CIDEGENT/ 2020/030).

CHAPTER III

Riders on the storm? Saharan dust disrupts movement patterns of an endangered top scavenger.

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Abstract

The effects of extreme climate events, such as heat waves, hurricanes and floods, on vertebrates have been paid significantly more attention, but dust storms remain poorly studied. This scenario limits our understanding of their impact on fauna and ecosystems. Using GPS data from 70 vultures for 2,555 days (2015-2021), we examined how Canarian Egyptian vultures (*Neophron percnopterus majorensis*) cope with recurrent dust storms from the Sahara Desert. We identified 63 dust storm events during the study period. Vultures daily movement (meters) reduced as dust concentrations in the atmosphere rose, with a steeper decline for males. Daily vulture movement decreased by 13.37% from the pre-storm to the storm period, but increased by 19.47% from the storm to the post-storm period. Subadults moved less than adults when dust storms occurred. We hypothesised that vultures' activity reduces during dust storms to mitigate adverse conditions, such as poor visibility, extreme heat and low humidity. This is the first long-term study linking animal movement to recurrent dust storms, which permits us to highlight the potential impacts of dust storms on non-migratory birds. As climate change progresses, understanding the effects of extreme climatic events on wildlife behavioural patterns is crucial to make future science-based conservation decisions.

Keywords: adaptive behaviour; sandstorms; scavengers, movement ecology, climate change

1.Introduction

There is a growing consensus that unusual climate patterns are causing widespread adverse effects on nature and humans (IPCC, 2012). The existing literature predominantly highlights the need to know the effects of steady climate changes on ecosystems or the economy, such as evaluating how rising average temperatures determine sea level, ecosystem productivity or species reproduction, rather than delving into the consequences of extreme and abnormal climate conditions (Vasseur et al., 2014). Indeed, extreme weather events will become more frequent and intenser (Ummenhofer & Meehl, 2017), with relevant consequences for the biota (Vasseur et al., 2014). The study of extreme climate events (ECEs) is a novel subject of interest in ecology that deserves scientific research and includes long-term monitoring (Van de Pol et al., 2017). In fact, the literature on ECEs has been pointed out to be biased towards short-term studies, which focus mostly on the effects of a single event (Bailey & van de Pol, 2016), such as extreme drought or volcano eruption, with consequences on plants as the most studied topic (Maxwell et al., 2019).

Of ECEs, much more attention has been paid to heat waves, hurricanes, floods and droughts than to other recurrent climate events like dust storms (Van de Pol et al., 2017). Dust storms (or sandstorms) are a meteorological phenomenon associated with the erosion, transport and deposition of dust and soil particles in the atmosphere by strong wind currents (Ghosh & Pal, 2014). From all the different sources of dust to the atmosphere, such as the Aral Sea, the Gobi Desert in Asia or the Lake Eyre Basin in Australia, the largest source of dust on Earth originates in the Sahara Desert, specifically in the Bodélé Depression in Chad (Goudie & Middleton, 2001; Middleton, 2017). Occurrence of dust storms has dramatically increased worldwide since the 1950s (Goudie & Middleton, 2001). Some studies affirm that recurrence of these events will increase in the forthcoming decades in the current climate scenario (Niang et al., 2008). Other studies conducted on the Canary Islands state that these events are less frequent for the study period, from 1980 to 2022 ((Suárez-Molina et al., 2024).

Dust deposition from the Sahara Desert is of the utmost importance for ecosystem functioning in many biomes worldwide. For instance, Saharan dust is the source of 30-40% of atmospherically delivered phosphorus, is the main source of iron in the Mediterranean Sea, and determines 15-70% of new primary productivity in the southeast Mediterranean (Guieu et al., 2002; Herut et al., 2002). The continental-scale transport of Sahara dust also plays a key role in the productivity patterns and functioning of the Amazonian rainforest (Kok et al., 2021; Koren et al., 2006) because

Saharan dust changes soil phosphorus availability, and even drives cloud formation and precipitation cycles in this region (Prenni et al., 2009). Nevertheless, profounder knowledge about how this ECEs type affects organisms from higher trophic levels, particularly vertebrates, is still lacking.

Under adverse environmental conditions, animal species can possess different behavioural mechanisms to cope with unpredictable weather conditions. One of the commonest responses is avoidance; i.e., leaving an area either temporarily or permanently as an immediate response to an extreme weather condition or as a reaction to posterior consequences of the event (Naveda-Rodríguez & Rush, 2023; Weimerskirch & Prudor, 2019). Other animal responses include staying and enduring extreme weather under harsh conditions by completely receding or waiting until the after effects of the ECE disappear (Burger, 1982). In this last scenario, one of the behavioural responses is decreased animal movement as a response to adverse weather. This response is defined as "allostatic overload", during which those conditions generated during ECEs trigger an emergency response and individuals cease their regular activities in an attempt to survive extreme conditions (Wingfield et al., 2017).

Taking advantage of the monitoring of 70 Canarian Egyptian vultures (*Neophron percnopterus majorensis*) tagged with GPS trackers over 7 years, we evaluated how an islander vulture population tackles recurrent dust storms from the Sahara. Our main hypothesis is that vultures reduce their daily activity during dust storms to cope with adverse weather conditions (poor visibility, extreme heat, low humidity). This response is also mediated by individual level responses, such as sex or age, as movement differences between sexes has been previously described (van Overveld et al., 2018). The results from this study shed light on how vertebrates cope with these understudied ECEs, and may allow future science-based conservation decisions to be made.

2. Methods

2.1 Study area and target population

The Canarian Egyptian vulture is a sedentary, endemic subspecies to the Canarian archipelago, Spain (between 27º37′ and 29º25N′, 13º20′ and 18º10′ W). It generally breeds in cliff cavities and forages on the semi-arid landscapes dominated by bare soils, grasslands and scrublands (Rodríguez Delgado, O., García Gallo & Reyes Betancort, 2000a). Once it was widely spread throughout the entire archipelago, but its population steeply declined in the late 20th century, mainly due to non-natural mortality like indirect poisoning or accidents with power lines

(Donázar, Palacios, et al., 2002). It currently survives only on the two easternmost Canary Islands (Fuerteventura and Lanzarote), with the bulk of its population (> 90%) on the former. Its population is increasing thanks to long-term conservation programmes (Badia-Boher et al., 2019a) and this population has been monitored since 1998. Extensive fieldwork (ringing of nestlings and trapping of adults) has currently allowed over 90% of its population to be individually identifiable (Badia-Boher et al., 2019a).

Egyptian vultures are obligate scavengers that scavenge a wide range of prey, from domestic livestock carcasses to wild small-sized animals that can either prey or be scavenged on (Margalida et al., 2012). On Fuerteventura, domestic carcasses are readily available at two supplementary feeding stations (van Overveld et al., 2018). Home range sizes vary from 50 km^2 to over 600 km^2 depending on social rank, sex and age (van Overveld et al., 2018). Individuals are also known to forage on the goat farms scattered across the island, and to gather on the urban waste facility located in the middle of the island (Donázar, Palacios, et al., 2002; García-Alfonso et al., 2020).

2.2 GPS tracking

From June 2013 to July 2021, 70 adults (30 males, 40 females) were trapped with cannon nets and tagged with solar-powered GPS transmitters. Individuals were genetically sexed, and their age was known because they were either individually tagged in nests when they were chicks or were dated when trapped for moult characteristics (Forsman, 1998). Two types of devices were used: 29 individuals were equipped with UvA-BiTS (https://www.uva-bits.nl/ Amsterdam, the Netherlands), 40 with E-obs (GmbH, https://e-obs.de/, Munich, Germany), and one individual was tagged with both devices during the study period. Both device brands have multiple sensors to measure altitude, speed and geographical coordinates according to a defined time interval (see below). Devices were attached as backpacks using a 0.84- and 1.12-cm wide Teflon harness. The total harnessing system weighed between 31 g (UvA-BiTS) and 54 g (E-obs), constituting 1.4-2.4% of the mean body mass of this species (Sergio et al., 2015). We used GPS data from 1 January 2015 to 31 December 2021 (2,555 days) because the GPS settings for the individuals tagged in 2013 to 2015 were programmed to collect data over much wider time intervals, and because it was impossible to compare the data from the first year and a half to the rest of the study period. All the devices applied during our study period were programmed with time intervals lasting between 1 and 5 min.

2.3 Dust data collection and processing.

Dust surface concentration data were downloaded from the WMO - Barcelona Dust Regional Centre (WMO SDS-WAS Regional Centre for Northern Africa, Middle East and Europe, https://dust.aemet.es/). We downloaded the daily data corresponding to our study period from the MULTI-MODEL forecasting model (Terradellas et al., 2022) available online. We processed the data with the Max-Planck operators CDO (Climate Data Operators, (Schulzweida, 2023)), which is a collection of command line operators to manipulate and analyse climate data. The MULTI-MODEL contains several parameters for dust data on a raster layer. We selected the "*Concentration*" parameter, which corresponds to the dust concentration at the surface level. Each daily file contains a record for every 3 h, and includes the corresponding day data and a forecast for the next 3 days. We selected only the records from the day of interest. Then we averaged records to, thus, obtain a single dust surface concentration per day in a grid (0.5º x 0.5º). Afterwards, we selected the pixels corresponding to the Fuerteventura Island and averaged them. The resultant data consisted in a single daily dust surface concentration for the Fuerteventura Island. We created the variable dust surface concentration (*Dust conc.,* kg/m^3) to test the raw effect of the dust concentration on vultures' movement.

Following the IPCC (Intergovernmental Panel on Climate Change) definition of an ECE as being whatever the value is that is near the upper (or lower) end of the range of the observed values (usually 5% or 10%), we took each day as *Dust Storm,* or not, accordingly. Therefore, the days with a dust surface concentration over 6.80×10^{-8} kg/m^3 (10% of the upper end of the range of dust observed for our study period) were considered to be *Dust Storm* days. When there were more than two consecutive days with these high concentrations, we considered all the consecutives days to be a *Dust Storm* event. When two *Dust Storm* days were separated by one day, we considered the three of them to be a single event because, although the concentration lowered on the day in between, it belonged to the same weather perturbation. Therefore, we created variable dust storm events (*Events*) as a categorical variable with three levels: (1) *Dust Storm,* day or days with a high concentration of dust at the surface level ($> 6.80 \times 10^{-8}$ kg/m^3); (2) from the first day of each *Dust Storm* event, we categorised the 10 days before as *Prev*.; (3) when the *Prev* period overlapped a *Dust Storm*, we selected instead the 10 days after the last day of the event as *Post*. Hence, we used a *Prev* or alternatively a *Post* period for each *Dust storm* event. We considered this time interval (10 days) because this would allow us to account for similarities in movement behaviour associated with the season or the climate conditions surrounding *Dust storm* events. This period was long enough to dilute the effects of the gradual rise or drop in the dust concentration on the days close to the *Dust storm* days. Therefore, the *Events* variable was composed of the day or consecutive days with high dust concentrations (*Dust storm*), the 10 days prior (*Prev*) and for those events that were less than 10 days apart (did not allow this to be established 10 days before) on the 10 days after (*Post*).

2.4 Statistical analyses and modelling

In order to evaluate how dust storms affected the long-term movement patterns of our focal species, we used Linear Mixed Models (LMM) and two separate modelling procedures depending on the included dust-related fixed explanatory variable (*Dust conc.* or *Events*). In both cases, the response variable was an estimate of daily movement based on GPS data. To standardise all the individuals across the different settings, we resampled all the fixes (i.e., GPS positions) to 30 min with a tolerance of 5 min (García-Alfonso et al., 2021). To standardise the data for calculating cumulative distance, the days with fewer than 20 fixes per day were discarded. Those individuals with fewer than 30 days of data for our study period were discarded (n=2 individuals). The fixes corresponding to night were also discarded, where night was understood as those fixes from dusk to dawn. Additionally, the days with over 4 hours of gap between fixes were discarded. Then we calculated the distance between the consecutives fixes per individual. Finally, we used the cumulative distance per day and individual as the response variable (*Daily distance*).

For both modelling procedures, we considered three other fixed explanatory variables: i) *Duration*: number of days that each dust storm event lasted, with 0 for the days with a dust concentration below 6.80×10^{-8} kg/m^3, 1 for the first day of the event, 2 for the second consecutive day, and so on; ii) *Sex* of each individual, *Male* or *Female*; iii) *Age* of each individual by considering two categories: *Subadults* (up to 5 years) and *Adults* (6 years or more, (Donázar, Palacios, et al., 2002)).

In both modelling procedures, we included the interactions of *Sex* and *Age* with the dust-related fixed explanatory variable (either *Events* or *Dust conc.*), and individual identity (*Individual*) was included as a random factor. For model selection purposes, we fitted all the possible combinations between the explanatory variables and ranked the resulting models based on Akaike's Information Criterion corrected for small sample sizes (AICc, (Sugiura, 1978). All the statistical analyses were performed using the R statistical software, version 4.1.2. To see functions, packages and versions see Supporting Information.

3. Results

We identified 63 dust storm events (n=229 days) during our study period (2015-2021), with 32 *Prev* and 15 *Post*. The average duration of these events was 3.86 days (±4.54 SD), with a maximum of 30 days in November and December, 2015. Dust storms occurred mainly in winter months, and concentrated in December and January (**Figure 1**). The year with more days with a high dust concentration was 2015 with 57 days of dust storms, and the maximum concentration was reached on 7 March 2015 with 9.92×10^{-7} kg/m^3.

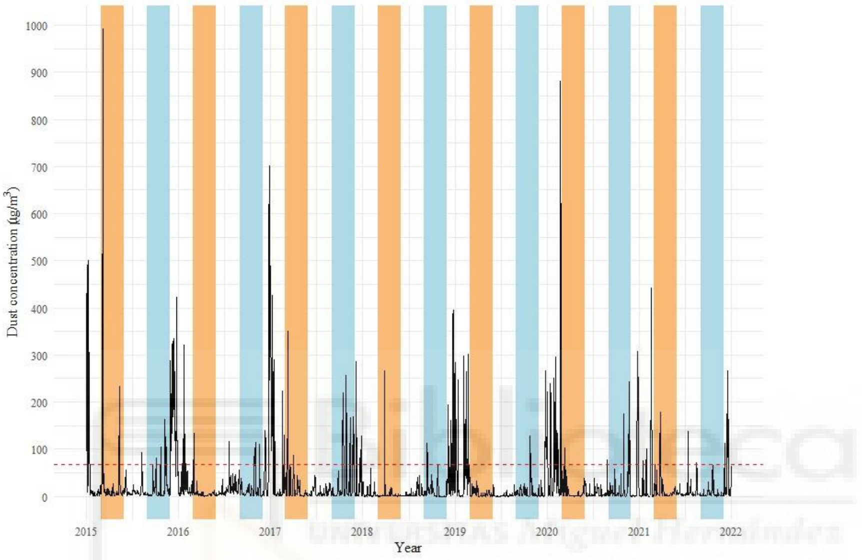

Figure 1: Daily Dust concentration (kg/m^3) at surface level for Fuerteventura Island during the study period. The red dashed line represents the threshold for the variable *Events* – Dust storm. The days above the dashed red line would correspond to days with a dust storm. Blue stripes represent the months ranging from September to November, and orange stripes represents the months from March to May (roughly the fall and spring months, respectively).

The modelling procedure that included the *Dust conc.* variable (Table S1) yielded a single model within ΔAICc < 2. This model achieved an R^2 of 13.07% (2.4% for the fixed and 10.6% for the random factors). The results of this single model showed that daily vulture movement was negatively affected by the dust concentration **(Table 1**).

Table 1: Results of the best model for both modelling procedures, the first including the variable *Dust conc* as fixed variable, and the second that included the categorical variable *Events*. CI stands for Confidence Interval. The reference level for *Sex* is *Female*, for *Events* is *Dust storm*, and for *Age* is *Adult*.

Analysis	Variables	Estimate	Std. Error	CI - 2.5%	CI – 97.5%
Dust conc	Intercept	-0.207	0.058	-0.321	-0.093
	Dust conc	-0.048	0.008	-0.065	-0.031
	Sex – Male	0.255	0.084	0.088	0.421
	Dust conc:Sex	-0.028	0.012	-0.052	-0.004
Events	Intercept	-0.291	0.057	-0.404	-0.179
	Events – Post	0.336	0.017	0.301	0.371
	Events – Prev	0.107	0.013	0.071	0.134
	Sex – Male	0.274	0.082	0.112	0.435
	Age – Subadult	-0.137	0.019	-0.176	-0.098

This implies that as the dust surface concentration roses, the daily distance (m) travelled by vultures decreased (**Figure 2**). Additionally, as males moved more than females (**Table 1**), the slope of the effect was greater for males, and in such a way that at high dust concentrations, both sexes similarly obtained low values for their daily travelled distance (**Figure 2**).

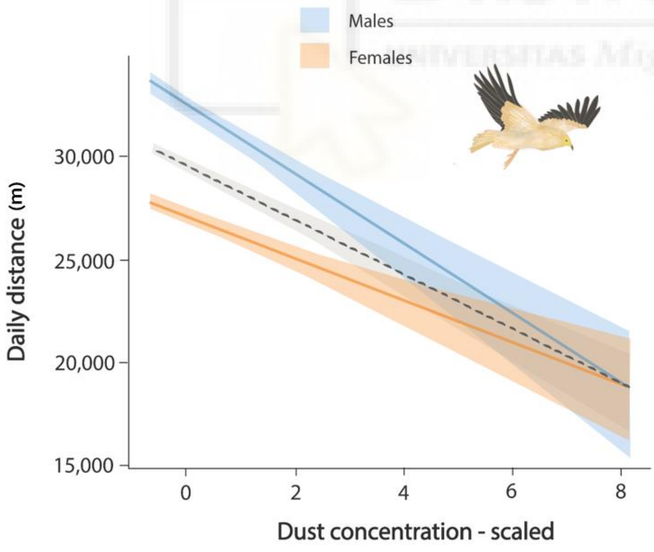

Figure 2: Linear relationship between the response variable *Daily distance* (m) and the fixed variable *Dust conc* (scaled) between sexes (*Female* and *Male*). In grey and dashed line is the mean *Daily distance* for both sexes combined.

The modelling procedure that included dust events as a categorical variable (*Events*) also yielded a single model within ΔAICc < 2 (Table S2). The R-squared for the model that included *Events* was 12.4%, (2.7% explained by the fixed and 9.6% by the random factors). Our analysis showed significant differences between the daily travelled distances across the three dust storm periods (Tukey post-hoc test, $p < 0.01$). Vulture movement reduced by 13.37% between the Pre- and Dust Storm, but increased by 19.47% from the Dust Storm to the Post period. *Sex* and *Age* were included in the first selected model. Males tended to travel longer daily distances than females under all the storm conditions (**Figure 3**). Additionally, subadults moved less than adults when faced with dust storms (**Table 1**).

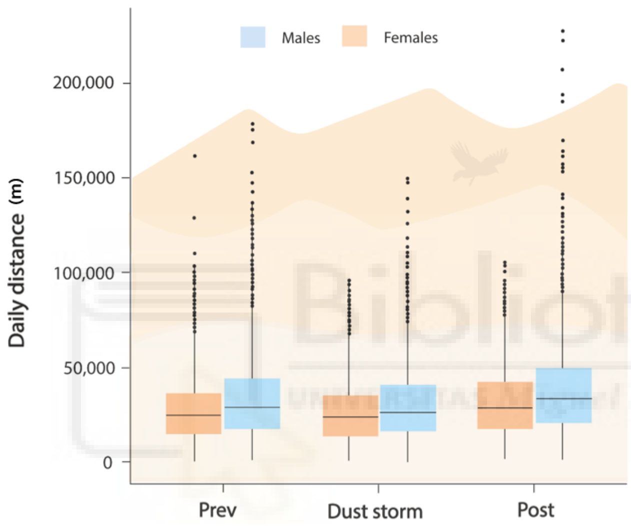

Figure 3: Differences in daily movement (m) between females and males of the GPS-tagged Canarian Egyptian vultures across different phases of dust storm. The categories are dust storm event (Dust storm), 10 days before (Prev), and 10 days after (Post). The boxplots represent the median, with the lower edge of the box representing the 25th percentile and the upper edge the 75th percentile. Whiskers represent the variability of the data outside the interquartile range, points are outliers that fall outside 1.5 times the interquartile range.

4. Discussion

Taking advantage of a long-term monitoring of 70 avian scavengers facing numerous dust storms, we observed a population-level behavioural response as the dust surface concentration rose. To the best of our knowledge, this is the first study to link animal movement and multiple dust storm recordings, which revealed an unusual reduction in the daily travel of non-migratory vertebrates to cope with extreme climate conditions. Together, our results suggest direct and indirect effects of dust storms on vertebrates due to changes in ecosystem stressors (visibility, humidity, temperature) that may ultimately affect ecological processes, such as foraging behaviour, intra- and interspecific species interactions or breeding success.

Although we do not have direct information of how poor visibility derived from the dust storms may condition the sight of the Egyptian vulture, there was indirect evidence from other natural catastrophes, such as volcanic eruptions (Weinzierl et al., 2012). In the past, eruptions have triggered massive exodus of gulls and forest birds from areas affected by airborne ash (Dalsgaard et al., 2007; Hayward, 1982), but contrastingly led to limited changes in movement patterns of Andean condors (*Vultur gryphus*) (Alarcón et al., 2016). Another climate event that creates poor visibility is fog, whose studies describe it to bring about changes in soaring migrating bird movement behaviour by altering flight speed, and by even causing disorientation during migration (Becciu et al., 2021). To our knowledge, the only study to link movement and dust storms indirectly is that by Strandberg et al 2010 (Strandberg et al., 2010), which assumes that anomalous changes in a few migrating raptors' flight courses might be because they encounter dust storms or strong headwinds.

Interestingly, we found that the daily travelled distances by individuals were different before, during and after a dust storm event. Vultures' activity markedly decreased during the event, and only increased afterwards. The ecological consequences of dust storms for this species can be separated into two scenarios. In the short-term scenario, ECEs are known to promote the redistribution of both plants and animals, therefore rearranging the food availability (Reyer et al., 2013; Waide, 1991). These changes or alterations can be temporary depending on the type, intensity and duration of events (Bailey & van de Pol, 2016; Maxwell et al., 2019). A natural consequence of an ECE is increased mortality as either a direct result of the event or an indirect one due to the ecosystem alterations triggered by the event (Sergio et al., 2018). This would lead to a higher mortality of wild primary consumers, which constitute an important feeding resource for Egyptian vultures. Thus, vultures would move more in the short term to exploit these ephemeral feeding resources (Alarcón et al., 2016; Naveda-Rodríguez & Rush, 2023).

In the long-term scenario, the ecological consequences of dust storms for Egyptian vultures can be related to cascading effects on the ecosystem, especially if the occurrence of these events becomes more frequent. For instance, dust storms increase ecosystem aridity, reducing primary productivity (Wang et al., 2006) and affecting primary consumers. Dust storms are also known for increasing the surface temperature in arid ecosystems (Otto et al., 2007) that, coupled with wind erosion, would negatively impact the island's ecosystem productivity. From previous works, we know that primary productivity is key for Egyptian vultures' breeding success

(Fernández-Gómez et al., 2023). This primary productivity is also key for primary consumers that are ultimately preyed on by Egyptian vultures, which is of utmost importance during the breeding season (Margalida et al., 2012).

With reduced vulture movement activity during dust storms, the consequences for individuals' fitness can be subtle, but significant. As our results reveal, this decreased movement was consistent between sexes, but this decrease was more pronounced for males. Reduced movement can be a behavioural response to the allostatic overload triggered by a dust storm. When individuals face a negative balance between used energy and the energy required to survive, an emergency or survival stage can be triggered. So available energy resources can be used purely for self-preservation purposes (McEwen & Wingfield, 2003). This response can be as extreme as stopping reproduction, interrupting migration or ending moulting (McEwen & Wingfield, 2003). In the present islander vulture population scenario, these types of responses can have detrimental consequences for the population. For example, reduction in movement can negatively impact the breeding outcome of reproductive adults by threatening population stability. For non-territorial birds and juveniles, reduction in movement can imply less success in prospecting new territories or natal dispersion.

Additionally, the individual response to dust concentration had a significant importance on the models. That is, the dust concentration showed twice the effect on random factors (individual identity) than on the fixed factors of models (daily distance, sex and age). Similar results were yielded for the dust storm events analysis, where the weight of the random factors tripled that for the fixed factors. This can be explained by two different, but complementary, reasons. On the one hand, personality or individual experience can drive individuals' movement (van Overveld et al., 2018) and they will, therefore, respond differently to changes in dust concentration. On the other hand, differences in the orography on the island can also provoke small-scale differences in dust concentrations (Suárez-Molina et al., 2024) that can condition vultures' movement depending on factors like each individual's territory spatial location (for adults, which can also have more previous experience) or preferred flying routes (for the entire population).

As global warming continues, dust and sandstorms are expected to worsen because new dust emission sources are currently being created in some areas due to aridification, increases in global temperatures and poor land-use management (Lababpour, 2020). However, on both the regional and global scales, projected dust emissions are contradictory (Webb & Pierre, 2018), with studies claiming that dust emissions will be higher (Stanelle et al., 2014), lower (Mahowald et al., 2006) or equal (Ashkenazy et al., 2012). In fact, the factors that condition the occurrence and intensity of dust and sand emissions to the atmosphere are still being discussed (Webb & Pierre, 2018). For our study area, a recent study done on the Canary Islands has suggested that the number of days with dust storms is showing a decreasing trend, but their intensity (measured as dust concentration) is increasing (Suárez-Molina et al., 2024). So, it is of utmost importance to learn how these dust and sandstorms affect wildlife and ecosystems in such an uncertain scenario.

CHAPTER IV

Foraging strategies of a top avian scavenger across breeding phases.

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Abstract

Balancing energy intake and expenditure is crucial for animal survival, influencing growth, reproduction, and resilience to environmental change. While foraging strategies of herbivores and carnivores are well-documented, scavengers—key players in ecosystem functioning—remain understudied. Many scavenger species rely on both natural and anthropogenic food sources, yet how their foraging strategies shift between these different sources, under variable environmental conditions and across life cycle remains unclear. This study examines the movement ecology of 49 GPS-tracked Egyptian vultures over five breeding seasons, assessing the combined influence of environmental factors and resource predictability on how their foraging strategies shift across breeding phases. Results showed significant differences in movement patterns across breeding phases. During chick-rearing, vultures travelled shorter distances and reduced time spent at predictable feeding sites, favouring natural foraging areas. Conversely, in periods of lower primary productivity, vultures expanded their home ranges thus increasing foraging effort to compensate for resource scarcity. These findings suggest a high dependence of the species on natural resources during the reproductive phase and emphasize the need for conservation strategies that account for spatiotemporal resource variability, and different sources of food. Efforts should prioritize habitat preservation, sustainable land-use practices, and maintenance of natural ecosystem processes to support vulture populations in arid landscapes. Understanding how scavengers respond to changing resource availability over their life cycle is essential for predicting broader ecological consequences of global changes and for improving conservation management.

Keywords: behavior; energy budget; home range; resource use; supplementary feeding

1. Introduction

Maintaining balance between energy intake and energy expenditure is essential for species, as it affects animal's capacity to grow, reproduce and withstand environmental challenges. Considerable time and effort are expended on foraging to maintain adequate levels of energy balance. In fact, individuals often change or expand the diet during specific periods such as migration or breeding season to cope with higher energy demands (Dhondt & Hochachka, 2001; Montague et al., 1986; Salamolard & Weimerskirch, 1993). This dietary shift is a strategic response to gain fat, in the case of migrating birds (McWilliams et al., 2004), or to either overcome the added stress of breeding or to provide the offspring with all the necessary nutrients for optimal growth and development. For instance, some birds may switch from a diet primarily composed of seeds to one that includes more insects, which are higher in protein content, ensuring their chicks receive adequate nutrition (Catry et al., 2016). Similarly, marine animals might increase their consumption of prey with higher caloric content to support both their own energy needs and those of their offspring (Saraux et al., 2011). These flexible foraging strategies highlight the intricate relationship among resource availability, dietary demand, reproductive success, and climate, demonstrating the importance of energy management in the life history strategies of animals.

Environmental factors not only influence species life-history but also shape energy fluxes within ecosystems. Temperature, precipitation, and other climatic variables can alter resource availability and energy transfer across the food web, affecting species interactions, reproduction, migration patterns, and population dynamics (McKinnon et al., 2012; Öberg et al., 2015; Robson & Barriocanal, 2011). For example, rising temperatures may stimulate plant growth in some regions while intensifying drought stress and reducing vegetation cover in others, ultimately limiting energy availability for herbivores (Nishar et al., 2017; Robertson et al., 2010). These changes in vegetation would in turn impact the next trophic level (primary consumers), which rely on vegetation for nutrition and/or shelter (Pettorelli et al., 2009). Consequently, this reduction in food availability for herbivores ultimately would lead to poorer body condition, lower reproductive success, and higher mortality rates (LaSharr et al., 2023). As consequence, we can expect that climate-driven shifts in primary productivity produce propagation effects throughout the food web, therefore affecting foraging behaviors of secondary consumers that depends on the lower levels of the food chain (Schmitz et al., 2000). Although these cascading effects between consecutive trophic levels such as plant-herbivore or herbivore-carnivore has been thoroughly studied (e.g. (Hunter & Price, 2008; Owen-Smith, 2015), there is a gap of knowledge in the literature about how these relationships would impact other trophic levels such as scavengers, a highly understudied guild which has been linked to increase connectance in food webs (Wilson & Wolkovich, 2011) and strongly related to nutrient recycling and ecosystem functioning (DeVault et al., 2003).

Scavengers have evolved to exploit carrion, an ephemeral resource that is to a certain extent unpredictable both spatially and temporally (DeVault et al., 2003). Obligate scavengers, such as vultures, have adapted to this unpredictability by developing large bodies and an efficient soaring ability that minimizes energy expenditure when displacing. These adaptations allow them to search for food over long periods and consume large food quantities when carrion is available, helping them to cope with its irregular availability (Ruxton & Houston, 2004). However, during some periods such as breeding season, vulture's movements are constrained and centred around the nest, as they are central-place foragers (Monsarrat et al., 2013). They must commute between the nest and their food sources. Therefore, they must optimize their movements to maintain a balance between energy expenditure and intake, as survival tends to take precedence over breeding in long-lived species like vultures (Hamel et al., 2010). Vultures rely on both natural and anthropogenic food sources, yet how their foraging strategies shift from different sources across breeding phases remains unclear.

In recent decades, supplementary feeding stations have become a highly common tool for conservation of vulture populations. These facilities, alongside other predictable places such as livestock farms, are sources of stable food for vultures in many ecosystems. Many authors have highlighted the positive effects of such facilities on enhancing population recoveries (Terrasse, 2006), to increase survival and breeding success (González et al., 2006; Oro et al., 2008), or to buffer the changes in the carrion availability (Donázar et al., 2009; Margalida & Colomer, 2012). However, detrimental effects of supplementary diet have also been reported, such as decrease in adult survival, productivity and increased intra and inter-specific competition (Bosè et al., 2012; Carrete et al., 2006; Cortés-Avizanda et al., 2012). In fact, predictable food can even alter the foraging behaviour and trigger a dependency on these food sources (Kane et al., 2016).

In this work, we aim to unravel the movement patterns of 49 GPS-tagged Egyptian vultures over 5 years during the breeding season, one of the most stressful life-history periods. As many scavenger species relies on both natural and anthropogenic food sources, here, we question how their foraging strategies shift between these different sources, under variable environmental conditions and across life cycle. Specifically, we want to tackle the use of the landscape in search for available resources, including not only highly predictable feeding places and farms but also considering other factors such as the environmental variables that potentially can affect the search for natural resource. Many avian species adjust or broaden their dietary niches during the breeding season to provide chicks with the necessary nutrients (Catry et al., 2016; Saraux et al., 2011). Accordingly, we hypothesize that during the chick-rearing phase, vultures will rely less on predictable feeding sites and prioritize wild-based food sources to meet the nutritional needs of their chicks (Fernández-Gómez et al., 2023, 2025; Margalida et al., 2012). Furthermore, since wild prey availability is closely tied to primary productivity (Gough et al., 2012; Letnic & Ripple, 2017), we anticipate that in less productive years, vultures will increase their foraging effort to compensate for the scarcity of natural resources. To address these hypotheses, we pose the following questions: i) How do the daily activity patterns of territorial individuals differ across the breeding phases, including nuptial behaviour and copulation (pre-breeding), incubation, chick-rearing, and post-breeding? ii) What percentage of time do vultures spend at predictable feeding sites (e.g., supplementary feeding stations and farms) during each breeding phase? iii) How does space use vary with primary productivity and weather conditions? Answering these questions will provide valuable insights into how environmental factors influence the fine-scale movement patterns of this endangered subspecies, contributing to improved conservation strategies.

2. Methods

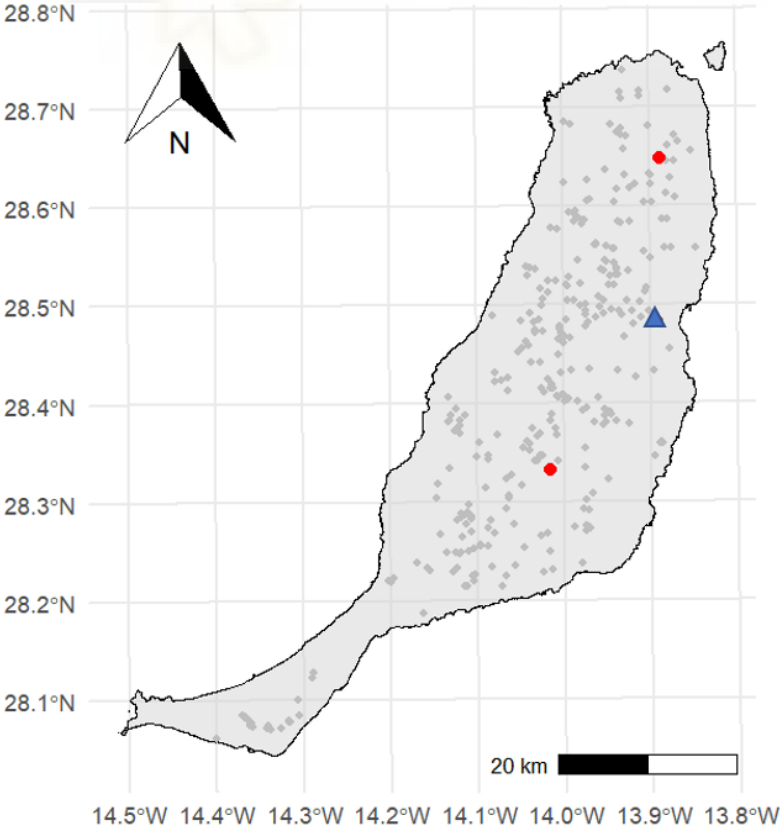
2.1 Study area

This study was conducted on Fuerteventura Island, the easternmost island of the Canary archipelago. The Canary Islands are located in the north-east Atlantic Ocean, between 27º 37′ and 29º25′N, and 13º 20 and 18º 10′W. It has an extension of 1,660 km^2, being the second largest island in the archipelago. It is considered a semi-arid ecosystem, being mainly dominated by grasslands and scrublands with almost complete absence of woodland (Rodríguez Delgado, O., García Gallo & Reyes Betancort, 2000a).

Livestock farming is based on goats and to a lesser extent, sheep (Gangoso et al 2006). Goats were introduced around 3500 BP, remaining livestock production as the main economic activity of the island (Gangoso et al., 2006a) until recent decades, when tourism gained importance (Hernández-Martín et al., 2021).

Traditionally, goats were kept in an extensive to semi-extensive system, but recently intensive farmland systems have emerged. The number of heads increased from 20,000 in 1970 to 150,000 in 2006, but from 2013 onwards suffered a steep decline, currently accounting for approximately 85,000 (Fernández-Gómez et al., 2023). Up to 2017, we have located 291 farms in Fuerteventura Island (See García-Alfonso et al., 2020 for detail).

In Fuerteventura, there are different food sources with a high degree of predictability. First, there are farms that are scattered throughout the island (Map 1). Secondly, the supplementary feeding stations that are located in the middle and the north of the island (Tiscamanita and Villaverde, respectively). Tiscamanita consists mainly of pig slaughterhouse remains, that are dumped there every two weeks, plus some goat carcasses that are left there by the farmers nearby. The Villaverde supplementary feeding station is composed by goat carcasses that are dumped by the farmers from the vicinity. Lastly, the Urban Waste facility (Dump) is the other place where vultures congregate to forage, spatially during non-breeding season (Donázar, Palacios, et al., 2002; van Overveld et al., 2018). For clarity reasons, we have grouped the two supplementary feeding stations and the dump as Highly Predictable Feeding Places (HPFP).



Map 1: Fuerteventura island with the Farms located throughout the island in grey dots. Red dots represent the two supplementary feeding stations, being Villaverde the one located in the north and Tiscamanita in the center of the island. Blue triangle represent the Urban Waste facilities associated to Puerto del Rosario city.

2.2 Population monitoring

The Canarian Egyptian vulture is a sedentary endemic subspecies (Donázar, Negro, et al., 2002). It generally breeds in cliffs and forages over the arid landscapes dominated by bare soil, grasslands, and scrublands (Rodríguez Delgado, O., García Gallo & Reyes Betancort, 2000a). This species was once widely spread throughout the entire archipelago, but during the late 20th century its population suffered a steep decline mainly due to non-natural mortality such as indirect poisoning or collisions with human infrastructures (Donázar, Palacios, et al., 2002). Currently, it only survives in Fuerteventura and Lanzarote, being the bulk (over 90% of the population) in the former. Egyptian vultures are obligate scavengers that feed on a wide range of prey, from domestic livestock carcasses to wild small-sized animals, which they can either prey upon or scavenge (Margalida et al., 2012). The species has a deferred sexual maturity, with an age of recruitment between 4 and 10 years for this population (Agudo et al., 2012).

This population has been monitored since 1998. Extensive fieldwork (ringing of nestlings and trapping of adults) has allowed that currently over 90% of the population is individually identifiable (Badia-Boher et al., 2019a). Egyptian vultures breed usually one egg per breeding season, sometimes two. As with other species of vultures, this species is highly philopatric to their breeding territories, occupying them for long periods of time (Carrete et al., 2007). The monitoring of the species also included frequent visits (minimum of 3 times a week) to the territories to identify the corresponding breeding individuals from each territory by fieldwork technicians. They also visually identified breeding behaviours such as nest preparation or mating, which occur usually in the month before the start of the breeding season (Morant Etxebarria et al., 2019). The dates of egg laying, and chick hatching were specified by behavioural changes in the parental individuals (taking turns on incubations, stand up to reposition the egg or the chick once it hatches) and by the estimated age of the chicks when the nests were accessed to ring the chicks as a part of the monitoring. The age of the chicks was calculated based on physical characteristics such as size, weight and the length of the primary feathers and the tarsus. As the primary growth rate is almost constant throughout the growing period for both single nestling and second hatched nestling (if applicable) (Donázar & Ceballos, 1989). The average date of egg laying was around the 24th-25th of March (sd = 19.24 days). The time of incubation is around 42 days for other populations (Morant Etxebarria et al., 2019). The average date of hatching is for our population the 6th-7th of May (sd = 15.32 days), which would result in approximately 42 days of incubation. Following Donázar and Ceballos 1989, the fledging occurs when the chicks are around 75 days old, but sometimes they remain attached to the breeding grounds for longer, so we considered the time of the fledging to be around 82 days for all the pairs that successfully bred.

2.3 GPS tracking

From January of 2015 to December of 2020 (n= 5 years), 70 adults and preadults have been trapped with canon nets and tagged with solar-powered GPS. Two types of devices were used: 29 individuals were equipped with UvA-BiTS (https://www.uva-bits.nl/ Amsterdam, Netherlands), 40 with E-obs (GmbH, https://e-obs.de/, Munich, Germany) and one individual was tagged with both of them during the time of study. From them, 30 were males and 40 were females. Both brands of devices have multiple sensors to measure altitude, speed according to a defined time interval (see below) and provide geographical coordinates. Devices were attached as backpacks in a harness using 0.84 and 1.12 cm wide Teflon. The total weight of the harnessing system was between 31 g (UvA-BiTS) and 54 g (E-obs), from 1.4-2.4% of the mean body mass of this species, below the limit recommendations for avoiding negative effects (3%, Sergio et al., 2015). All devices were programmed with time intervals between 1 and 5 min. We resampled all the fixes (i.e., GPS positions) to 30 min to standardize all the individuals across the different settings.

2.4 Statistical analyses and modelling procedures

We performed three different analyses for disentangling how the use of the available resources and space will differ between the breeding phases, and how the environment drives the movement during chick rearing. First, we determined the movement patterns during the different breeding phases, and how this movement can be conditionate by the environment. We added variables such as temperature, precipitation, wind and dust concentration since they might have an impact in the flight conditions, altering therefore the movement patterns. Secondly, we calculated the percentage of time (time budget) that vultures spent in the different predictable feeding sites (i.e., Tiscamanita supplementary feeding station, Villaverde supplementary feeding station, farms and the Urban Waste facilities (Dump)). Again, we also consider in the models the environmental variables such as temperature, precipitation, wind and dust because they can alter the daily flight, hindering the movement and conditioning the time budget. Finally, for those individuals that successfully raised a chick, we assessed the space use by examining how the home range size fluctuates in relation with the weather (temperature and precipitation) and also with the NDVI.

Per each analysis, we fitted a Generalised Additive Mixed Model (GAMM). The response variables were the NSD for the breeding movement pattern analysis, the percentage of time spent at each predictable feeding location for the time budget analysis (one for the farms, other for the HPFP), and for the home range one model for the size of the KUD 95 and other for the KUD 50 (core area).

Explanatory variables fitted per each modelling procedure are detailed in **Table 1**. At first, we fitted as random effects the year and the individual in all three modelling procedures. However, for both the breeding movement pattern analysis and the time budget analysis, the year did not explain any of the variance, so we removed it from the models. For the space use analysis, the year was fitted as random factor. All the variables were scaled prior to fitting the GAMM. All pairs of variables with a Spearman correlation coefficient higher than |0.5| were excluded from the analysis. In the following sections, we detail how we calculated each of the response (NSD, time budget, space use) and explanatory variables such as different weather variables and environmental such as dust concentration or NDVI.

2.4.1 Breeding movement patterns

From the 70 vultures with GPS information, we selected those tagged individuals during our study period (n = 49) that were territorial, i.e. they actively defend an area and exhibit breeding behaviour such as mating and selecting a cavity or a cliff to breed (nest). Then, we selected all the GPS fixes from February to September, including data from the egging lay to the independence of chicks from parental care. Then, we classified the GPS information regarding each breeding phase. That is, we classified the GPS data as *Pre-breeding* when they were obtained from 1st February until the egg laying date. Subsequently, we classified the GPS data as *Incubating* class when they were obtained from the egging laid period until the hatching date. From the hatching date to 82 days after (date when the chicks are independent), we classified the GPS data as *Feeding.* And from this date until the end of September, we classified that period as *Post-Breeding*. We classified as *Non-Breeders* those individuals that did not attempt to breed even though they presented breeding behaviour and defended a territory. If any individual at any phase of the breeding failed, the remaining days until the end of September would also be categorised as non-breeder. For example, if any given individual incubated an egg, but it does not hatch, this individual would have a pre-breeding phase, an incubating phase and for the remaining of the breeding season would be categorised as a non-breeder.

Using the GPS information from the above-mentioned classes separately, we calculated the Net Squared Displacement (hereafter, NSD, Börger & Fryxell, 2012) to assess detailed differences in movement among the phases of breeding. The NSD function allows to calculate the distance between a focal location and each of the subsequent locations over time. In our case, we used the coordinates of the nest as the focal location, so all the displacements (in m) were calculated taking the nest as a reference point. Therefore, we calculated the distance from each GPS location per individual to the nest by calculating the difference in meters. As NSD inherently incorporates the temporal dynamics of movement, this measurement would allow us to track how movement evolves over each breeding phase.

2.4.2 Time budget

For the same 49 individuals analyzed in the breeding movement patterns section, we also calculated the time each individual spent at i) farms or ii) Highly Predictable Feeding Places (HPFPs). The HPFPs refer to three highly predictable feeding sites in terms of stable food in Fuerteventura: the two supplementary feeding stations (Tiscamanita and Villaverde), and one Urban Waste facility (Dump). To calculate the time budget (time individuals spent at each type of feeding place), we first determined whether the GPS fixes fell within a 180-meter buffer surrounding the centroid of each farm and HPFP (García-Alfonso et al 2020). The sizes of the feeding stations were as follows: 110x100 meters for Tiscamanita, 140x70 meters for Villaverde, and 170x150 meters for the portion of the Dump used during the study. Then, we measured the time intervals between GPS location fixes during the study period (February 2015 to September 2020). Then, per individual and day, we calculated the total amount of time that each individual spent in each category (*Farm* or *HPFP*) divided by the total amount of time that we had GPS information that day.

2.4.3 Space use

To define the space use of the territorial tagged individuals during the chick rearing period, we calculated the home range per individual and year. We firstly estimated the utilization distribution per individual and year for the chick rearing period, and then we calculated the 95% Kernel Utilization Distribution (home range) and the 50% Kernel Utilization Distribution (or core area). The KUD quantifies the probability distribution of an animal's use of space based on its location data. The KUD 95 represents he area where a vulture spends 95% of its time. This is considered the animal home range, and it captures the majority of its activity while excluding outlier movements or excursions. Therefore, it allows us to determine how much space an individual need to fulfil its ecological needs (e.g. foraging, roosting, breeding). The KUD 50 or core area refers to the areas of higher use, critical for survival. Usually, they correspond to nesting sites/territory in central-place foragers. For calculating both estimators, we used the default smoothing parameter (h=href) and bivnormal distribution (bivariate normal kernel).

2.4.4 Environmental variables

As animal movement is usually conditioned by temporal and spatial changes in environment conditions, we extracted two different sets of weather variables, one for the breeding movement pattern analysis and the time budget, and other for the space use analysis. The latter includes the spatial component, since is based on shapes of the home range and the core area for a determined period of time, meanwhile the first two analysis is on a daily time scale. For both the breeding movement patterns analysis and the time budget, we extracted the daily maximum temperature, wind speed and the accumulated precipitation from the Puerto del Rosario meteorological station (see **Table 1** for further details).

The dust surface concentration data was downloaded from the WMO - Barcelona Dust Regional Centre (WMO SDS-WAS Regional Centre for Northern Africa, Middle East, and Europe, https://dust.aemet.es/). We downloaded the daily data corresponding with our study period from the forecasting MULTI-MODEL (Terradellas et al., 2022) model available at the website. We processed the information with the Max-Planck CDO operators (Climate Data Operators, https://code.mpimet.mpg.de/projects/cdo) which is a collection of command line operators to manipulate and analyse climate data. The MULTI-MODEL contains several parameters regarding dust data in a raster layer. We selected the "*Concentration*" parameter, which corresponds with the dust concentration at surface level. Each daily file contains a record per each 3h and includes the corresponding day information and a forecast for the following 3 days. We selected only the records from the day of interest and remove the forecasting information. Then, we average the records, thus obtaining a single dust surface concentration per day in a grid of 0.5ºx0.5º. Afterwards, we use the Fuerteventura shape for clipping each raster layer and subsequently we average all the pixels, resulting in a single daily dust surface concentration per day. Thus, the variable used in both analyses (breeding movement patterns and time budget) was the concentration of dust at surface level per each day.

Table 1: Explanatory variables fitted in each of the GAMMs fitted for the modelling procedures. Per each variable, the Analysis column indicates in which of the analyses is fitted. The nomenclature indicates the names of the variables in the remaining tables. PVC was used as a random factor for all the analyses, meanwhile Year was only used in space use as a random factor

Name	**Definition**	**Nomenclature**	**Analysis**
Wind speed	From the Puerto del Rosario Airport Meteorological Station, the average speed of the wind per each day.	Wind	Breeding movement patterns, time budget.
Dust surface concentration	Per each day, the dust concentration at surface level.	Dust	Breeding movement patterns, time budget.
Maximum temperature	From the Puerto del Rosario Airport Meteorological Station, the maximum temperature per each day.	Temperature_max	Breeding movement patterns, time budget.
Accumulated precipitation	From the Puerto del Rosario Airport Meteorological Station, the accumulated precipitation per each day.	Precipitation_acc	Breeding movement patterns, time budget.
Sex	If the individuals were males (M) or females (F).	Sex	Breeding movement patterns, time budget, space use.
Age	Age (in years) per each individual.	Age	Breeding movement patterns, time budget, space use.
Distance to Tiscamanita	Per each individual and year, the distance of the nest to the Tiscamanita Supplementary Feeding Station.	Dist_Tisc	Breding movement patterns
Distance to Villaverde	Per each individual and year, the distance of the nest to the Villaverde Supplementary Feeding Station.	Dist_Villav	Breding movement patterns
Distance to Dump	Per each individual and year, the distance of the nest to the Urban Waste facility (Dump) located nearby the city of Puerto del Rosario.	Dist_Dump	Breding movement patterns
Breeding phase	Taking advantage of the monitoring information, we defined five breeding categories or phases. From the beginning of the breeding season (February) to the date of egg laying, it is considered *pre-breeding*. Fron the egg laying to the hatching, it is considered as *incubating*. From the hatching to day 82 (chick fledging) is *chick rearing*. From this last	Breeding_ph	Breeding movement patterns, time budget.

	date until the end of the breeding season (September) is considered *post-breeding*. In addition, those individuals that did not bred or they failed at any of the previous phases was considered as *non-breeder*.		
NDVI	For each individual and year, the mean NDVI (Normalized Difference Vegetation Index) for the *chick rearing* breeding phase within the 95% and the 50% KUD (Kernel Utilization Density). We gathered the NDVI images from between the dates of hatching and the fledging of the chicks (82 days) and processed it with google earth engine.	NDVI	Space use.
Temperature	For each individual and year, the mean of the maximum temperature for the *chick rearing* breeding phase within the 95% and the 50% KUD (Kernel Utilization Density). We gathered the images from between the dates of hatching and the fledging of the chicks (82 days) and processed it with google earth engine.	Temperature_sp	Space use.
Precipitation	For each individual and year, the accumulated precipitation for the *chick rearing* breeding phase within the 95% and the 50% KUD (Kernel Utilization Density). We gathered the images from between the dates of hatching and the fledging of the chicks (82 days) and processed it with google earth engine.	Precipitation_sp	Space use.
Number of farms	For each 95% and 50% KUD (Kernel Utilization Density) the number of farms within the boundaries of the kernel.	N_farms	Space use
PVC	The individual identifier of each vulture.	PVC	Breeding movement patterns, time budget, space use.
Year	The corresponding year.	Year	Space use

For the space use analysis, we extracted the NDVI (Normalized Difference Vegetation Index), the accumulated precipitation and the maximum temperature per each home range (KUD 95) and core area (KUD 50) per individual and year. NDVI has been pointed out as a good proxy for monitoring vegetation response to climate, and to estimate ecosystem-level productivity (Pettorelli et al., 2005; Schloss et al., 1999). Using Google Earth Engine platform, we extracted the NDVI from the MODIS/MOD09GA_006_NDVI Image Collection, corresponding with MODIS satellite. This product has been previously corrected and filtered for clouds, and for atmospheric gases and aerosols at low levels. Accumulated precipitation was calculated using UCSB-CHG/CHIRPS/DAILY Image Collection by the Climate Hazards Group Infrared Precipitation with Stations (CHIRPS) and for temperature we used NOAA/CDR/PATMOSX/V53 Image Collection corresponding with the National Oceanic and Atmospheric Administration (NOAA) satellite. The specific start date and end date for extracting the variables per year and individual was the date of hatching and the date when the chick is fully feathered and usually independent from parental care (fledging date, 82 days after hatching).

3. Results

3.1 Breeding movement patterns

The first analytical procedure showed that the movement patterns during the different breeding phases was significantly different. The Net Squared Displacement (NSD) of our tagged vultures was lower for those individuals that were in active breeding (intercept: Non-Breeders, all remaining categories of breeding phase were negative). Particularly, the lowest accumulated displacement was during the post-breeding and chick rearing period, followed by pre-breeding and lastly the incubating (**Table 2**). The distances to Tiscamanita supplementary feeding station and Villaverde, although significative, did not yield any response. All the smoothing factors were significative (**Table 2**, see **Table A1** and **FigureS1** in Supplementary Material for gam check results and smoothing effects with residuals).

Table 2: Result from the GAMM model for disentangling the breeding movement patterns. The response variable is the Net Squared Displacement. The reference level for the Breeding phase variable is Non-Breeders, and Female for the variable Sex. Std Error stands for Standard Error. P-values significances are detailed in the footnote of the table.

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	-5.136	3.602	-1.426	0.1540	
	Breeding_ph – Chick rearing	-0.718	0.073	-9.851	0.0000	***

Component	Term	Estimate	Std Error	t-value	p-value	
	Breeding_ph – Incubating	-0.341	0.090	-3.779	0.0002	***
	Breeding_ph – Post-breeding	-0.828	0.110	-7.523	0.0000	***
	Breeding_ph – Pre-breeding	-0.502	0.071	-7.097	0.0000	***
	Dist.Tisca	0.000	0.000	15.630	0.0000	***
	Dist.Villaverde	0.000	0.000	2.316	0.0206	*
	Dist.Dump	0.000	0.000	0.146	0.8841	
	Sex – M	1.629	3.758	0.434	0.6646	
Component	**Term**	**Edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth terms	s(Wind)	2.920	2.995	11.140	0.0000	***
	s(Precipitation_acc)	2.857	2.985	6.396	0.0003	***
	s(Age)	2.902	2.993	44.692	0.0000	***
	s(Temperature_max)	2.995	3.000	653.962	0.0000	***
	s(Dust)	2.469	2.793	41.562	0.0000	***
	s(PVC)	31.633	32.000	354.970	0.0000	***

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05

Adjusted R-squared: 0.161, Deviance explained 0.162

-REML : 546213.595, Scale est: 66.479, N: 155232

Wind speed was negatively related to the displacement, suggesting lower travelled distance as wind speed increases (**Figure 1**). A similar pattern was found regarding the dust concentration and the precipitation, with a negative relationship between those variables and the Net Squared Displacement. Although NSD seems to increase above 15 mm of precipitation, this trend appears biased by an outlier (see **Figure 1**). Overall, we found that NSD increases with higher temperature. Moreover, travelled distances increase until intermediate ages, with a shifted decrease trend after 10 years old (**Figure 1**).

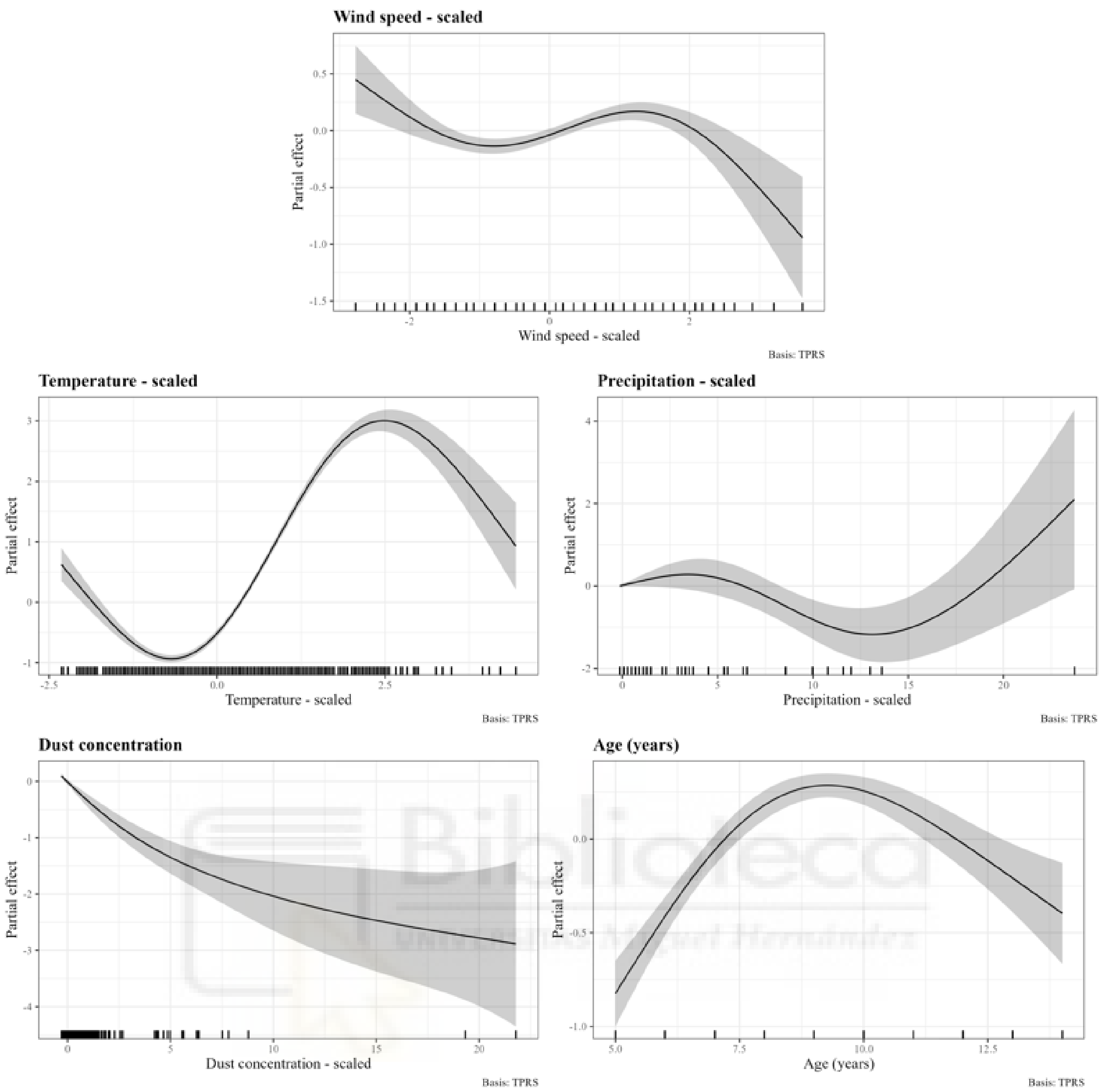


Figure 1: Significative smoothing effects of all the explanatory variables fitted in the GAMM (Generalized Additive Mixed Model) for the movement patterns analysis. Grey coloured shaded area corresponds to the 95% confidence interval, ticks in the X-axis represent location of observations along the predictors.

3.2 Time budget

For the Highly Predictable Feeding Places (HPFP), we found that vultures spent less time in the two supplementary feeding stations and the garbage dump during the chick rearing phase and the pre-breeding phase when compared with non-breeders (**Table 3**, see **Table A2** and **Figure S2** in Supplementary Material for GAM check results and smoothing effects with residuals). The rest of the breeding categories did not yield robust results, nor the sex variable. Regarding the smoothing terms (**Table 3**), only maximum temperature and wind were significative (**Figure 2**). In particular, vultures spent more time in HPFP in days with strong winds and less time in days with intermediate temperature levels.

Table 3: Results from the time budget analysis. In the intercept for the Breeding phase variable is Non-Breeder, and Female for the variable Sex. HPFP stands for Highly Predictable Feeding Places.

A) HPFP

Component	**Term**	**Estimate**	**Std Error**	**t-value**	**p-value**	
A. parametric coefficients	Intercept	19.216	0.582	33.021	0.0000	***
	Breeding_ph - Chick rearing	-5.860	2.354	-2.489	0.0129	*
	Breeding_ph – Incubating	-2.439	3.148	-0.775	0.4385	
	Breeding_ph - Post-breeding	4.907	3.737	1.313	0.1892	
	Breeding_ph - Pre-breeding	-5.625	2.292	-2.454	0.0142	*
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth terms	s(Temperature_max)	2.368	2.958	3.338	0.0271	*
	s(Wind)	1.000	1.000	4.515	0.0337	*
	s(Dust)	2.222	2.615	1.385	0.3475	
	s(Precipitation_acc)	1.390	1.669	1.198	0.2061	

B) FARMS

Component	**Term**	**Estimate**	**Std Error**	**t-value**	**p-value**	
A. parametric coefficients	Intercept	13.451	0.228	58.937	0.0000	***
	Breeding_ph - Chick rearing	-2.902	0.699	-4.150	0.0000	***
	Breeding_ph – Incubating	-1.892	0.882	-2.144	0.0321	*
	Breeding_ph - Post-breeding	3.197	1.288	2.482	0.0131	*
	Breeding_ph - Pre-breeding	-0.516	0.639	-0.808	0.4191	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth terms	s(Temperature_max)	5.440	6.541	11.831	0.0000	***
	s(Wind)	1.716	2.180	2.169	0.0975	.
	s(Dust)	5.728	6.842	2.819	0.0078	**
	s(Precipitation_acc)	1.189	1.350	0.593	0.3985	

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05

For the farms model, vultures spent less time at farms during chick rearing phase and the incubating, followed by an increased time spent on farms during the post-breeding phase. The other categories did not yield significative results (**Table**

3). For the smoothing terms, only the temperature, the wind speed and the dust were significative (**Table 3**, see **Table A2** and **Figure S2** in Supplementary Material for GAM check results and smoothing effects with residuals). The vulture’s response to the wind and temperature were similar to the ones found for the HPFP. The time spent at farms was greater in days with strong winds, and also during days of high temperature (**Figure 2**). The response to dust concentration showed a negative tendency linked to the increase of dust. However, there is a single point linked to extremely high dust concentration that forced the trend to adapt upwards (see **Figure 2** and **S2** in Supplementary Material for trend with residuals). This shape is probably the result of an outlier, since it belongs to a single day with an extreme concentration.

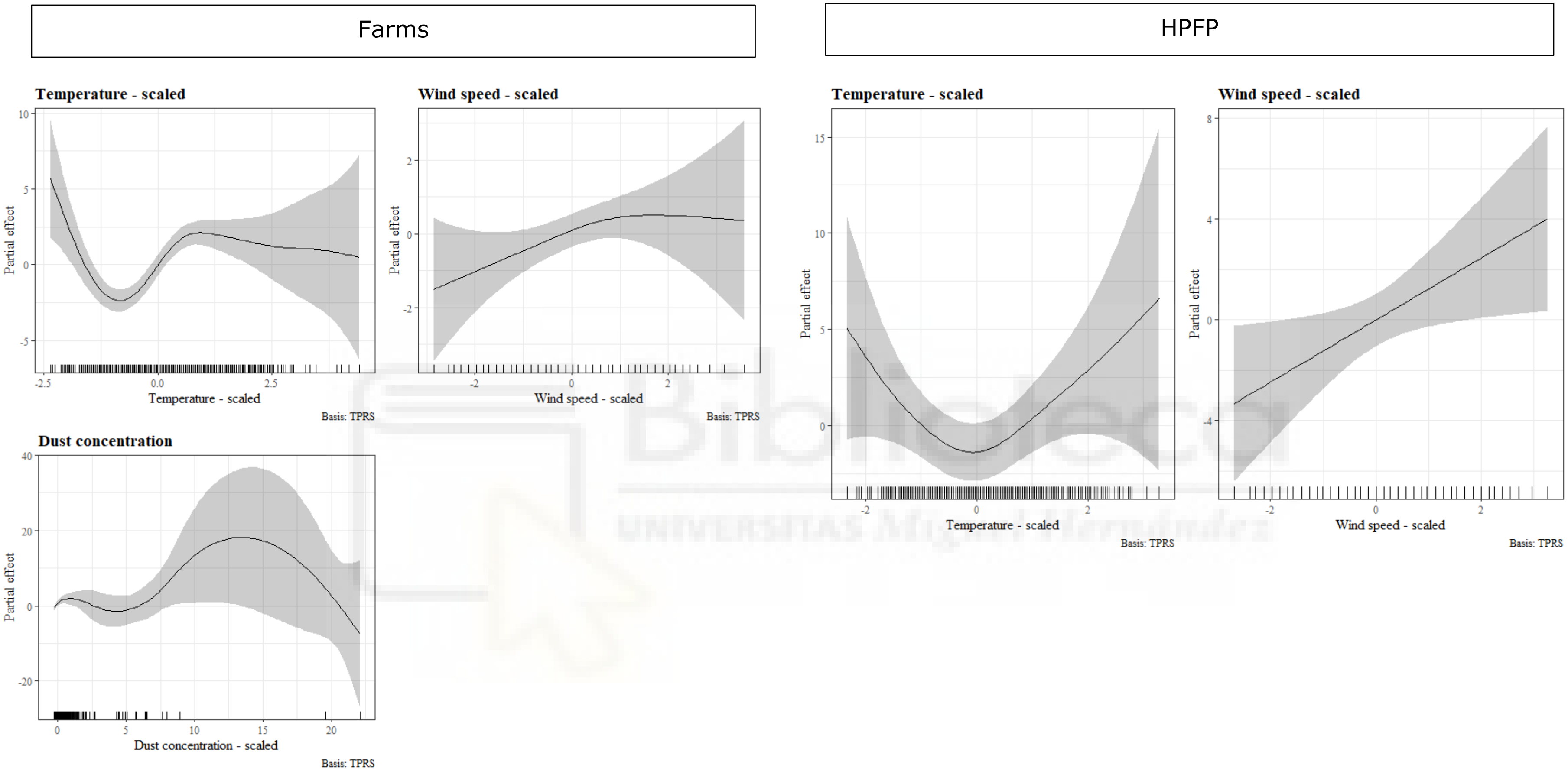


Figure 2: Significative smoothing effects for the models corresponding with those localizations at farms and Highly Predictable Feeding Places (Tiscamanita and Villaverde feeding stations and the Urban Waste facility). Grey coloured shaded area corresponds to the 95% confidence interval, ticks in the X-axis represent location of observations along the predictors.

3.3 Space use

We found that NDVI yielded a negative linear relationship with the size of the home range, measured as 95% KUD (Kernel Utilization Density) (**Table 4**, **Figure 3**, see **Table A3** and **Figure S3** in Supplementary Material for GAM check results and smoothing effects with residuals). In addition, there was also a positive linear relationship between the size area of the home range and the number of farms within the limits of the home range (**Figure 3**).

Table 4: Results from the space use analyses. In the A) table are the results from the 95% isopleth of the Kernel Utilization Distribution (KUD 95, home range) and the B) is for the 50% of the Kernel Utilization Distribution (KUD 50, core area). Std Error is for Standard error. Significances are detailed in the footnote of the table below.

A) KUD 95

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	0.034	0.085	0.402	0.6900	
	Age	-0.031	0.047	-0.662	0.5116	
	Sex – M	-0.059	0.115	-0.514	0.6098	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth terms	s(NDVI)	1.000	1.000	48.010	0.0000	***
	s(Temperature_sp)	1.000	1.000	0.158	0.6929	
	s(Year)	4.937	8.000	3.967	0.0002	***
	s(N_Farms)	1.000	1.000	1,159.815	0.0000	***

B) KUD 50

Component	Term	Estimate	Std Error	t-value	p-value	
A. parametric coefficients	(Intercept)	0.194	0.134	1.451	0.1553	
	Age	-0.309	0.140	-2.201	0.0341	*
	Sex – M	-0.305	0.213	-1.430	0.1612	
Component	**Term**	**edf**	**Ref. df**	**F-value**	**p-value**	
B. smooth terms	s(NDVI)	1.000	1.000	14.540	0.0005	***
	s(Temperature_sp)	2.459	2.459	3.989	0.0132	*
	s(Precipitation_sp)	1.000	1.000	0.105	0.7475	
	s(Year)	0.000	8.000	0.000	0.4408	
	s(N_Farms)	1.000	1.000	32.234	0.0000	***

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05

The size of the core area (50% KUD) showed a negative relationship with age of the vultures (**Table 4**). This means that older individuals present smaller core areas. The smoothing parameters that yielded significative results were the average NDVI, the temperature and the number of farms within the core area (**Table 4**, see **Table A3** and **Figure S3** in Supplementary Material for gam check results and smoothing effects with residuals). NDVI exhibited a negative linear relationship with core area size, suggesting that in more productive areas, where resources are more abundant, vultures are able to reduce the extent of their core areas. The temperature exhibited a slightly quadratic response but overall negative tendency, meaning that although intermediate temperatures lead to an increase in the size of the core area (50% KUD), the core area diminishes with high temperatures. Lastly, we found a positive linear relationship between the number of farms and the size of the core area (**Figure 3**).

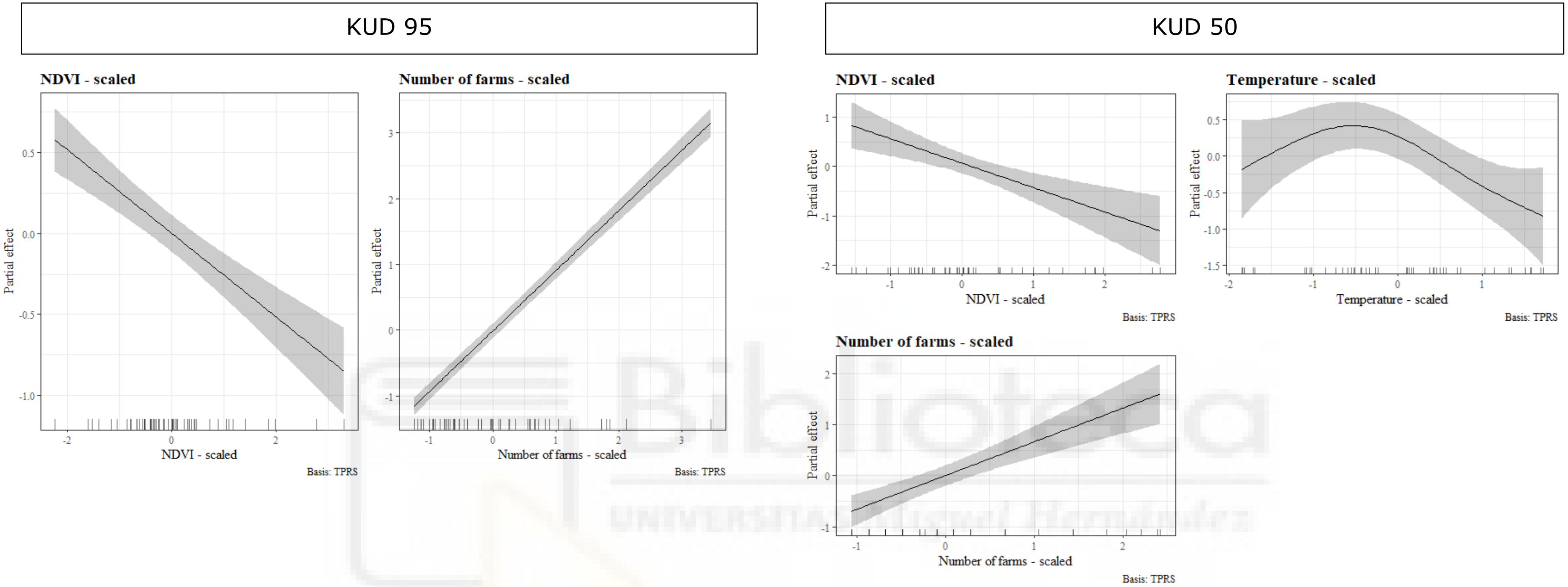


Figure 3: Significative smoothing effects of all the explanatory variables fitted in the models for the space use analyses (KUD95 and KUD50). Grey coloured shaded area corresponds to the 95% confidence interval, ticks in the X-axis represent location of observations along the predictors.

4. Discussion

Our results show that an obligate scavenger fits its movement behavior to the changing needs of resources throughout the breeding season. The foraging strategy shifts in Egyptian vultures between natural and anthropogenic food sources are closely linked to breeding phase, moderated by climatic conditions and ecosystem productivity. Movement behavior varied significantly across reproductive stages, with individuals exhibiting reduced ranging and increased reliance on natural foraging areas post-hatching, coupled with decreased use of predictable anthropogenic resources such as farms and supplementary feeding stations. Foraging effort, in terms of both spatial extent and temporal investment, was determined by the use of human-provided resources during each breeding phase. During the chick-rearing period, individuals exhibited energy-efficient behavior by concentrating foraging in areas of higher primary productivity. Together, our results emphasized the need for conservation strategies that account for spatiotemporal variability of different food resources in the landscape.

Through long-term monitoring of this vulture population, initiated in 1998, we identified distinct phases within the breeding cycle based on movement patterns, as quantified using Net Squared Displacement (NSD). Among these phases, the post-breeding and chick-rearing periods were characterized by the lowest NSD values, indicating reduced spatial displacement from the nest. During the chick-rearing phase, vultures must optimize their movements to cope with the increased energy demands of foraging, as they need to feed both their chick(s) and themselves. As a result, they likely prioritize food sources located near the nest to minimize effort and energy expenditure (Boyd et al., 2014; Mills et al., 2020).The pattern observed during the post-breeding phase may result from the attachment exhibited by some chicks, despite being fully developed. Although individuals older than 82 days are considered independent, they sometimes remain in or near the breeding grounds. Consequently, their parents may also stay in the vicinity, which could explain the lower net squared displacement (NSD) values recorded during this phase. This pattern contrasts with the incubation period and the behavior of pre-breeding individuals, who exhibited higher NSD values. We believe that the non-brooding parent, during incubation duty, likely tried to maximize foraging time and explore a wider range of food sources or travel to more distant locations to meet the high energy demands of incubation, hence having large NSD values. A similar strategy has been observed in pelagic seabirds, where parental shifts can last over 24 hours, with trips for foraging of over 500km from the nest (Salamolard & Weimerskirch, 1993). Additionally, the foraging parent may forage over other feeding sources to store body fat to sustain itself through the remainder of the breeding season. In fact, (Donázar et al., 2020) found that territorial adults store more fat (measured as body mass) than non-territorial individuals. While they attributed this to the higher dominance rank of territorial vultures, this rank may also grant them preferential access to predictable food sources such as highly predictable feeding sites (*HPFP*), *Farms* and other key resources.

Interestingly, during the chick-rearing period vultures were observed to spend less time at Highly Predictable Feeding Places (*HPFP*) and on *Farms*. Egyptian vultures, in particular, are known for their broad dietary range among European vultures, feeding on a variety of prey including small mammals (e.g., rodents, birds, lizards, and livestock (Balaban & Yamaç, 2018; Milchev et al., 2012). The fact that they are able to consume a wide arrange of prey and their impact on the breeding success has been suggested by several authors. Margalida et al., (2012) studied the diet composition and diversity and proposed that wild prey would be key for the breeding success. Later, Fernández-Gómez et al., (2023) linked highly productive areas in terms of NDVI with better breeding success on this population, and a negative relationship with the amount of livestock, suggesting that overgrazing affected negatively to the vegetation, hindering the wild herbivores. Then, Fernández-Gómez et al., (2025) determined that higher diversity was related to more chicks successfully raised, and that the amount of wild prey found in the nests was negatively related with the presence of livestock, further consolidating this hypothesis; vultures spent more time foraging for wild prey during chick-rearing breeding phase. The importance of wild prey is stressed by the fact that small-sized animal remains supply essential micronutrients that are present to a much lesser extent in the soft tissues of domestic ungulates (Houston, 1978; Reynolds & Perrins, 2010). Additionally, small animals (e.g., lizards which are common in our study area) are usually consumed whole, which provides certain elements like calcium, which is necessary for the bone mineralisation of chicks (Houston, 1978).

The results from the Kernel Utilization Density (KUD) models at both 95% and 50% levels support the idea that vultures' reduced reliance on anthropogenic and predictable food sources is driven by their consumption of wild prey. Specifically, our findings confirm a negative relationship between the size of the vultures' home range and primary productivity, as measured by the Normalized Difference Vegetation Index (NDVI). NDVI, widely recognized as a reliable proxy for primary productivity (Pettorelli et al., 2005), indicates that more productive areas—with higher vegetation density—are associated with smaller home ranges. This relationship likely arises because productive habitats support a greater abundance of herbivores that utilize vegetation for foraging and shelter (Letnic & Ripple, 2017). As a result, vultures concentrate their foraging efforts in these productive regions, taking advantage of the availability of wild prey carcasses instead of depending on supplementary feeding stations or garbage dumps (van Overveld et al., 2018). This behavior is particularly important during the breeding season, as there is a clear link between movement, energy expenditure, and the need to save energy to provide enough food for chicks. By restricting their movements, vultures optimize energy use and feeding efficiency, highlighting the importance of natural food sources during this period. These findings further confirm the results presented by Fernández-Gómez et al., (2023) and (2025), where authors stressed the importance of primary productivity and wild prey for the breeding success of this population. This foraging strategy has substantial implications for conservation, as it underscores the need to protect natural habitats that support these feeding behaviors. Interestingly, our findings contrast with the foraging strategies of other scavengers, such as griffon vultures and albatrosses, which often rely on predictable feeding sites to enhance feeding efficiency for their offspring (Monsarrat et al., 2013; Weimerskirch et al., 1997). In contrast, the vultures in our study rely more on natural and less predictable environments, reflecting a distinct foraging strategy shaped by environmental conditions and resource availability.

This strong use of highly productive areas during such a sensitive period highlights the intricate relationship between environmental conditions and the fitness of vultures. In regions with high primary productivity, vultures are likely to exhibit more localized foraging behaviour, reducing competition and energy expenditure (Dodge et al., 2014). This is particularly advantageous during energetically demanding periods such as incubation and chick-rearing when consistent food availability near the nest can significantly enhance reproductive success (Dodge et al., 2014). Fluctuations in primary productivity can lead to adaptive shifts in the space use over time (Pettorelli et al., 2011). During periods of drought or reduced vegetation productivity, species dependent on primary productivity (such as herbivores) are forced to expand their home ranges (Viana et al., 2018), potentially increasing their exposure to natural or anthropogenic threats (Emsens et al., 2013; Godet et al., 2017; Mancinelli et al., 2018). For the Egyptian vulture in Fuerteventura Island, electrocutions, collision with wind turbines and poisoning were the main causes of non-natural death of this species in the past (Badia-Boher et al., 2019a). This suggests a delicate balance between environmental conditions and survival strategies. Changes in primary productivity not only influence foraging efficiency but also expose vultures to broader ecological risks. Increased movement has been linked to lower survival rates due to anthropogenic threats, such as poisoning, collisions with human infrastructure, and exposure to contaminants (Arrondo et al., 2020; Curk et al., 2024; S. C. Krüger et al., 2022).

Interestingly, environmental variables had a significant effect on several analyses. The temperature influenced the net squared displacement, with a reduction in the movement during the extreme temperatures. This could be due to different reasons. Because of the timing of the summer and the breeding, when the extreme temperatures occur is when the chick is already born and is one of the periods with less movement due to parental duty. However, this could also be explained by the thermal constrains on movement (Poessel et al., 2018). Vultures, as large soaring birds, that rely on thermal uplifts and orographic updrafts to fly (Duerr et al., 2015). These conditions are mostl frequent at moderate and high temperature (Spiegel et al., 2013), thus explaining both the increase in the displacement along the temperature rise. Some species have adapted to cope with extreme heat by either flying at higher altitude (Sjöberg et al., 2021), or shortening the flight time (Guillemette et al., 2016). This could explain why at extreme temperatures the displacements are shorter and why they spend more time at the HPFP and Farms on days with extreme heat. To avoid hyperthermia during flight under suboptimal thermal conditions, birds may reduce foraging effort and instead remain in areas with predictable food availability ((Arkumarev et al., 2021), as coping with heat stress imposes additional energetic costs (Lewden et al., 2023). This would also align with the results from the wind. Wind is also intimately related to flight performance (Mandel et al., 2008; Scacco et al., 2023). Energy saved from flight performance can have key impacts on fitness (Morant et al., 2022), particularly during breeding season for species that breeds in cliffs (Lempidakis et al., 2022). Therefore, in days with strong winds that are not suitable for foraging, the displacement is minor and they spend more time in HPFP and Farms, where the food is predictable. Similarly, during days with precipitation, the displacement was less. Precipitation generally reduce raptor flight activity (Naves-Alegre et al., 2025), with consequences for the reproductive output at extreme conditions (Fisher et al., 2015). Comparably, we also observe a reduction in the movement as a result of the increase in dust concentration at surface level. Dust storms can also pose a diminishment of visibility (Suárez-Molina et al., 2024; Xi, 2021), since the air is saturated with particulates. Hence, vultures would travel less distance under adverse conditions. Additionally, that also would explain that they spend more time on foraging farms, since they are a stable food resource that is scattered over the island, being more accessible that foraging over wider areas, that would imply soaring under low visibility conditions.

The findings presented in this paper have important conservation implications. Given the species’ sensitivity to environmental variability, efforts to preserve and restore natural habitats with consistent primary productivity should be prioritized. This could involve promoting sustainable land-use practices that mitigate habitat degradation, ensuring the protection of key foraging areas, and enhancing connectivity between resource-rich zones. Ultimately, the present study underscores the critical need for conservation approaches that account for both spatial and temporal resource variability in an arid landscape.

GENERAL DISCUSSION

In the face of major global change, understanding the interplay between ecosystem functioning and wildlife dynamics is crucial for predicting ecological responses to environmental shifts. Ecosystems are dynamic networks where biotic and abiotic factors—including climate variability, land-use changes and human activities— regulate energy flow, nutrient cycling, and species interactions. This thesis explores in depth these ecological dynamics by examining the role of environmental shifts and ecosystem processes on scavengers, linking both climatic and anthropogenic drivers to higher trophic levels through direct and indirect pathways.

A key contribution of this work is its elucidation of how climate-driven fluctuations in ecosystem functioning propagate through food webs to influence scavenger population dynamics. While direct climatic effects on species are well documented, the indirect cascade effects mediated by resource availability remain understudied (Cahill et al., 2013). This research demonstrates that shifts in ecosystem productivity alter the availability of carrion and prey, which in turn affects the breeding success of a top avian scavenger (**Chapters I** and **II**). These findings underscore the importance of bottom-up and top-down processes in shaping scavenger demography, particularly in systems where scavengers act as keystone regulators of decomposition and nutrient redistribution. In the study system, the Egyptian vulture serves as a primary provider of ecosystem services associated with scavengers (García-Alfonso et al., 2019).

In arid ecosystems, where resource pulses are inherently constrained by climatic variability, anthropogenic pressures such as livestock overgrazing can disrupt bottom-up controls on resource availability, key to preserving the ecosystem functioning. This thesis illustrates how high-density goat farming impacts vegetation biomass, leading to a decrease in ecosystem-level primary productivity, the baseline for ecosystem function. Beyond climate, these practices fragment and degrade habitats and reduce biodiversity, further limiting wild herbivore populations, creating a trophic bottleneck: the decline in wild herbivore populations due to habitat depletion limits wild-origin carrion availability for obligate scavengers like the Egyptian vulture (*Neophron percnopterus*). However, minor alleviation of grazing pressure due to changes in the European funding of farming revealed a recoverable linkage between primary productivity and scavenger breeding success (**Chapter I**). As vegetation regenerated, populations of wild prey species (e.g., rabbits, reptiles) are likely to rebound, diversifying the vultures' diet and increasing the number of chicks reared (**Chapter II**). These findings exemplify a human-mediated trophic cascade, wherein overgrazing disrupts arid ecosystem functioning by decoupling it from climatic drivers. By linking grazing pressure, primary productivity, and scavenger fitness, this work emphasizes that conserving scavengers requires addressing not only direct threats (e.g., poisoning, collisions with human infrastructures, lead intoxication, Donázar et al., 2002) but also the fundamental ecosystem processes that sustain their trophic niche. Scavengers play a pivotal role in maintaining ecosystem stability by accelerating detrital breakdown, reducing disease transmission, and facilitating energy transfer across trophic levels (DeVault et al., 2016; Selva & Fortuna, 2007). However, their dependence on climate-mediated resource pulses makes them particularly vulnerable to anthropogenic disruptions, such as land-use change and altered carcass availability (Barton et al., 2013; Oro et al., 2013). By integrating ecosystem-level drivers into scavenger ecology, this research advances our understanding of how environmental changes reverberate through food webs, with significant implications for ecosystem resilience.

While this work demonstrates how trophic cascades—mediated by primary productivity—shape scavenger populations, the increasing frequency of extreme climatic events adds complexity to these dynamics. Movement ecology analyses revealed that Egyptian vultures exhibit high behavioral flexibility, adjusting their movements in response to challenging flying conditions during dust storms (**Chapter III**). These storms not only reduce visibility (a key constraint on vulture flight) but also exacerbate aridification (Ebrahimi-Khusfi et al., 2022), further degrading an already fragile ecosystem due to livestock overgrazing. Over time, recurrent storms may diminish the vultures' capacity to buffer climate-driven resource scarcity. This vulnerability is particularly critical during energetically demanding life stages, such as breeding season (**Chapter IV**).

Supporting these concerns, we examined how Egyptian vultures balance natural and anthropogenic resources across breeding phases (**Chapter IV**). During chick rearing—a period of exceptional metabolic demand—individuals significantly reduced flight activity, contracted their home ranges in areas with higher ecosystem primary productivity, and paradoxically decreased visits to supplementary feeding stations. This behavior suggests a strategic prioritization of energy-efficient foraging in high-quality natural patches when provisioning offspring. Such adaptations highlight the species' reliance on functional natural ecosystems, yet also expose a vulnerability: that is, if climate-driven aridification degrades these productive patches or disrupts their phenology, vultures may lose their preferred food source during chick rearing. Compounding these threats, dust storms, which are projected to be more intense under climate change (Suárez-Molina et al., 2024), could further limit their ability to locate ephemeral natural resources, forcing dependence on anthropogenic subsidies that may lack nutritional suitability for breeding success (**Chapter II**). Most studies on extreme climatic events focus on single episodes or short-term responses, overlooking the chronic, cumulative pressures revealed by long-term studies like in the present thesis (**Chapter III**). This has strong conservation implications. Under current scenario of global change, where predictions are leaning towards extreme aridification and major habitat loss due to the increasing agricultural and farming intensification, conservation strategies must explicitly link the protection of climate-resilient natural patches (e.g., high productive zones identified in our study) with careful regulated anthropogenic resource provisioning. This dual approach (bolstering natural ecosystem functionality while mitigating resource gaps during climatic stressors) could provide a critical buffer against the interacting threats of habitat loss/degradation, changes in land use and climate instability.

IMPLICATIONS FOR CONSERVATION

This thesis collectively presents findings that could fundamentally transform conservation strategies for the endangered Egyptian vulture. While human-vulture relationships have historically centered on livestock (Moleón et al., 2014), our research highlights two critical dimensions often overlooked in conservation planning: (1) significant variation in nutritional and energetic requirements among vulture species, and (2) intraspecific seasonal fluctuations in these needs. The Egyptian vulture's reliance on a diverse prey base - unlike many sympatric European vultures - makes it particularly vulnerable to conventional conservation approaches. Traditional reliance on supplementary feeding stations provisioned with domestic carcasses assumes uniform resource needs across scavenger communities, despite evidence that Egyptian vultures experience competitive disadvantages in multi-species scavenger guilds (Cortés-Avizanda et al., 2010; Moreno-Opo, Trujillano, Arredondo, et al., 2015). However, previous comparative studies of scavenger guild dynamics have not sufficiently examined: (a) the effects of a diverse diet on breeding success, including more natural prey sources (**Chapter II,** although see Margalida et al., 2012), nor (b) seasonal variation in energy requirements based on movement energy expenditure and feeding requirements between breeding and non-breeding periods (**Chapter IV**). In this respect, our work has demonstrated the intrinsic relationship between primary productivity and breeding success (**Chapter I**), the positive implications of wilder, diverse diet on chick rearing (**Chapter II**), the implications regarding movement as proxy of energy expenditure of climate and extreme climatic events (**Chapter III**), and the distinctive behavioral and energetic adaptations across life-history stage (**Chapter IV**). Together, these findings challenge the efficacy of generalized conservation measures and emphasize the necessity for seasonally adaptive, informed management strategies that account for the species' unique trophic niche.

FUTURE DIRECTIONS

Understanding the indirect ecosystem-level pathways that influence scavenger communities opens new paths for future research. While this study sheds light on how climate-driven productivity and human land use interact to shape scavenger dynamics, many key questions remain, especially regarding the long-term consequences of ongoing global change. Crucial among these is how slowly unfolding processes like habitat degradation, aridification, and altered trophic interactions play out over decades. One of the most urgent needs is the continuation and expansion of long-term ecological monitoring, which remains rare but essential for detecting gradual trends and validating conservation outcomes. The insights gained here were only possible thanks to over twenty years of uninterrupted field data—highlighting the great value of such datasets. Establishing similar monitoring efforts across other regions and ecosystems will be key to evaluate whether the patterns identified here hold true under different environmental conditions and species assemblages.

Future research should also delve deeper into the limits of behavioral plasticity in scavengers. While Egyptian vultures exhibit impressive flexibility in response to climatic challenges—modifying movement patterns to track ephemeral resources or endure fasting periods—it remains uncertain whether such strategies are sustainable as climate extremes become more frequent and severe. Coupling movement ecology with energetic modelling and fitness assessments may help forecast thresholds beyond which behavioral adjustments can no longer compensate for deteriorating conditions. Moreover, targeted experimental interventions at landscape scale could offer critical insight into the mechanisms needed to restore ecosystem functionality. Management measurements such as habitat rewilding would ensure availability of more natural and diverse carcass, thereby supporting more robust scavenger populations. Understanding how these management actions influence ecological linkages across trophic levels will be key for designing effective conservation strategies. As global change accelerates, our ability to sustain key ecosystem services provided by scavengers will depend on how well we understand and manage these intricate dynamics at both local and global scales.

CONCLUSIONS

1. Climate-driven fluctuations in ecosystem productivity can trigger trophic cascades that influence population dynamics of species across food webs. These bottom-up processes are critical for understanding how populations and ecological communities respond to environmental change.

2. Anthropogenic land-use practices, such as livestock farming, can decouple natural climatic controls on ecosystem functioning, leading to habitat degradation and disrupted resource availability for higher trophic levels such as scavengers.

3. Supplementary feeding with anthropogenic resources may not completely replace the natural food resources, especially in systems where nutritional quality and timing are heavily linked to life-history stages and reproductive success.

4. Extreme climatic events, such as dust storms, are becoming more frequent and intense under current climate projections, particularly in arid regions. These disturbances can interfere with the species foraging behaviour, reduce habitat quality, and intensify existing ecological stressors. Therefore, we need to incorporate climate variability and unpredictability into long-term conservation planning.

5. Behavioural flexibility allows species to adjust to changing environmental conditions, but there are limits to how much they can compensate for accelerating habitat degradation and climate change. Identifying environmental shifts is essential for anticipating species’ vulnerability and long-term survival under increasingly unpredictable conditions.

6. Conservation strategies must incorporate ecosystem-level processes, not just species-specific threats. Preserving and restoring climate-resilient habitats is essential for sustaining ecological interactions and services, especially in vulnerable or arid ecosystems.

7. Long-term ecological monitoring is key to capture changes in ecosystems and to evaluate the effectiveness of conservation programs. These datasets are invaluable for revealing indirect and delayed ecological responses to global change.

CONCLUSIONES

1. Las fluctuaciones en la productividad del ecosistema impulsadas por el clima pueden desencadenar cascadas tróficas que influyen en la dinámica poblacional de las especies a lo largo de las redes alimentarias. Estos procesos de tipo ascendente (bottom-up) son fundamentales para comprender cómo responden las poblaciones y las comunidades ecológicas al cambio ambiental.

2. Las prácticas de uso del suelo de origen antropogénico, como la ganadería, pueden desacoplar los controles climáticos naturales sobre el funcionamiento del ecosistema, lo que lleva a la degradación del hábitat y a una disponibilidad de recursos alterada para los niveles tróficos superiores, como los carroñeros.

3. La alimentación suplementaria con recursos de origen humano puede no reemplazar completamente los recursos alimenticios naturales, especialmente en sistemas donde la calidad nutricional y el momento de disponibilidad están estrechamente vinculados a las etapas del ciclo de vida y al éxito reproductivo.

4. Los eventos climáticos extremos, como las tormentas de polvo, están volviéndose más frecuentes e intensos según las proyecciones climáticas actuales, especialmente en regiones áridas. Estas perturbaciones pueden interferir con el comportamiento de forrajeo de las especies, reducir la calidad del hábitat e intensificar los factores de estrés ecológico existentes. Por lo tanto, es necesario incorporar la variabilidad y la imprevisibilidad climáticas en la planificación de la conservación a largo plazo.

5. La flexibilidad conductual permite a las especies adaptarse a condiciones ambientales cambiantes, pero existen límites en cuanto a cuánto pueden compensar la degradación acelerada del hábitat y el cambio climático. Identificar los cambios ambientales es esencial para anticipar la vulnerabilidad de las especies y su supervivencia a largo plazo en condiciones cada vez más impredecibles.

6. Las estrategias de conservación deben incorporar procesos a nivel de ecosistema, no solo amenazas específicas para cada especie. Conservar y restaurar hábitats resilientes al clima es esencial para mantener las interacciones ecológicas y los servicios ecosistémicos, especialmente en ecosistemas vulnerables o áridos.

7. El monitoreo ecológico a largo plazo es clave para captar los cambios en los ecosistemas y evaluar la efectividad de los programas de conservación. Estos conjuntos de datos son invaluables para revelar respuestas ecológicas indirectas y retrasadas ante el cambio global.

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ANNEX:

Supplementary Material for Chapter I

Ecosystem productivity drives the breeding success of an endangered top avian scavenger in a changing grazing pressure context.

Figure S1: Raw data for the response variable and the explanatory variables fitted in the MARSS model corresponding with the first model selected by AICc. In red, the year 2012 where we propose the regime shift. We have added the annual NDVI for comparative purposes between the NDVI from 6 months before breeding season and the annual NDVI.

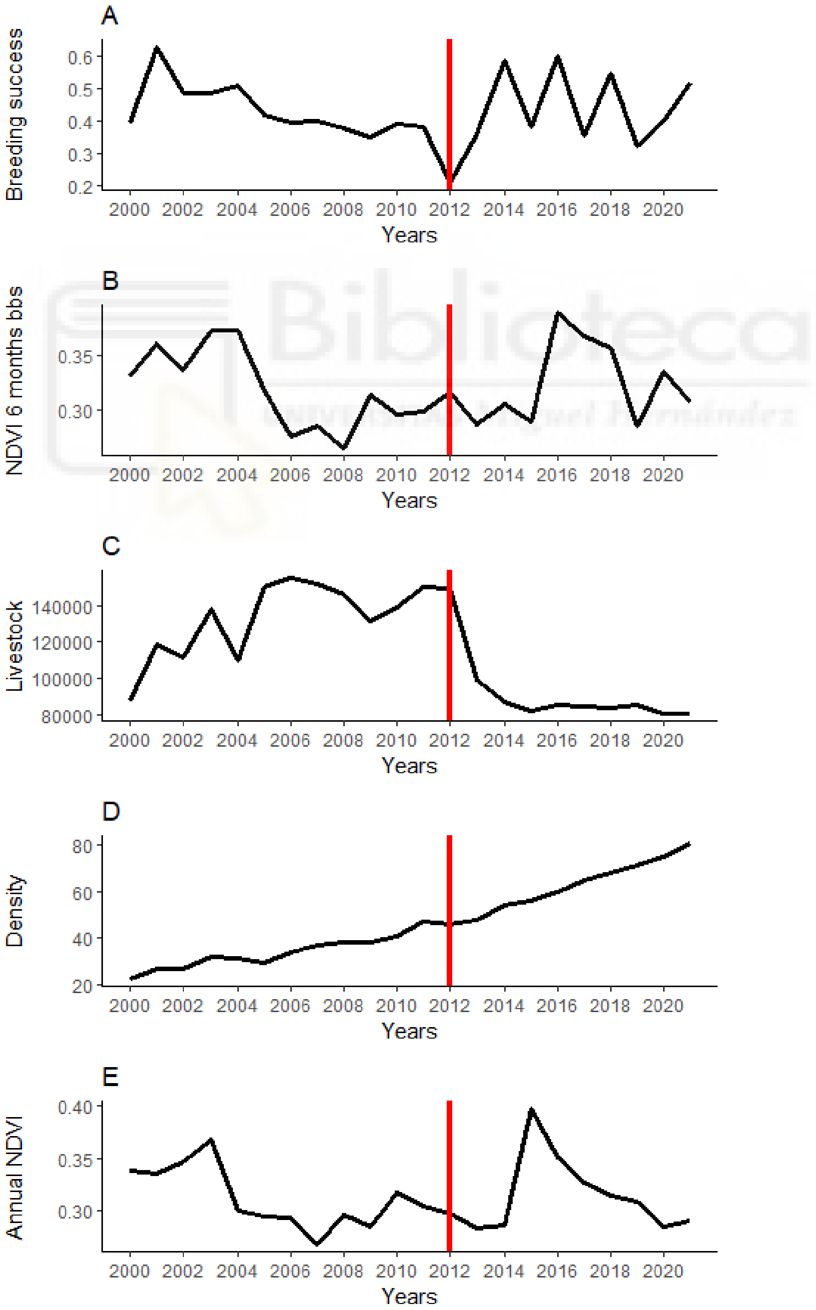
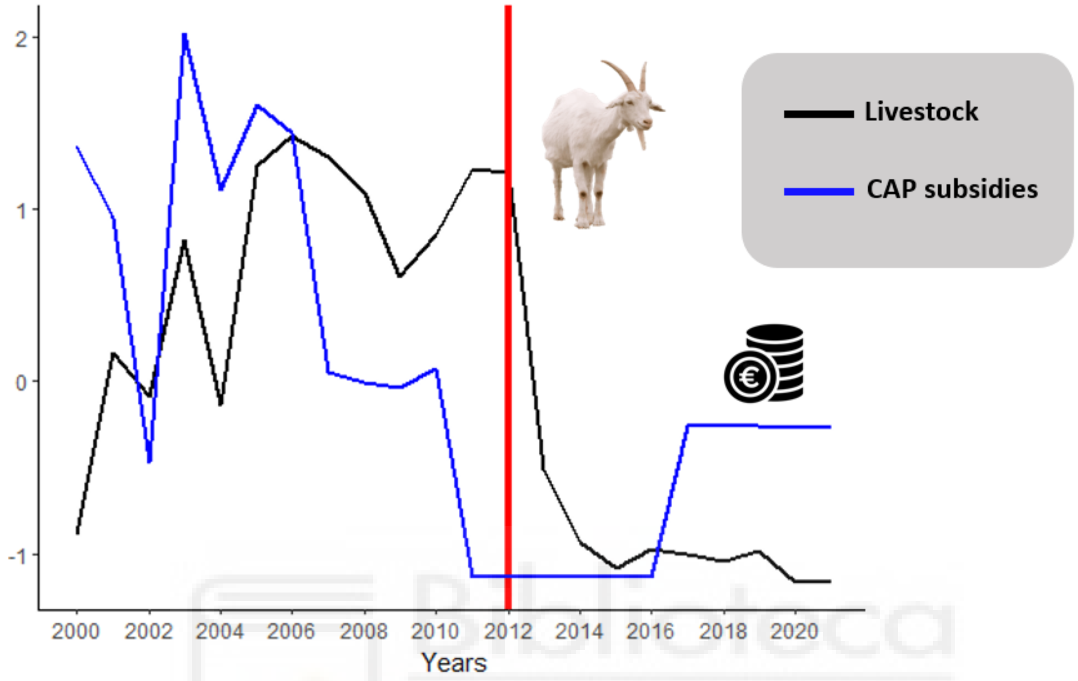


Figure S2: Amount of livestock (black line) and direct financial aid from the Common Agricultural Policy (CAP, blue line) among the years. The vertical red line corresponds with the year 2012 and represents the threshold where we propose the regime shift. Both variables are scaled for comparative purposes.



Supplementary Material for Chapter II

Overgrazing triggers cascading effects on a top avian scavenger: long-term changes in diet and breeding success.

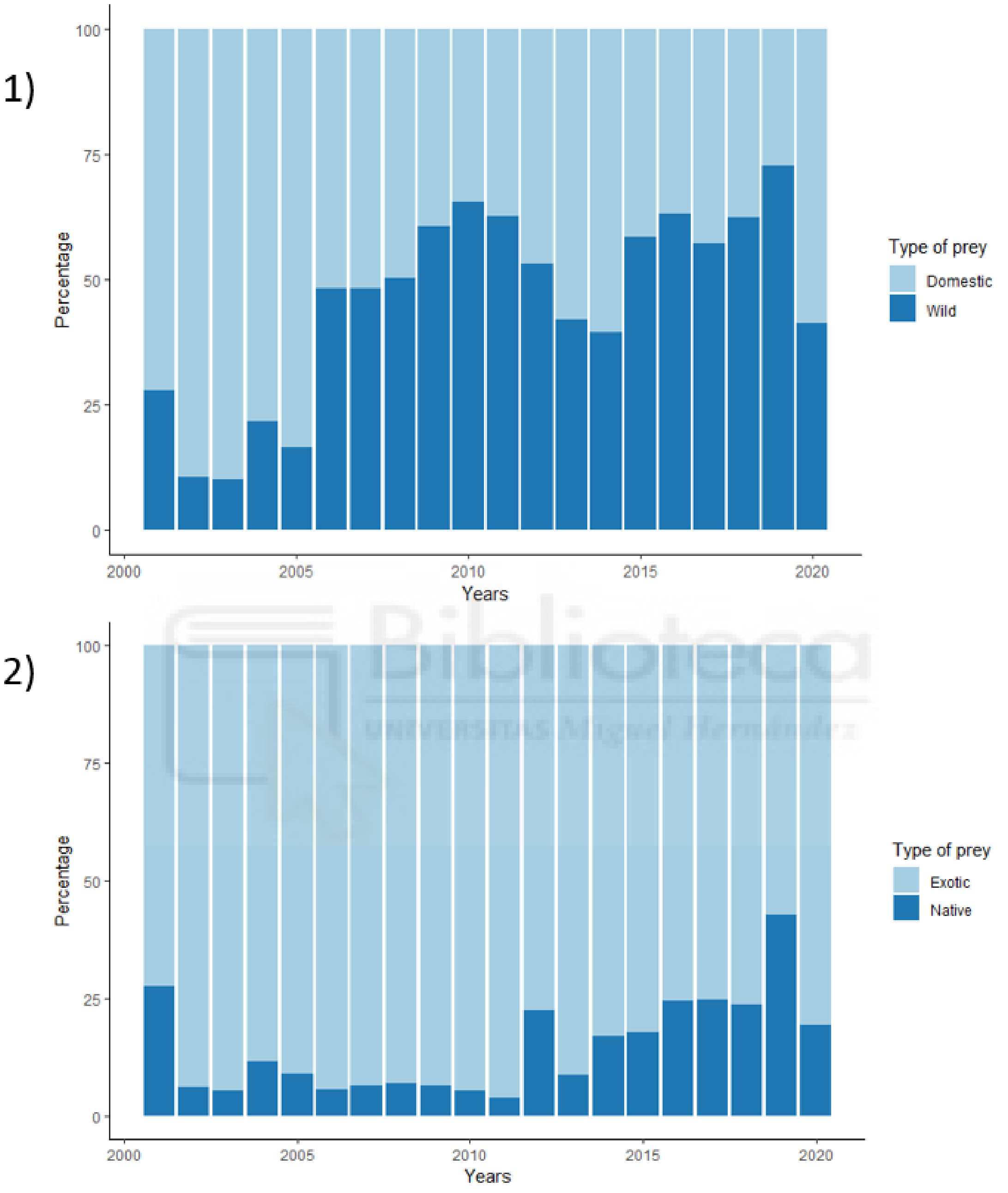


Figure S1: Percentage of 1) Domestic vs. wild prey and 2) Native and exotic prey in the 15 territories of Egyptian vultures.

Table A1: Comparison of the first ten models resulting from the dredge procedure performed for the response variables *Diversity* and *Breeding success*. Models are ordered by AICc. AICc stands for Akaike's Information Criterion corrected for small samples, delta is the ΔAICc, logLik is the log Likelihood and df is degrees of freedom.

Variables for Diversity models	df	logLik	AICc	delta	weight
Wild + Grazing + Wild:Grazing	5	-91.2	192.6	0.0	0.5
Wild + Grazing + Wild:Grazing + Precipitation	6	-91.0	194.4	1.8	0.2
Wild + Grazing + Wild:Grazing + NDVI	6	-91.1	194.6	2.0	0.2
Wild + Grazing + Wild:Grazing + Precipitation	7	-90.9	196.4	3.8	0.1
Wild + Grazing	4	-95.1	198.4	5.8	0.0
Wild + Grazing + Precipitation	5	-94.9	200.0	7.4	0.0
Wild + Grazing + NDVI	5	-95.1	200.5	7.9	0.0
Wild + Grazing + Precipitation + NDVI	6	-94.9	202.2	9.5	0.0
Wild	3	-101.0	208.1	15.5	0.0
Wild + Precipitation	4	-100.4	209.0	16.3	0.0

Variables for Breeding success models	df	logLik	AICc	delta	weight
Diversity + Wild + Grazing	4	-204.9	418.0	0.0	0.1
Wild + Grazing	3	-206.4	419.0	1.0	0.1
Diversity + Grazing	3	-206.7	419.5	1.5	0.1
Diversity + Wild + Grazing + Marine	5	-204.6	419.5	1.6	0.1
Diversity + Wild + Grazing + Precipitation	5	-204.6	419.6	1.6	0.1
Diversity + Wild + Grazing + NDVI	5	-204.8	419.9	1.9	0.1
Wild + Grazing + Precipitation	4	-206.2	420.7	2.7	0.0
Diversity	2	-208.4	420.8	2.8	0.0
Diversity + Grazing + NDVI	4	-206.3	420.8	2.8	0.0
Wild + Grazing + NDVI	4	-206.3	420.9	2.9	0.0

Supplementary Material for Chapter III

Riders on the Storm? Saharan dust disrupts movement patterns of an endangered top scavenger

Supporting Information Text

Methods.

All the statistical analyses were performed using the R statistical software, version 4.1.2, with the *stats* package (R Core Team, 2013) for confidence intervals, the *lme4* package (Bates et al., 2015) for the LMM analysis, the *dredge* function for model ranking (MuMIn package, (K. Barton, 2019)), the *rsq.glmm* function from the *rsq* package for R^2 and *lsmeans* (Russell L, 2018) for Tukey’s post-hoc test.

Table S1. Comparison of the models resulting from the modelling procedure that included the variable Dust conc (Dust concentration) as a fixed variable. In bold, the best model selected.

Intercept	Age	Duration	Dust conc	Sex	Dust conc:Sex	df	logLik	AICc	delta	weight
-0.216			**-0.061**	**+**	**+**	**6**	**-117,758.3**	**235,528.5**	**0.000**	**0.970**
-0.215			-0.074	+		5	-117,763.1	235,536.3	7.741	0.020
-0.215		-0.002	-0.057	+	+	7	-117,762.0	235,538.0	9.413	0.008
-0.083			-0.074			4	-117,767.6	235,543.2	14.675	0.000
-0.215		-0.002	-0.070	+		6	-117,767.0	235,545.9	17.374	0.000
-0.082		-0.002	-0.070			5	-117,771.4	235,552.8	24.281	0.000
-0.211		-0.012		+		5	-117,941.2	235,892.4	363.802	0.000
-0.078		-0.012				4	-117,945.5	235,899.1	370.508	0.000
-0.218				+		4	-118,031.8	236,071.5	542.976	0.000
-0.085						3	-118,036.2	236,078.4	549.801	0.000

Table S2. Comparison of the models resulting from the modelling procedure that included the variable Events as a fixed variable. In bold, the best model selected.

Intercept	Age	Duration	Events	Sex	Age:Events	Events:sex	df	logLik	AICc	delta	weight
-0.2915	**+**		**+**	**+**			**7**	**-30,942**	**61,898**	**0.000**	**0.787**
-0.2639	+		+	+		+	9	-30,942	61,902	3.472	0.138
-0.1640	+		+				6	-30,946	61,904	5.219	0.057
-0.3118	+	0.0025	+	+			8	-30,945	61,907	9.013	0.008
-0.2868	+		+	+	+		9	-30,945	61,909	10.812	0.003
-0.2843	+	0.0026	+	+		+	10	-30,945	61,911	12.258	0.002
-0.1840	+	0.0025	+				7	-30,949	61,913	14.310	0.001
-0.2615	+		+	+	+	+	11	-30,945	61,913	14.765	0.000
-0.1593	+		+		+		8	-30,949	61,914	16.050	0.000
-0.3090	+	0.0031	+	+	+		10	-30,948	61,916	17.959	0.000
-0.2835	+	0.0030	+	+	+	+	12	-30,948	61,920	22.131	0.000
-0.1810	+	0.0030	+		+		9	-30,952	61,922	23.291	0.000
-0.3235			+	+			6	-30,963	61,938	39.783	0.000
-0.2951			+	+		+	8	-30,962	61,941	42.638	0.000
-0.2023			+				5	-30,966	61,942	43.507	0.000
-0.3283		0.0005	+	+			7	-30,969	61,952	53.269	0.000
-0.3004		0.0006	+	+		+	9	-30,968	61,954	56.064	0.000
-0.2072		0.0005	+				6	-30,971	61,955	56.987	0.000
-0.1566	+	-0.0057		+			6	-31,098	62,208	309.181	0.000
-0.0289	+	-0.0057					5	-31,101	62,213	314.534	0.000
-0.1648	+			+			5	-31,111	62,232	334.050	0.000
-0.0366	+						4	-31,115	62,238	339.692	0.000
-0.1852		-0.0071		+			5	-31,121	62,252	353.486	0.000
-0.0642		-0.0071					4	-31,124	62,256	357.233	0.000
-0.2023				+			4	-31,146	62,300	401.449	0.000
-0.0822							3	-31,149	62,304	405.198	0.000

Supplementary Material for Chapter IV

Table A1: Results from the gam.check performed on the first analysis (Breeding movement pattern).

Variable	k'	EDF	k-index	p-value
s(Wind)	3	2.92	0.99	0.310
s(Precipitation_acc)	3	2.86	1.01	0.725
s(Age)	3	2.90	1.00	0.620
s(Temperature_max)	3	2.99	0.98	0.145
s(Dust)	4	2.56	0.98	0.095
s(PVC)	34	31.63		

Table A2: Results from the gam.check performed on the second analysis (Time budget).

Location	Variable	k'	EDF	k-index	p-value
HPFP	s(Temperature_max)	5	2.37	0.99	0.33
	s(Wind)	5	1.00	0.99	0.275
	s(Dust)	5	2.22	0.95	0.015
	s(Precipitation_acc)	5	1.39	0.93	<2e-16 ***
Farms	s(Temperature_max)	9	5.44	1.00	0.56
	s(Wind)	9	1.72	0.99	0.28
	s(Dust)	9	5.73	0.99	0.13
	s(Precipitation_acc)	9	1.19	1.00	0.52

Table A3: Results from the gam.check performed on the space use analysis (KUD95 and KUD50).

Analysis	Variable	k'	EDF	k-index	p-value
KUD95	s(NDVI)	9	1	0.88	0.16
	s(Temperature_sp)	9	1	1.23	0.94
	s(year)	8	4.94		NA
	s(N_Farms)	9	1	1.15	0.8
KUD50	s(NDVI)	9	1	0.98	0.36
	s(Temperature_sp)	9	2.46	1.19	0.82
	s(Precipitation_sp)	9	1	0.83	0.09
	s(Year)	8	0		NA
	s(N_Farms)	9	1	0.88	0.16

APPENDIX 2:

Figure S1: Smoothing effects of all the explanatory variables fitted in the GAMM (Generalized Additive Mixed Model) for the movement patterns analysis. Grey colored shaded area corresponds to the 95% confidence interval, ticks in the X-axis represent location of observations along the predictors. Blue dots represent the residuals of the model.

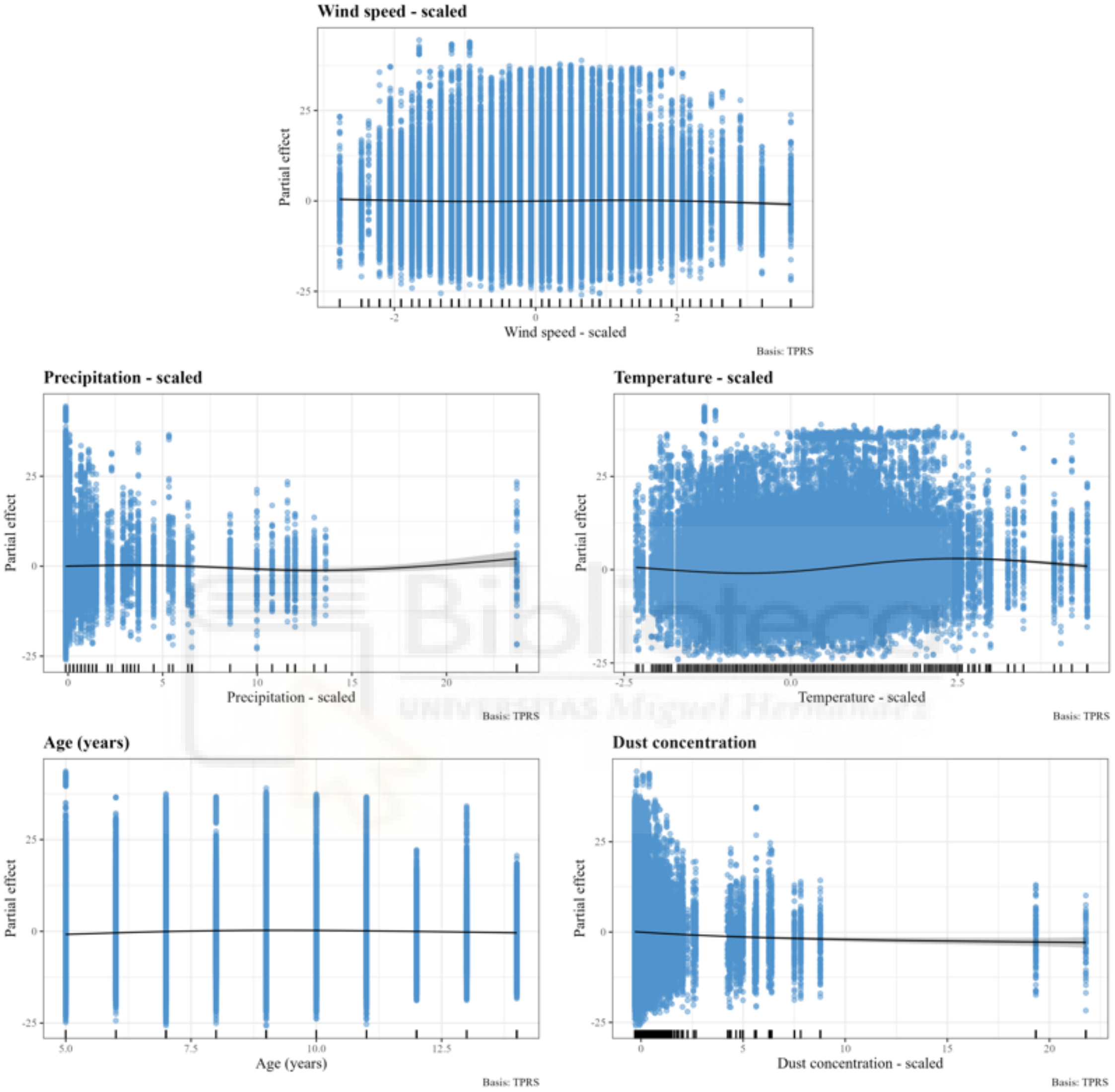


Figure S2: Smoothing factors for the models corresponding with those localizations at farms and Highly Predictable Feeding Places (Tiscamanita and Villaverde feeding stations and the Urban Waste facility). Grey coloured shaded area corresponds to the 95% confidence interval, ticks in the X-axis represent location of observations along the predictors. Blue dots represent the residuals of the model. For the farm models, only temperature, wind speed and dust concentration were significative. For HPFP, only temperature and wind were significative.

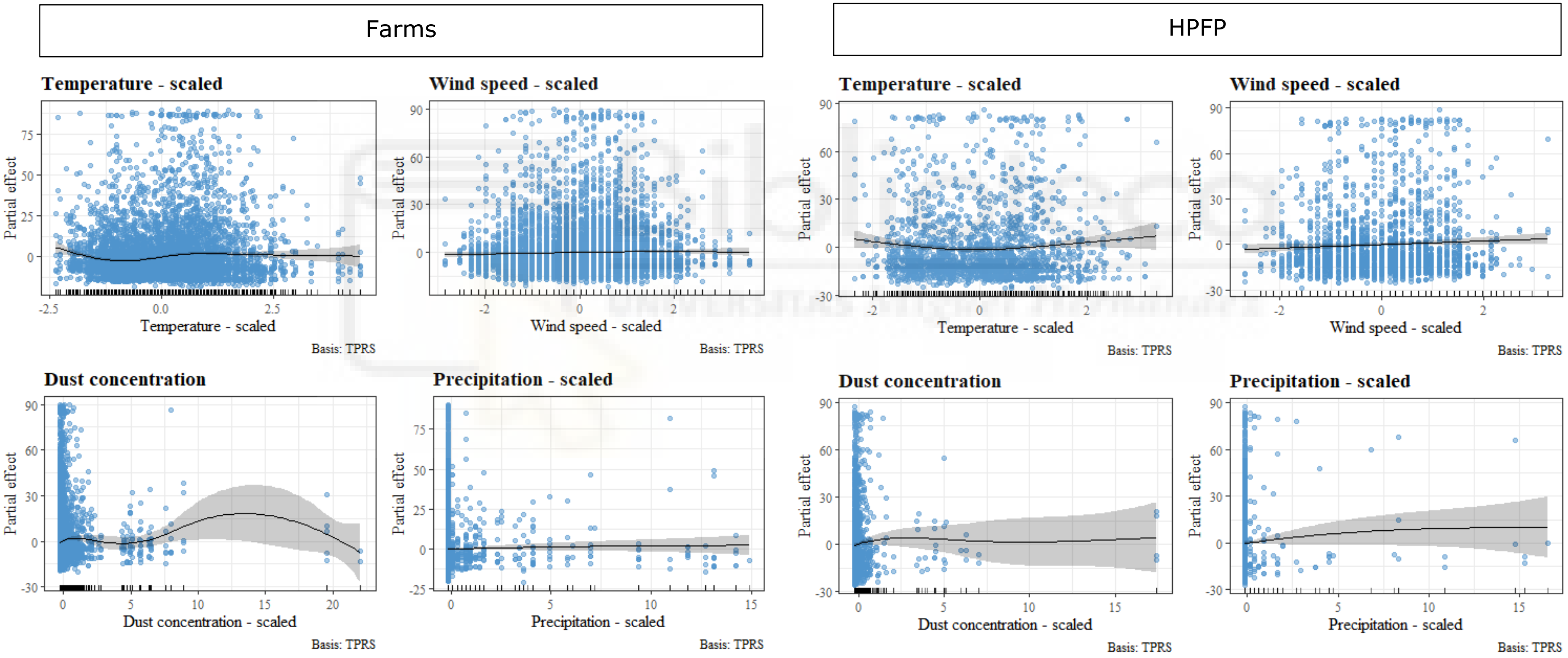
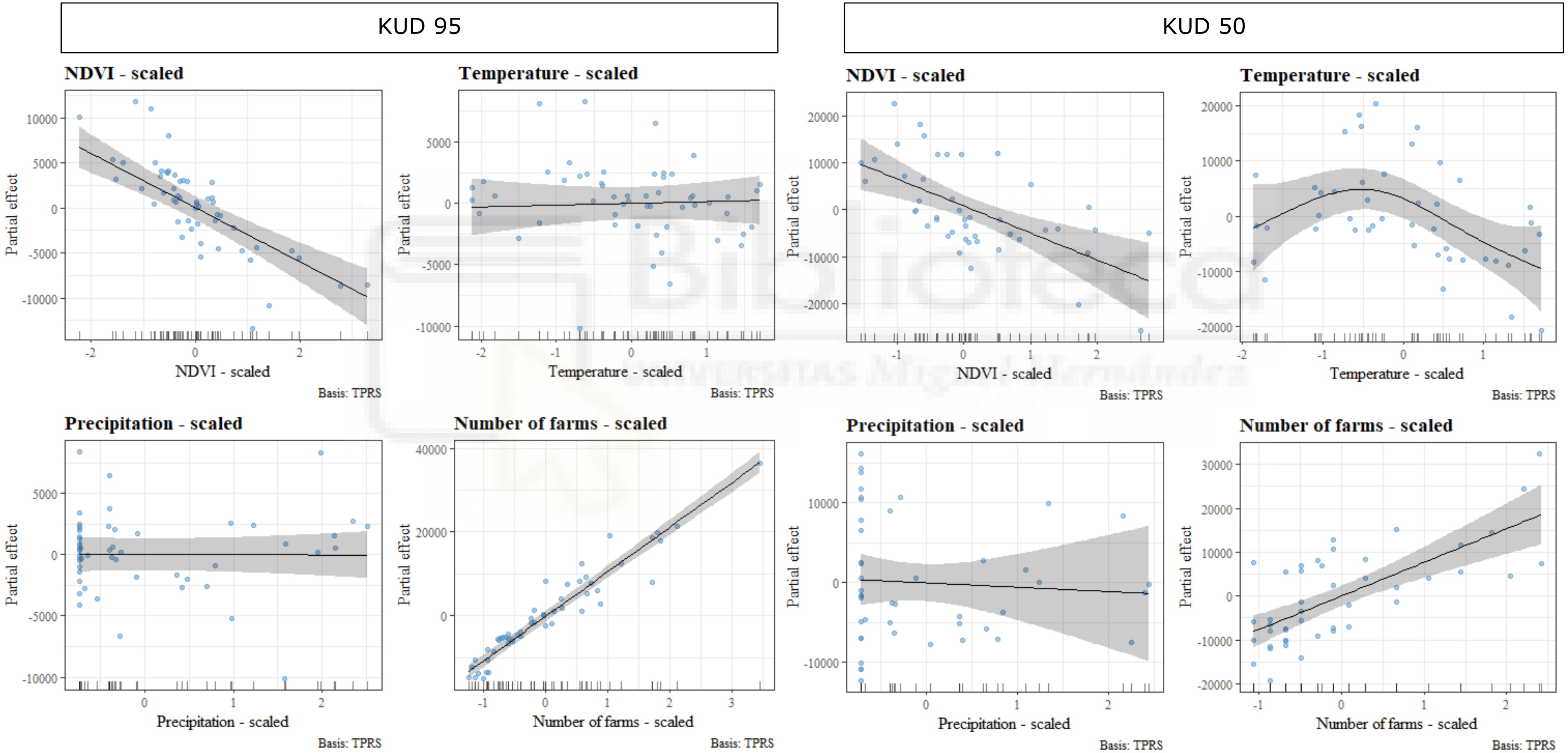


Figure S3: Smoothing effects of all the explanatory variables fitted in the GAMM (Generalized Additive Mixed Model) for the space use analyses. The graphic A is for the KUD 95, and the B is for the 50 KUD. Grey coloured shaded area corresponds to the 95% confidence interval, ticks in the X-axis represent location of observations along the predictors. Blue dots represent the residuals of the model.



AGRADECIMIENTOS

Comencé esta tesis doctoral en octubre de 2020, año de la pandemia, donde por no poder, no podíamos estar más de tres personas por despacho, ni más de 5 en una mesa en un bar. Con esas me mudé a Elche, el punto de partida de esta aventura. A lo largo de estos cinco años, han sido muchas las personas en acompañarme (y a veces, empujarme). Intentaré no dejarme a ninguna.

Lo primero de todo, gracias infinitas a mis directores, Toni y Jomar. Toni, gracias por los paseítos por el campo, por ir "a ver que se cuece" por Fuerteventura, Cazorla, Espuña…Por la paciencia y por los consejos de la vida y esas llamadas cuyo objetivo era: "¿Estás bien? ¿Estás contenta?". Jomar, gracias por las charlas y las risas, también por los paseos y por las conversaciones sobre la ciencia y la vida. A ambos, gracias por incentivar mi creatividad, por darme la libertad de explorar mis ideas y por guiarme siempre por buen camino. Esta tesis, definitivamente, no hubiera sido posible sin vosotros.

A mi familia, qué decir. Gracias por el apoyo, el cariño y los ánimos. A mis padres, por la infancia con las rodillas peladas, las uñas con barro y la banda sonora de verano constante de las chicharras y las tórtolas. Por siempre animarnos a estar fuera, que nos diera el aire y jugáramos en el campo e, inconscientemente, inculcar en mí la curiosidad por lo natural. A mi madre, especialmente, por siempre creer en mí, a lo "madre Pantoja" y llevarme por bandera allá donde iba. Esta tesis es un poquito tuya también.

A toda la gente que me guio y acompañó desde los inicios en la EBD. A Pedro, que fue mi primer amigo de este mundo de la investigación. A día de hoy, eres familia. Sin tu ayuda y apoyo desde el minuto uno, esta tesis jamás hubiera existido. A Martina Carrete, por darme la oportunidad de iniciarme en la ciencia. A Álvaro Luna, por animarme a seguir en la ciencia, y por tu ayuda vital con el TFG. A Marina y Eneko, que me guiaron en este mundillo de buitres desde el primer día con mi TFM, y que hoy día siguen siendo referentes en muchas otras cosas. A Josean y Ainara, mis directores del TFM, por iniciarme en este mundo de la investigación, y en particular Josean, por haber sido mi "director en la sombra" todos estos años. A Manuel de la Riva, por los correítos y las mil dudas y la paciencia. También en esa misma época, a mis compis de máster, a mi Nudicom, por todo lo compartido ese y el resto de los años. En especial Patri, Mireia y Anna. Esas cervezas obligatorias en la alameda post-reunion con los tutores de TFM salvaron mi salud mental.

Centrándome ya en el periodo de la tesis doctoral, he de agradecer a mis primeros compis de despacho, Roberto P., Nati y Lara. Gracias por acogerme como un pollito más cuando no sabía ni por donde me venía el aire. Robe, por los ánimos, Nati, por los ratitos pajareros y los consejos, Lara, por las charlas sobre la ciencia y los libros, y por el apoyo y la amistad que vinieron detrás. Andrea, que justo nos incorporamos juntas, gracias por escucharme cuando necesitaba ventilar, y por navegar juntas estos años de incertidumbre doctoral. Marina, por los eternos cafés y los intercambios de consejos y trucos aprendiendo el MARSS model. Creo que tendré pesadillas con ese modelo unos cuantos años más. A los pocos años de empezar esta aventura, se incorporó Irene, a darle un poco de salsa a la sala predoc. Irene, gracias por los ánimos y los piropos, y por estar dispuesta a unas risas, llantos y charlas sobre feminismo y política. No siempre en ese orden. Adrian (sin tilde), gracias por la frescura y los ratitos de campo, y los consejitos de maquetación. A los profes, Paco, Andrés y Eva. Paco, gracias por la sabiduría, los cafés y ayudar a relativizar y simplificar la vida. A Andrés y Eva, por la paciencia cuando me tocó aprender a dar clase y por la ayuda sobre cómo afrontar esa y otras etapas. A Esther, gracias por el apoyo y las charlas sobre la mujer y la ciencia, y por ofrecer tu perspectiva y ánimo siempre.

A los moradores de la sala postdoc: Vicky, Roberto R., Josema, Mario…Gracias a todos por los consejos y los ratitos compartidos. Especial agradecimiento a Roberto R., por no sólo organizarnos la agenda cultural y de ocio del departamento, sino por siempre sacar un huequito para hablar, preguntar y siempre estar dispuesto a ayudar con todo, a pesar de tener más agenda que un ministro. Al hilo de esto, Marcos, gracias por las risas, el teatro y las arepas. No podía dejarme atrás, sobre todo en el tema risas y comidas, a los chicos de la sala de abajo; el team tortu: Nuria, Andrés, Dani, Piqueras, Will, Marta…Gracias por dar vida allá por donde pasáis. Otro morador temporal de la sala de abajo fue Jon. Eternamente agradecida por los consejos, los códigos de R y siempre tener una oreja lista para escuchar y aconsejar.

Con el paso de los años en esta nuestra universidad, empezaron a sumarse caras nuevas: Claudio, Mario y David. Gracias por la ayuda en el campo, los cernícalos, alcaravanes, garcillas…y todos los relíos pajareros que se nos ocurrirán. Y hablando de relíos pajareros, no podía faltar Oscar, esa gran presencia (silenciosa). Gracias por los días anillando en el Clot, censando dormideros, por sacarme al campo cuando necesitaba desconectar, y por compartir la infinita sabiduría que tienes de todo lo natural.

Tampoco podían faltar aquí toda la gente que me acompañó durante mi estancia en la Universidad de Swansea. A Luca, por ser mi mentor y dedicarme tantas horas y paciencia delante del ordenador haciendo números, y por acogerme en tu casa en las fiestas donde a mí me faltaba la mía. To all the phD students and postdocs from the Biosciences department: Felipe, Lucie, Hywel, Lucía, Elliot, Marco, Manos, Ale, Marina (and Andrea)…Thank you so much for making Swansea a temporary home, not just a place to stay. To Felipe, particularly, thanks for the mid-week beers. They worked wonders on my mental health. Also, thanks to Emily and Rory, the conversations in Spanish were a breath of fresh air (from home) during my stay.

Ya va llegando el final de esta parrafada, y toca dar las gracias especiales a dos personas que han hecho de Elche un hogar donde querer quedarse. Juanma, gracias por ser amigo, mentor, compañero de paseos perrunos, y marido del trabajo. Isa, gracias por ser amiga, confidente, compañera de paseítos e incitadora de vermús. Habéis sido las grapas de mi cordura en más de una ocasión. Gracias por las noches de terracita y cerveza, y por ser compañeros de aventuras.

Y, por último, lo mejor para el final. Si hay una persona que se merece un gracias tan extenso como esta tesis, eres tú. Antonio, gracias por ser el mejor compañero de vida. Gracias por los ánimos constantes, por los cafés por la mañana los días que sabías que iban a ser duros. Por acompañarme en esta aventura que nos llevó a nuevas tierras sin dudar ni un segundo. No podría haber elegido mejor copiloto de viaje. Te quiero.