Individual and environmental drivers of resource use in an endangered vulture:

Integrating movement, spatial and social ecology

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TESIS DOCTORAL

Individual and environmental drivers of resource use in an endangered vulture:

Integrating movement, spatial and social ecology

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al título de Doctora por la Universidad de Sevilla

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Abstract

The study of animal movement makes possible to understand how the spatial context influences individuals and populations, something especially important for species with high movement abilities able to wander routinely over large areas and face diverse human-mediated threats at different spatial scales. Vultures are long-lived scavenging vertebrates with delayed maturity and low fecundity, often exhibiting complex social behaviours. European and most of the Old World vulture populations have been historically dependent on the spatial distribution of human-provided resources. Currently, they are endangered worldwide suffering regional dramatic declines of up to 90% mainly provoked by direct and indirect persecution, infrastructure development and decrease in food resources. Effective vulture conservation requires spatially-explicit understanding of how vultures cope with resource availability and human induced transformation.

In this thesis, we used spatial data collected between 2013 and 2018 from 49 GPS-tagged Canarian Egyptian vultures (*Neophron percnopterus majorensis*). The bulk of this endemic subspecies is concentrated in Fuerteventura Island where it depends on extensive goat farms, currently changing towards semi-intensive and intensive regimes. In addition, it suffers from high mortality in power lines. Movement information is combined with individual characteristics, life-history stages, and detailed data on the spatial distribution of territories, feeding resources, and human facilities. Particularly, we examined i) drivers of the use of power lines, ii) foraging tactics according to spatiotemporal variation in food predictability and individual characteristics, iii) drivers of use of livestock farms, and iv) farmers' perception about the target species in relation to the observed spatial behaviour.

Vultures' behaviour was influenced by the distribution, predictability and amount of feeding resources, as well as by the spatial distribution of conspecifics and sources of human disturbance. At the same time, individual attributes such as sex, age, territorial status or social rank interacted with environmental cues to shape movements. Overall, vultures somewhat avoided humans by selecting farms and electric pylons far from roads or urban areas. Importantly, the predictable food resources provided by the main feeding station determined an intensive use of electric pylons and farms in its proximity. Use of both resources were however complex according to individual traits and life-history stages. Territorial status and social position in the dominance hierarchy shaped sex-specific patterns of feeding preferences, with dominant breeding females, but not males, using predictable food more intensively and choosing to settle in nearby territories. The distribution of territories affected

in turn the selection of pylons and farms by both territorial and non-breeding individuals, highlighting the close interdependency and feedback between the spatial structuring of the population and the distribution of resources. Non-territorial individuals avoided resources located close to occupied breeding territories meanwhile territorial ones preferred those close to their nest, these spatial constrains being less obvious during the non-breeding season. After disentangling how those factors influence the intensity of use electric pylons, we combined predictions combined with actual mortality showing that prioritizing mitigation measures on relatively few pylons could drastically reduce accidents.

Finally, farmers perceived Egyptian vultures as the most beneficial avian scavenger in the island, but owners of larger farms, which were more visited but frequently more mechanized than smaller ones, were less aware of vulture presence in their exploitations. This suggests a potential influence of modernization in livestock practices on disconnecting people from ecosystem services provided by wildlife. Moreover, the consistency between awareness and GPS data increased when vultures were more present in farms or their surroundings, indicating that scarce and endangered species are more susceptible of suffering misperception.

Our findings are important from an applied point of view in a context of rapid changes in traditional livestock practices and power development, offering sound scientific knowledge that allows to make informed management decisions. The complex network of factors and patterns should be considered in the management of electric infrastructures, predictable and semi-predictable resources, or social actions for vulture conservation. General solutions ignoring population structure and the spatial distribution of territories, feeding sources or human footprint should be avoided since those could lead to unbalanced impacts between population fractions that could compromise the effectiveness of management and conservation actions.

Introduction

Conservation biology is the scientific discipline that study causes and solutions for the massive loss of biodiversity that the planet is currently suffering by anthropogenic activities (Pimm et al., 1995; WWF, 2018). Knowledge about ecosystems, communities, populations, species and their threats is essential to conserve them. The detrimental impact of human activities could not be completely removed because human footprint is inherent to the development of human-beings. Hence, we should afford conservation issues looking for a balance between human actions and nature. As our resources are limited, the prioritization on more severe threats is necessary to achieve more efficient remedies (Brooks et al., 2006), which has become biodiversity conservation into one of the most important environmental challenges. For this reason our main goal is to increase the knowledge needed to face this challenge. Together with researches at ecosystem or community levels, the comprehensive study of populations is still necessary because general approaches may not be able to solve the problems faced by particular species. Focusing on conservation of animal species, the study of behavioural ecology is considered the most cost-effective way to improve conservation (Berger-Tal and Saltz, 2016; Bro-Jørgensen et al., 2019; Caro, 2016; Greggor et al., 2016). How and why animals behave the way they do partially explains fitness outcomes (fecundity, survival) under anthropogenic-altered conditions (Candolin and Wong, 2015; Sih et al., 2011, 2004; Tuomainen and Candolin, 2011).

Within this context, animal movement has a major role. Movement, considered as any change in the spatial location of an individual, determines the whole life of animals, affecting populations, and percolating to communities, ecosystems, and ultimately biodiversity (Nathan et al., 2008 and references there). Until recently, the basic limitations for studying this aspect were mainly the lack of technology for collecting movement data and the absence of a sound conceptual framework. Just 20 years ago, collecting movement information required huge efforts, but recent advances in tracking technology had led to exponential improvement in the study of accurate and precise animal movements through space and time (Kays et al., 2015). Additionally, a robust theoretical background has not been developed until recent years (e.g. Nathan et al., 2008). The field of movement ecology emphasizes the need of understanding how animals time their movements through space and the scale at which movement occur, and this has the potential of providing relevant data to guide management decisions (Allen and Singh, 2016; Barton et al., 2015; Wilmers et al., 2015). Individuals access resources, interact with conspecifics or avoid risks by movement behaviour (Lima and Zollner, 1996), thus movements research in populations of endangered species is a crucial step to address conservation challenges (Kays et al., 2015; Wittemyer et al., 2019). For example, detailed movement data allows making precise inferences regarding resource and habitat use and their drivers, understand in much more detail how the spatial context influences demographic parameters and population dynamics, or anticipate how animals will adapt to environmental changes at different spatial scales.

Most studies of resource use, habitat selection and population dynamics has traditionally consider all individuals as ecologically interchangeable, focusing on average population-level processes because of being the most “parsimonious” (Bolnick et al., 2003; Kendall and Fox, 2002; Vindenes and Langangen, 2015). However, mainly during the past decade, the so-called individual heterogeneity or intraspecific variation has been increasingly recognized as a strong factor shaping ecological and evolutionary processes, thus having great conservation implications (Biro and Stamps, 2010; Bolnick et al., 2011, 2003; de Valpine et al., 2014; Kendall and Fox, 2002; Killen et al., 2017; Sih et al., 2015; Vindenes and Langangen, 2015). Conspecific individuals differ in many traits, not only in obvious features such age, sex or morphology, but also in behaviour or physiology, which affect their expected fate (Bolnick et al., 2011; Greenwood, 1980; Kendall and Fox, 2002; Penteriani et al., 2013; Serrano and Tella, 2007). In the same way, when studying movement behaviour, averaging populations may prevent clarifying why and how individuals move.

Vultures

In order to account for between-individual heterogeneity in movement patterns, which could be organized by sex, age, or other ways, it is necessary to develop individual-based researches (Delgado et al., 2018; Holyoak et al., 2008). For these reasons, this thesis has been developed with individual-level data to take into account intraspecific variation in movement patterns, using a vulture species as study model. Vultures are long-lived scavengers that contribute to maintain energy flow fast in food webs and act as facilitators for facultative scavengers (Putman, 1983). They are responsible for carcass removal and indirectly regulating population of others scavengers which are disease vectors (Pain et al., 2003; Prakash et al., 2003), so they control the spread of diseases (Ogada et al., 2012a, 2012b; Whelan et al., 2008) thus providing ecosystem services and ecological functions which have an important role on both human and ecosystem well-beings (Moleón et al., 2014; Sekercioglu et al., 2016). Currently, they are severely threatened worldwide mainly due to non-natural causes, with 69% of species endangered or near-threatened according to the IUCN and being the most endangered avian functional guild

(Ogada et al., 2016, 2012a; Sekercioglu et al., 2016). Their decline began in the mid-19th century in Europe and North America (Mingozzi and Estève, 1997; Snyder, 1983) and it has been particularly fast and dramatic in Asia and Africa, where about 90% of vulture populations have disappeared in the last decades (Koenig, 2006; Ogada et al., 2012a; Proffitt and Bagla, 2004). The main causes of mortality according to Ogada et al., 2012a are: (1) Indirect or unintended poisoning; (2) Lead ingestion; (3) Human persecution; (4) Accidents with power lines; (5) Collisions with wind turbines blades; (6) Lack of food; and (7) Changes in habitats. For these reasons, vultures are common targets of conservation actions (Badia-Boher et al., 2019).

Vultures are usually social species, having complex social dynamics and concentrating massively at specific places, such as roosting places or predictable feeding points. In areas with scarcity of trees, the use of power lines for perching and roosting is frequent with the subsequence risk of mortality by electrocution (Angelov et al., 2012; Benson, 1981; Donázar et al., 2002b; Lehman et al., 2007; Mainwaring, 2015; Phipps et al., 2013), which increases in more social species due to communal roosting habits (Arkumarev et al., 2014; Donázar et al., 2002b, 1996a). Additionally, they are highly dependent on the spatial distributions of feeding resources, so the concentration of carrion derived from human activity in certain places (farms, supplementary feeding stations) involves major effects at the individual level (García-Heras et al., 2013), on the spatial structure of populations (Carrete et al., 2007) and on within-guild relationships (Cortés-Avizanda et al., 2012).

Vultures, as an ecological group with common adaptations and common roles in ecosystems, are of particular interest in the study of animal movement. These birds have evolved in a context of highly unpredictable resources, developing flight skills to cover vast areas expending relatively little energy. This has strong conservation implications since their foraging movements easily involve several administrative units (e.g. localities, regions, countries) that hinder management and conservation measures. From an ecological point of view, these movement patterns lead to a huge and complex amount of environmental interactions at large spatial scales, which makes difficult collecting information and unravelling the potential factors influencing their behaviour, ecology and conservation. Moreover, vultures have deferred-maturity which involves a long pre-adult stage. The life style regarding movement decisions and resource selection could be radically different after recruitment and presumably highly dependent on all the information collected during their pre-breeding period. Their long lifespan and delayed maturity involves the opportunity to establish complex interactions with the environment and conspecifics making it difficult to disentangle the motivation and constraints of their movements. Additionally, these trade-off and interactions could depend on other individual traits, so a comprehensive understanding of movement should focus on individual attributes.

Canarian Egyptian vultures as study model

For assessing some key factors in conservation of vulture populations, we focus on the study of the movement ecology of the Canarian Egyptian vultures (*Neophron percnopterus majorensis*), an endangered subspecies endemic from the Canary Islands that still survives in Fuerteventura and Lanzarote. We assess internal and external factors influencing the use of resources, specifically electric pylons for roosting and perching, and feeding stations and farms as feeding sources. We also probe into stakeholders' social perception and its drivers.

Egyptian vulture has large wingspans, which makes it more sensible to electrocution on power lines as happens with other large birds (APLIC, 1996; Bevanger, 1998). Additionally, this species frequently live in open habitat where this mortality cause is especially pressing due to the scarcity of perches that provoked some birds to use electric infrastructures instead (Angelov et al., 2012; Benson, 1981; Donázar et al., 2002b; Lehman et al., 2007; Mainwaring, 2015; Phipps et al., 2013). Moreover, highly social species as Egyptian vultures conform large aggregation of birds in communal roosts being even most susceptible of electrocution when roost are located on electric pylons (Arkumarev et al., 2014; van Overveld et al., 2018). For all these reasons, we focus on electrocution which is the main cause of mortality for vultures on Canary Islands.

Canarian Egyptian vultures depend heavily on livestock carcasses derived from animal husbandry. This is a general trend in Europe, where the replacement of most wild ungulates by domestic ones has changed the spatial and temporal distribution of carrion. Although human expansion may not have changed food availability, there is no doubt that it has become more predictable by concentrating animals in farms and creating *muladares* (outdoor dumps for dead livestock) (Grande et al., 2009). As a result, in Europe the majority of vultures' diet comes from livestock carcasses, but current changes in livestock husbandry practices from extensive field grazing to intensive industrialised farming is diminishing carcass availability (Caballero, 2007; Donázar, 1993; Donázar et al., 2009a, 1997; López-López et al., 2014). Moreover, sanitary regulations imposed in 2001, after the outbreak of BSE, determined that livestock carcasses had to be destroyed, which resulted in a dramatic decline of carcass availability for vultures (Donázar et al., 2009b). To counteract this drop, there was a proliferation of supplementary feeding stations, despite some important negative effects of increasing carrion predictability have been described (Cortés-Avizanda et al., 2016, 2012; García-Heras et al., 2013). In 2011, EU legislation changed to make possible again the abandonment of carcasses in the field (Arrondo et al., 2018; Margalida et al., 2012), but it has been implemented unevenly and not in all regions. Altogether, this new scenario is changing the predictability and amount of feeding resources for vultures, but scientific knowledge on its consequences is lacking except from general guidelines (Cortés-Avizanda et al., 2016, 2010; Moreno-Opo et al., 2015). Fuerteventura still holds a high number of goat farms under extensive regime, but it is changing to semi-intensive and intensive practices (García-Martínez et al., 2009). The abandonment of carcasses is still prohibited, but it occurs in some farms. Additionally, there are two supplementary feeding stations and a garbage dump. The European emerging scenario of different predictabilities is quite reflected in Fuerteventura, where the scavenger community is relatively simple, including only one vulture species and other 3 avian scavengers (see chapter 4 for details). Hence, the island constitutes an appropriate system to assess how vultures are reacting to such changes. In this thesis, we deep on vulture resource specializations and the factors affecting both those resource preferences and the specific use of livestock farms.

Finally, Canarian Egyptian vultures have been historically related to human activities in Fuerteventura linked to traditional goat farming practices (Gangoso, 2006). However, the social perception is an aspect hardly ever considered in combination with ecological aspects such as resource use and animal movement. Social misperception may determine the emergence of wildlife-human conflicts (Everard et al., 2017) hindering conservation efforts against practices harmful for beneficial endangered species (Badia-Boher et al., 2019; Margalida et al., 2014b, 2013a; Ogada et al., 2012a), and even leading to the disappearance of those species (Allen, 1893). Scavengers provide crucial ecosystem services, so they have been always perceived as beneficial to humans (Moleón et al., 2014; Sekercioglu et al., 2016; Whelan et al., 2008). Nevertheless, as we mentioned above, avian scavenger declines are strongly related to unintended poisoning and human persecution besides other anthropogenic causes. Further, disconnection of ecosystems from human societies is a recent conservation concern (Bennett et al., 2016; Cowling et al., 2008; Martín-López and Montes, 2015; Olea and Mateo-Tomás, 2009). Thus, we probe into the perception of livestock farmers about avian scavengers on Fuerteventura Island and factors affecting awareness accuracy to enhance our understanding of the social dimension of vulture conservation.

Objectives

The specifics objectives of this thesis are:

1. To determine drivers responsible for the intensity of use of power lines by Egyptian vultures using predictive models. Then, to contrast the resulting predictions with detected mortality due to power lines.

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2. To assess individual plasticity and repeatability in movements and in the exploitation of food resources varying in predictability. Additionally, to determine the preferences for such resources and the underlying individual characteristics.

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3. To investigate how livestock farms determine the probability of use by vultures according to both farm and individual characteristics

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4. To evaluate if Canarian Egyptian vultures are acknowledged by local farmers as beneficial ecosystem service providers. In addition, to contrast presence and abundance of vultures at farms as derived from GPS data with farmers' awareness of those patterns, while disentangling the factors influencing such adjustment.

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Study system

Target species and study area

The Egyptian vulture is a migratory, long-lived scavenger that is declining in virtually all parts of its range, apparently due to increasing mortality from non-natural causes, so it is classified as “endangered” according to IUCN (Birdlife International, 2017). It mainly lives in open landscapes of rugged and arid regions where it consumes carcasses of animals of medium or small size. It nests in cliff cavities of variable size, maintains breeding territories during the breeding season and normally lays two eggs (Cramp and Simmons, 1980; Donázar, 1993), of which one or two chicks fledge the nest. They have a delayed maturity with an age of about 7 years old for the first breeding attempt. Although they are territorial, during such a long pre-adult stage, individuals are highly social congregating in large numbers at feeding locations and communal roosts, a behaviour showed mainly by non-adult individuals (del Hoyo et al., 1994). The species has occupied historically some archipelagos even at great distances of the mainland: Canary Islands, Balearic Islands, Cape Verde and Socotra (Donázar et al., 2002a; Freitas et al., 2019; Porter and Suleiman, 2012). It maintained very dense populations in these insular systems but strong declines took place during the 20th century in the Atlantic regions. In the Canary Islands the Egyptian vulture probably was present in all the islands, but it approached the extinction at the end of the 20th century. Currently it survives only in the most-easterly islands, Fuerteventura and Lanzarote (Fig. 1), with the bulk of the population congregated in Fuerteventura (Agudo et al., 2010; Bannerman, 1963, 1912; Donázar et al., 2002b; Martín, 1987). The Canarian Egyptian vulture is an endemic subspecies locally known as “Guirre”. Their insular context adds further ecological components of great interest: it is the only vulture species in the Canary Islands and this relict population is sedentary with a virtually non-existent immigration, being highly disconnected from others population.

The Canary Islands are situated in the Northeast Atlantic ocean, between 27º 37’ and 29º 25’ N, and 13º 20’ and 18º10’ W. Fuerteventura is the nearest island to the African continent (97 km). The island measures 100 km long x 25 km width (1660 km2 ICE, 2008). In contrast with the remaining islands of the archipelago, their mean altitude is low; 54% of the land is below 200 m a.s.l., and 87% below 400 m a.s.l. (Donázar et al., 2002b). 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). In addition, aridness is increased by strong northerly winds, the so called “allisios” (with an average speed of 20 km/h) that are particularly strong during spring and summer (Johnson and Stevens, 2000). The landscape is dominated by grass and scrublands with an almost total absence of woodland (Rodríguez Delgado et al., 2000). On this island crops are extremely scarce, only 16.75% of the territory are potential arable lands (Molina, 2002) of which only 0.27% are being cultivated (Cabildo de Fuerteventura, 2007). Resident human population in 2019 was almost 123.000 people (INE 2019), mostly living in the town of Puerto del Rosario (32%). Furthermore, almost two million tourists visit the island every year (Frontur Canarias, 2015). Lanzarote (846 km2 ICE, 2008) is the closest island being 11 km northern of Fuerteventura and there is an islet named Isla de Lobos (4.58 km2 ICE, 2008) between them (Fig. 1). Lanzarote is the third island most populated on Canary Islands having about 151.000 people (INE 2019).

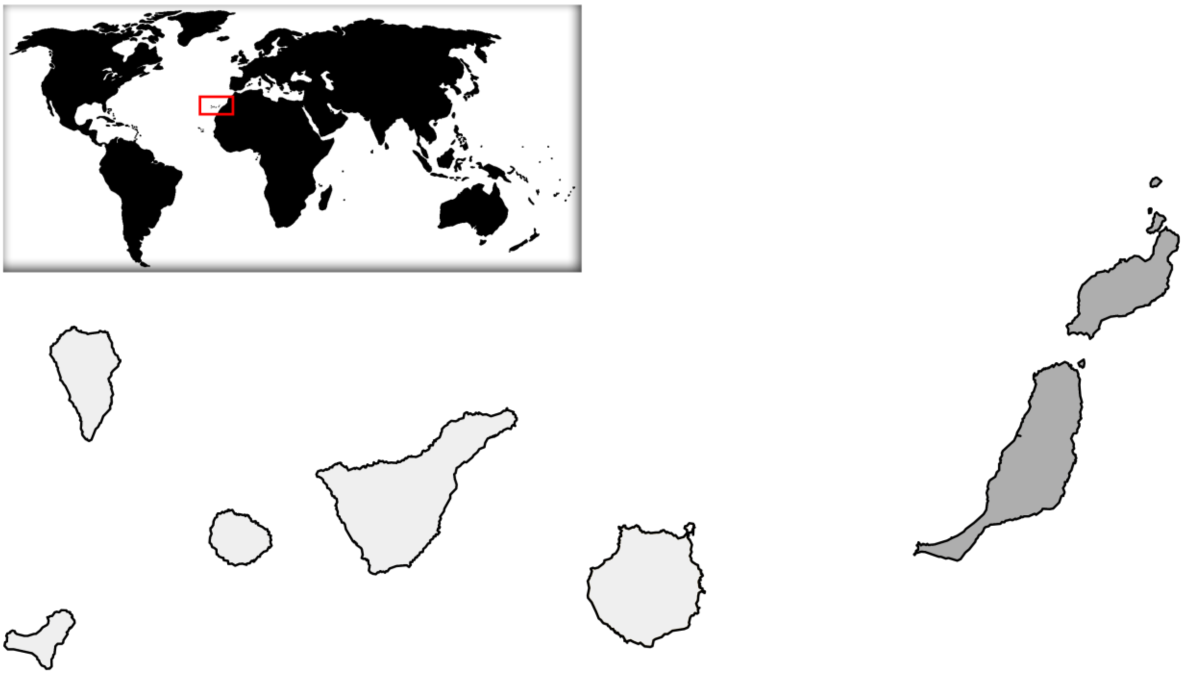

Figure 1. Canarian archipelago and their location on the world. The most easterly islands are Fuerteventura (south) and Lanzarote (north) on dark grey.

Population monitoring

This Canarian population has been monitored since 1998 intensively by a team of the EBD-CSIC. Every year a 2 or 3-people team conducts field work during six months covering the whole breeding season (from late February to late June). During this time all occupied territories in both islands (Fuerteventura and Lanzarote) are localized and controlled. Each territorial individual's ring is identified and number of fledglings at the end of the breeding season was determined when nests were accessible for ringing and/or fully visible with spotting scopes.

The population changed from only 21 territories in 1998 to 77 in 2019, which represents an average annual growth rate of 6%. Population size in 2019 reached 361 individuals, 198 non-breeding and 163 breeding conforming 154 breeding pairs and 9 trios. 89% of the individuals carried out metal and/or plastic rings in 2019.

Breeding success has been extremely low as compared to other studied populations during all the study period (Donázar et al., 2002b and own data) and shows an apparent long-term decrease throughout the study period (Fig. 2).

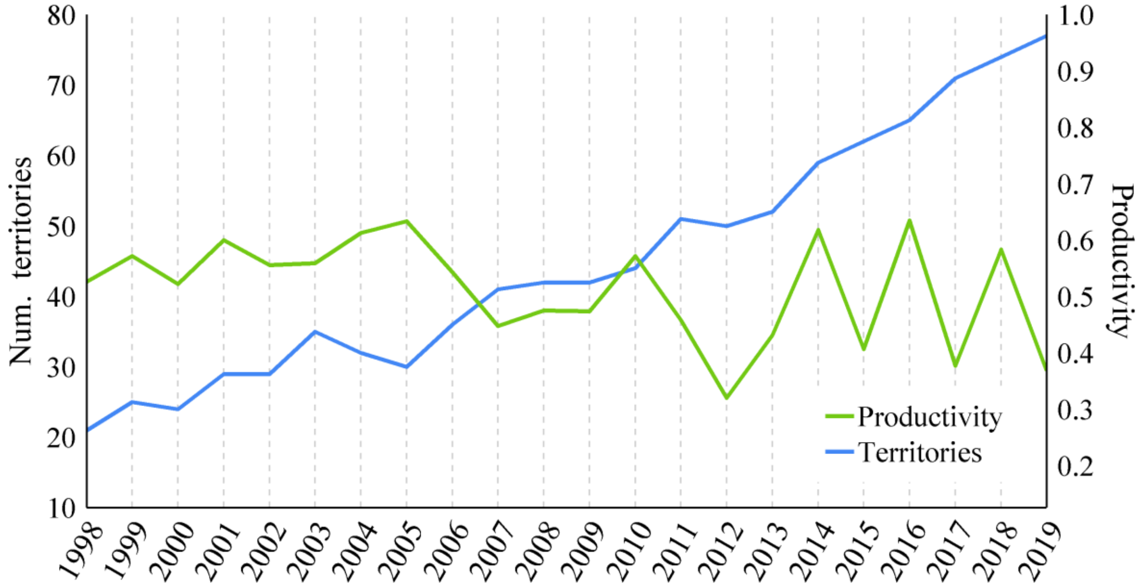

Figure 2. Number of breeding territories occupied by Egyptian vultures during the studied period and productivity calculated as the number of fledglings per number of occupied nest using only nest with known breeding success.

Between 1998 and 2017, 429 fledglings were captured in their nests (mean age 55 days old, from mid-May to early August). In addition, 26 juvenile (1-year old), 240 subadult (2- to 5-years old) and 101 adult (≥6-years old) birds were captured using cannon-nets baited with carcasses. Birds could be aged until their fifth year of age according to plumage patterns (Cramp and Simmons, 1980; Forsman, 2016), but later they acquire the adult plumage. All the birds were ringed with both plastic and metal rings engraved with an individual alphanumeric code, and blood samples, feathers, typical measures and pictures were taken (Fig. 3). Individual sex was determined by genotyping in the Laboratory of Molecular Ecology (EBD-CSIC).

Figure 3. Images of field work during monitoring and trapping of Egyptian vultures on Fuerteventura (Canary Islands). Between 1998 and 2019 field monitoring has been done (in chronological order) by César J Palacios, Ana Trujillano, Carmen Díez, Marcos Mallo, Sandra Sierra, Juan Ramírez, Toni Mulet, Walo Moreno, Julio Roldán, and José Sarrión.

Individual movement monitoring

In order to assess movement behaviour of Canarian Egyptian vultures, 49 different individuals have been tagged with GPS devices between 2013 and 2017 (SM1 chapter 1). Two type of devices were used: 27 UvA-BiTS (Bouten et al., 2013) and 21 E-obs (GmbH, Munich, Germany) that were fixed respectively to 30 (including reusing) and 21 individuals. Both kinds of devices are solar-powered and have multiple on-board sensors providing the geographical coordinates, altitude and speed of each individual according to a defined time interval. The collected information is stored in the devices which have a limited memory.

UvABiTS devices (Fig. 4) use a type of Bluetooth-network to download the collected data, requiring a base-station which consists of an antenna and a laptop. Data are downloaded to the laptop when birds are in the reception area that can be extended by using a relay. It is not possible to localize target individuals using radiotracking. These devices offer the possibility of defining two different time blocks, making possible the establishment of high frequencies of collecting data during day and low frequencies during night.

Figure 4. Details of an UvABiTS device on the left and a Canarian Egyptian vulture equipped with an UvABiTS device on the right.

E-obs devices (Fig. 5) use the GSM-GPRS signal, which is the same as mobile phones use. A base-station is not needed, though to ensure connections where there is not signal they include a high-speed radio-link for wireless on-site data download. Normally, data collected is daily downloaded and when a device does not connect for any reason, data are kept until a new connection. It is possible to localize target individuals using radiotracking, so recovering of dead individuals is easier than using UvABiTS. However, e-obs do not offer the possibility of defining two different times blocks.

Figure 5. Details of an e-obs device on the left and a Canarian Egyptian vulture with e-obs device being equipped on the right.

In both devices, all downloaded data are removed from the transmitter, recovering space in the memory. Settings for collecting data can be changed at any moment and devices will detect such changes in the next connection.

Due to requirements of UvABiTS devices, 2 base-stations and 3 relays are currently installed (Fig. 6). Batteries of relays have to be replaced every 3 months and the whole system requires frequent watching for occasional maintenance. The battery of the devices has to be periodically controlled in order to redefine the settings when facing low voltages, so periods without collecting information are avoided.

Figure 6. Details of the required system for the correct functioning of UvABiTS devices. (A) Laptop installed close to the main supplementary feeding station conforming the base station number 1. (B) Antenna connected to the laptop 1. (C) Relay used during the installation of a supporting relay for base station 1. (D) Laptop installed close to the garbage dump conforming the base station number 2. (E) Antenna connected to the laptop 2. (F) Relay installed inside the garbage dump supporting the base station 2. (G) Another relay installed inside the garbage dump supporting the base station 2.

Main threats and conservation measures

The main causes of mortality identified since 1998 were illegal poisoning, followed by fatalities due to power lines (mainly collisions and entanglements) (Figure 2 chapter 1). Other causes of minor impact were shootings, ingestion of lead bullets and natural causes (Donázar et al., 2002b; Gangoso and Palacios, 2002; Gangoso et al., 2009a). Additionally, two fatalities due to collisions with wind turbines were detected (one in 2018 and another in 2019, unpublished data)

A LIFE-Nature Project (LIFE04NAT/E/000067) was developed between 2004 and 2008 to mitigate non-natural mortality in this subspecies by means of the implementation of anti-entanglement and anti-collision systems (applied in 2005), and environmental education campaigns about the highly damaging effects of poisoning. Illegal poisoned baits were probably not targeted to vultures but to ravens and feral dogs (Badia-Boher et al., 2019), and for this reason some actions focused on environmental education and awareness activities towards stakeholders, as well as awareness campaigns using communication media to improve the visibility of the species and its conservation. Additionally, the monitoring team has been interacting with stakeholders since 1998, which may have led to an increase in the awareness about positive effects of vultures and could have diminished the use of poisoned baits (Badia-Boher et al., 2019).

After implementing the actions, poisoning has become a minor cause of mortality and entanglement or collisions with power lines have been no longer detected, giving way to electrocution as the main cause of mortality, which is not surprising considering that anti-electrocution systems were applied only to 10 electric pylons (Badia-Boher et al., 2019). Henceforth, the population has showed survival prospects higher than 90% (Badia-Boher et al., 2019) increasing the rate of annual growth (Fig. 2) and currently a LIFE-Nature project (LIFE16 NAT/IT/000659) is aimed to improve the conservation status of Egyptian vulture populations in Italy and the Canary Islands. Among the expected results of the project is the reduction in the electrocution risk by 60% on the Canary Islands.

Chapter 1

Applying movement ecology to identify drivers of power line use by vultures

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Chapter 2

Food predictability and social status drive individual resource specializations in a territorial vulture

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Abstract

Despite increasing work detailing the presence of foraging specializations across a range of taxa, limited attention so far has been given to the role of spatiotemporal variation in food predictability in shaping individual resource selection. Here, we studied the exploitation of human-provided carrion resources differing in predictability by Canarian Egyptian vultures (*Neophron percnopterus majorensis*). We focussed specifically on the role of individual characteristics and spatial constraints in shaping patterns of resource use. Using high-resolution GPS data obtained from 45 vultures tracked for 1 year, we show that individual vultures were repeatable in both their monthly use of predictable and semi-predicable resources (feeding station vs. farms) and monthly levels of mobility (home range size and flight activity). However, individual foraging activities were simultaneously characterized by a high degree of (temporal) plasticity in the use of the feeding station in specific months. Individual rank within dominance hierarchy revealed sex-dependent effects of social status on resource preference in breeding adults, illustrating the potential complex social mechanisms underpinning status-dependent resource use patterns. Our results show that predictable food at feeding stations may lead to broad-scale patterns of resource partitioning and affect both the foraging and social dynamics within local vulture populations.

Keywords: GPS-tracking, food predictability, *Neophron percnopterus*, resource specialisation, social rank, vultures.

Introduction

Foraging tactics are often highly plastic, allowing individuals to respond adaptively to spatial and temporal fluctuations in resource availability and environmental changes. Yet, despite plasticity in foraging, individuals of the same species typically tend to use only a subset of the resources available in the environment, often displaying distinct foraging specializations and/or dietary preferences (Bolnick et al., 2003). Such individual divergence in resource use may arise from phenotypic differences (e.g., morphology, behaviour, and physiology) and environmental constraints affecting foraging trade-offs (Bolnick et al., 2003). As such, foraging specialisations are generally thought of as different foraging optimization strategies (Pyke et al., 1977; Stephens and Krebs, 1986). However, the extent to which the interplay between ecological conditions and individual resource preferences affects (or determine) population spatial dynamics remain poorly understood (Araújo et al., 2011).

A major determinant of individual foraging strategies is the spatial clumping and temporal predictability of resources, affecting decisions on patch choice, patch departure times and inter-patch movements (Stephens and Krebs, 1986). Although temporal predictable food patches (pulsed resources) characterize most natural systems (e.g., upwelling, insect outbreaks, carcasses Yang et al., 2010), the presence of anthropogenic food resource pulses (e.g., fishing discards, refuse dumps, feeding stations) are increasingly impacting the natural dynamics of food supply, creating new ecological conditions upon which many animals base their foraging decisions (Oro et al., 2013). Predictable food patches can greatly alter the costs and benefits of foraging, either by reducing the time and energy needed for food searching (Bartumeus et al., 2010) or by increasing levels of competition among individuals attracted to the same resource and hence, the costs associated with food acquisition (Goldberg, 2001; Grand and Grant, 1994).

While high levels of competition and interference at predictable food may lead to the exclusion of subordinate individuals from these resources, the mechanisms underlying the usage of locally superabundant food are likely more complex. First, the ‘economic defendability’ of this resource is typically low (Brown, 1964). While dominant individuals may be able to monopolize a large share of the food, there will always be some food available to lower-ranked individuals. For example, predictable food patches are often visited by individuals for which the costs of food searching may be high, such as young, inexperienced individuals or immigrants from other populations with limited knowledge of their environment (Sanz-Aguilar et al., 2015). Second, for territorial birds, central place foraging constraints during breeding may importantly affect the ability of making use of predictable food (García-Heras et al., 2013). Such constraints may in turn differ among individuals depending on social rank if, for instance, the location of predictable food influences local territory quality (Carrete et al., 2006b; Sergio et al., 2007). Although there is increasing evidence that predictable anthropogenic resources are used by only a subset of the population, including seabirds (Patrick et al., 2015; Tyson et al., 2015; Votier et al., 2010) and storks (Sanz-Aguilar et al., 2015), studies examining the potential trade-offs responsible for the asymmetric use of anthropogenic food are still scarce (but see Sanz-Aguilar et al., 2015).

European vultures currently rely on feeding stations (where abundant food is supplied on a regular basis) (Cortés-Avizanda et al., 2016) and, to a lower extent, on the surroundings of cattle farms (more places, but where food is scarcer and less predictable) (Cortés-Avizanda et al., 2012). Despite concerns about the potential impact of such large feeding stations on the natural foraging habits and social structure of local vulture populations (Carrete et al., 2006a; Fluhr et al., 2017; Margalida et al., 2013b), a mechanistic understanding of how the use of surplus food varies within and among individuals is still lacking. The extent to which changes in the spatial distribution and predictability of resources may influence behavioural processes key to understand spatial population dynamics therefore still remain poorly understood.

Here, we assessed individual plasticity and repeatability in the exploitation of food resources varying in predictability by a territorial, but highly social avian scavenger. We took advantage of a twenty-year research program on a closed island population of the endangered Canarian Egyptian vulture (*Neophron percnopterus majorensis*). Continuous monitoring has resulted in 90% of the birds (total population size c.a. 300 individuals) being ringed in 2016, 16% of them carrying GPS-transmitters (n = 45). Firstly, we described seasonal variation in the monthly use of food resources varying in their spatiotemporal predictability (i.e. highly predictable feeding stations and garbage dump, versus semi-predictable goat/sheep farms) and how vultures allocated their time into flight and non-flight behaviour. Next, we tested our main hypothesis that individual vultures differ in resource preferences as a result of trait-specific foraging optimization strategies. In a first step, we assessed whether individual vultures were repeatable in their preferences for food resources differing in predictability (farms vs. feeding stations) and levels of mobility (home range size and flight activity). Second, we specifically test whether birds preferring predictable food reduce their overall food searching activities (i.e., showing both smaller home ranges and reduced flight activity) by analysing both within- and among-individual correlations between resource use and mobility. Finally, we examine whether predictable food is of higher value to dominant birds, owing to their superior competitive skills, by analysing the effects of individual rank within a dominance hierarchy, as well as sex, age, and territorial status. In addition, in territorial birds, we examine the role of spatial constraints in shaping individual resource use and patterns of mobility, by analysing how territory location (i.e. distance to predictable feeding sites) may affect resource use and ranging behaviour, again, in relation to individual traits.

Materials and Methods

Study species and population

The Canarian Egyptian vulture is a sedentary and endemic long-lived scavenger occupying the eastern part of the Canarian Archipelago (between 27.62º - 29.42º N, and 13.33º - 18.17º W). The species was once abundant throughout the archipelago (Bannerman, 1963), but is currently classified as 'critically endangered' owing to severe population declines since the 20th century. Fuerteventura Island (1662 km²) is the stronghold of the population, which is home to 60 breeding pairs and has an estimated population size of about 300 individuals in 2016 (authors unpublished). Extensive fieldwork (ringing of nestling and trapping of adults) has resulted in over 90% of the individuals being individually marked in 2016.

Egyptian vultures are facultative scavengers that forage solitary (or sometimes in couples). The species leads a vagrant but very social lifestyle prior to recruitment, but afterwards adults are much more solitary and territorial. Throughout the year, they may form large aggregations at places with an abundance of food and roosting often occurs communally (Donázar et al., 1996b). On Fuerteventura, the species heavily relies on human-provided carcases available at goat and sheep farms throughout the island (Fig. 1, further details see below). At these farms, livestock carcasses appear irregularly in time. Slaughterhouse remains (pork heads and intestines, ± 200 kg per week) are provided once or twice a week at each of the two feeding stations, one being located in the centre of the island (created in 1998) and one in the north (created in 2008) (Fig. 1). Local farmers regularly add additional livestock carcasses to both feeding stations. The feeding stations are separated by approximately 40 km distance. Vultures sometimes also forage at the garbage dump near the capital city Puerto del Rosario. Apart from these human-provided food resources, vultures may consume randomly encountered carcasses, especially those of feral goats and small-sized vertebrates such as wild rabbits (*Oryctolagus cuniculus*) and feral pigeons (*Columba livia*) (Gangoso et al., 2006).

GPS tracking

Vultures were captured with cannon-nets about 3km away from the main feeding station in the centre of the island. GPS trackers (UvA-BITS, www.uva-bits.nl, University of Amsterdam, n = 26; e-obs, e-obs Digital Telemetry, Grünwald, Germany, n = 19) were attached to the bird using backpack harnesses. The total weight of the system varied between 31 g (UvABiTS) and 54 g (e-obs) (1.4-2.4% of the weight of the bird) which is assumed to be harmless to the individual (Sergio et al., 2015). In total, we used GPS-tracking data from 45 birds (24 females (14 territorial and 10 non-territorial) and 21 males (11 territorial and 10 non-territorial) collected over a 12-month period (October 2015- September 2016). GPS loggers were programmed to record locations every 1 to 5 minutes, but data were re-sampled to an interval of 10 minutes (range 9-11 minutes, R-function developed by D.S. Viana) to allow direct comparisons between individuals. Because of low-battery levels and/or poor satellite reception, intervals exceeding15 minutes were removed from the dataset. We only used GPS-fixes between sunrise and sunset. We included all months with continuous recording of GPS-locations, independent of downloading error (which was small due to sunny weather conditions). However, we excluded months for which we had incomplete logging data (e.g. due to exceedance of data logging capacity and mortality (N = 2). We also excluded all movements made to the neighbouring Lanzarote island (e.g. one bird breeds on Lanzarote, but spent its time outside the breeding season on Fuerteventura). In total, we had data available for 486 individual-month (994.179 fixes), comprising 12 months for 35 individuals and between 3 to 11 months for 10 individuals. The median percentage of time explained per month by GPS fixes was 94.8% (range 16.13 – 100 %, further details below).

Monthly activity budgets

To construct monthly activity budgets we distinguished between time allocated to flight vs. non-flight behaviour (including resting and foraging) using a threshold ground speed 3 m/s for data obtained from both GPS devices (see Fig. S1). Non-flight behaviour was further subdivided into time allocated to foraging at two types of food resources: highly predictable places (the two feeding stations and the garbage dump) and semi-predictable places (goat-sheep farms). To classify GPS data into resource use, we used the number of GPS locations within a buffer zone of 75 m around the centre of the two feeding stations and a buffer zone of 250m around the centre of the garbage dump, covering respectively the total fenced area and the total surface of the garbage dump. Since farmers drop carcasses at variable distances from their farms, we used a buffer zone of 250m to determine the use of farms as source of food (i.e. based on 10 farms where we knew the exact distance (median 254 m, range 60– 610m, García Alfonso et al. under review). In total, we were able to retrieve the coordinates of 319 out of 437 farms (73%). Farms differed greatly in size (median 202 animals, range 10-4217, n = 292). Our data included all farms with more than 500 animals (N = 67). Annual mortality rate of sheep and goats (including lambs) at farms is estimated at about 10% (see Margalida and Colomer, 2012). We described monthly variation in average time-budgets of all individuals (flight vs. non-flight behaviour), specifically detailing the time spent at resources differing in predictability in the non-flight category (the two feeding stations, garbage dump and all farms pooled). See Fig. S2 for an overview of average monthly time-budgets.

Ranging behaviour

Monthly ranging behaviour per individual was quantified by calculating utilization distributions (UD) using the fixed kernel contour method on the adehabitHR package, R version 3.0.3 (Calenge, 2014). Since we were interested in food searching behaviour and/or explorative movements, ranging behaviour was defined using the 95% kernel density estimate (95KDE, in km²). We excluded all non-flight GPS fixes at the feeding stations, garbage dump and farms to improve the independence of our home range estimate. Since the use of a reference smoothing factor (href) led to unrealistic estimates of home ranges (see Fig. S3 for details), we checked manually home range sizes using different smoothing parameters (h) (Wand and Jones, 1993) and realistic estimates were found for h between 500-1000m (see Fig. S4 for examples and more details on selection of smoothing parameters). We therefore chose to set the width around each point location to 750 m, using a constant kernel width for each individual allowing comparing ranging behaviour between individuals. To check for effects of temporal/spatial autocorrelation of locations on home range estimates, we recalculated 95%KDE using Brownian Bridge Movement Models (BBMM), which method specifically integrates movement paths in estimates of home range sizes (Walter et al., 2011). However, both methods produced highly similar 95%KDE when using similar smoothing parameters, or estimates were highly correlated when using various custom made smoothing factors (details provided at Fig. S4-S5).

Dominance data

Data on social dominance were collected in February 2016 (early breeding season) and August-September 2016 (post-breeding season). We noted all agonistic displacements between colour-ringed individuals around baits at the central feeding station (from a hide) between sunset and sunrise. In total, we observed 4593 displacements between 141 individuals that were involved in more than 20 displacements (average 65.1 ± 3.0 S.E., range 20-175), including 40 birds fitted with GPS loggers (19 males and 21 females: average 65.5 ± 6.4 S.E. displacements, range 20-175). Rank scores for each individual were determined using David's score using the 'compete' package in R (Curley, 2016), corrected for chance of encounter and thus independent of group size or visiting rate, see Suppl. Mat. text S1 and Fig. S6 for details (Gammell et al., 2003). Scores obtained from the total dataset were used (details in Fig. S7). Rank was scaled between 0-1 with 1 being the most dominant bird.

Statistical analyses

We conducted all statistical analyses using SAS 9.4 software (SAS Institute Inc., Cary, NC). We used a three-step approach to analyse our data. First, to quantify individual differences in the use of predictable and semi-predictable resources and movement behaviour we tested for repeatable individual differences in resource use (time spent at the main feeding station and farms, both square-root transformed), resource preference (ratio time spent at feeding station: farms, arctangent-transformed) and mobility (ranging behaviour by 95KDE, log-transformed, and time spent flying by 'flight activity', square-root transformed). All transformed response variables were scaled by the standard deviation and mean-centred. Repeatability (R) was calculated based on a null model without main effects (i.e., non-adjusted), as the among-individual variance divided by the sum of the among-individual and the residual within-individual variance (Dingemanse and Dochtermann, 2013), using univariate mixed-effect models with bird ID as a random effect and a Gaussian error distribution. To interpret factors influencing individual repeatability in behaviours, non-adjusted repeatability indices were compared with adjusted repeatability in full models including individual traits and environmental factors (see below). To test the significance of repeatability, we compared models with and without the random effect of bird ID using a likelihood ratio test LRT (Pinheiro and Bates, 2000; Zuur et al., 2009).

Second, links between individual preferences for resources differing in predictability and mobility patterns were tested by analysing within- and between-individual correlations in monthly resource use, ranging behaviour and flight activity (based on average daily measurements) using bivariate mixed-effects models (Dingemanse and Dochtermann, 2013). Significance of within-individual correlations was tested by comparing unconstrained models with models where the within-individual covariance was constrained to zero, again by applying an LRT test (to compare the χ^2 against $P(\chi^2, df = 1)$.

In the last part of our analyses, we tested the effects of individual attributes and territory location on resource preferences and mobility (dependent variables). First, we fitted LMMs with bird ID as random effect and included month, sex (male or female), dominance rank, age (in years) and territorial status (yes or no) as fixed effects. Since exploratory analyses showed that resource use and patterns of mobility varied strongly across the year in a non-linear manner (Fig. S2), we included month squared in all analyses. To test whether effects of dominance rank on resource use varied between the sexes and between territorial and non-territorial birds, we included two interactions: sex × rank and territorial status × rank in all models. We also included another two interactions (month squared × sex and month squared × dominance rank) to test for sex- or dominance-specific seasonal relationships. All covariates were mean and variance standardized. Finally, for territorial birds, we tested whether distance from the territory (nest location) to the central feeding station affected resource use and mobility, and whether territory location was explained by social rank (for males and females separately), using a LMM again with bird ID included as a random effect. Full models included all main fixed effects, random effects and interaction terms irrespective of their significance. Note that adjusted repeatability indices were calculated based on these full models.

Results

Temporal dynamics in resource use and movement pattern

The overall monthly proportion of time spent at human-provided food resources (feeding stations, farms, garbage dump; all pooled, see Fig. 1 for an overview) was 14.7% ± 9.8 SD. Vultures spent most time at the central feeding station and to a lesser extent at farms (average monthly proportion of time 8.5% ± 9.0 SD and 3.9% ± 4.6 SD, respectively). The garbage dump and the feeding station located in the north, were rarely used (average 1.5% ±

2.4 SD and 0.9% ± 2.3 SD, respectively). Monthly time budgets varied strongly over the course of the season. As a general pattern, average monthly flight activity was generally low during the non-breeding season (July-December) and substantially increased during the breeding season (January-June). By contrast, average monthly time spent at the central feeding station, and to a lesser extent at farms, decreased during the breeding season and again increased during the non-breeding season (Fig. S2, details in text S2 and below).

Individual repeatability and plasticity in resource use and mobility

There was significant among-individual variance in the intercepts (i.e. non-adjusted individual repeatability) of the time spent at the central feeding station (variance ± SE = 0.43 ± 0.10, $\chi^2_1 = 175.6$, $p < 0.001$), farms (0.45 ± 0.11, $\chi^2_1 = 203.4$, $p < 0.001$) and the ratio feeding station: farms ('resource preference': 0.47 ± 0.11, $\chi^2_1 = 209.1$, $p < 0.001$). Both measures of mobility were also individually repeatable: logKDE95 (0.43 ± 0.10, $\chi^2_1= 184.8$, $p < 0.001$), and flight activity (0.18 ± 0.06, $\chi^2_1= 39.8$, $p < .0001$).

There was no significant within-individual or among-individual covariance between the use of farms and feeding stations (Table 1), nor among-individual covariance between resource use and mobility parameters (Table 1, for territorial and non-territorial males and females, Fig. 2. a.1-d.1). Positive within-individual covariance was found between the use of the feeding station and LogKDE95 ($\chi = 34.4$, $p < .0001$, Table 1), while negative within-individual covariance was found between time spent at the central feeding station and flight activity ($\chi = 89.1$, $p < 0.001$, Table 1), indicating that individual birds increased home-ranges and decreased flight activity in those months when they visited the feeding station more frequently. A similar relationship was found for resource preference ($\chi = 27.1$ and 20.6, both $p < 0.001$, for covariance with flight activity and LogKDE95, respectively), but not the use of farms, indicating that the effects of resource preference on mobility were driven by the use of the feeding station (Table 1). Within-individual covariance between time spent at the central feeding station and mobility parameters (home-range size and flight activity) were both significant in territorial birds, with females: 0.23 ± 0.04, $\chi = 39.3$, $p < 0.001$ (Fig. 2. a.2-a.3) and -0.37 ± 0.07, $\chi = 39.1$, $p < 0.001$; and males: 0.25 ± 0.06, $\chi = 24.2$, $p < 0.001$ and -0.26 ± 0.06, $\chi = 21.6$, $p < 0.001$ (Fig. 2. b.2-b.3), while for non-territorial females and males, significant within-individual covariance was found only between time spent at the central feeding station and flight activity with $p <0.001$ for non-territorial females (Fig. 2. c.2-c.3) and males (Fig. 2. d.2-d.3).

Effects of social status on resource use and mobility

Females were socially dominant over males, whle within sexes, territorial birds were socially dominant over non-territorial birds (territorial females > non-territorial females > territorial males > non-territorial males, Fig. 3.a). Social status also increased with age (Spearman rank correlation $r = 0.52$, $p < .001$, $n = 40$).

Resource specialization

Resource preference differed between the sexes in relation to dominance rank and territorial status (Table 2), and these effects varied strongly across the season (month squared × sex × dominance rank: $F_{3,387} = 8.38$, $p < 0.001$; month squared × sex × territorial status: $F_{2,387} = 6.80$, $p = 0.001$). Resource preference also varied according to age, with young birds spending more time at the central feeding station than farms compared to older birds (Table 2). Overall, females preferred the central feeding station over farms, while males showed the opposite pattern (Fig. 3.b). The importance of individual traits in explaining resource preference is further illustrated by a decrease in among-individual variance changing individual repeatability (non-adjusted: $R = 0.47$ vs. adjusted: $R = 0.28$, Table 2).

However, within territorial birds, a reversed effect of social status on resource use was found in males and females (sex × dominance rank $F_{1,18} = 9.6$, $\beta = 1.58 \pm 0.52$, $p = 0.006$), showing a positive and negative correlation respectively (females: Fig. 4.a-b; males: Fig. 5.a-b). Within non-territorial males and females, no correlation was found between dominance rank and time spent at either the central feeding station or farms ($p > 0.11$), nor were there significant sex-difference in time spent at different resources (Fig. 6.a-b). Subdominant territorial females visited more farms ($p = 0.02$), which showed a clear peak in use during the late chick-rearing phase (Apr-May) ($p = 0.01$, Fig. 4.f). In male territorial birds there was no relationship between dominance rank and number of farms visited ($p = 0.15$, Fig. 5.f). Details on statistics are provided in Table S1.

Mobility

Links between social status and mobility varied according to sex and territorial status, but these patterns were highly seasonal and/or only present during specific periods of the year (Table 2). Repeatability indices for home-range size and flight activity changed due to respectively a decrease in among-individual variance component (non-adjusted: $R = 0.43$ vs. adjusted: $R = 0.32$, Table 2) and increase in within-individual variance component (non-adjusted: $R = 0.18$ vs. adjusted: $R = 0.34$, Table 2), indicating effects of individual traits on the ranging behaviour and confounding seasonal effects on flight activity.

Subdominant territorial males and females had larger home ranges during late summer (Oct-Dec) and the pre-egg laying phase (Jan-Mar) compared to dominant individuals, but these differences disappeared during the remaining part of the year (month squared × dominance rank; females: $p = < 0.001$, Fig. 4.c; males: $p = 0.052$, Fig. 5.c). In both territorial males and females, flight activity peaked during the breeding season ($p < 0.001$ for both sexes; females: Fig. 4.d; males: Fig. 5.d). Non-territorial birds, but males in particular, made large scale movements during the breeding season ($p = 0.001$, Fig. 6.c), corresponding to a peak in flight activity and large flight distance relative to the feeding station around the egg-laying phase (Mar-Apr) of breeding birds ($p < 0.001$ for both sexes, Fig. 6.d and 6.e). Overall, non-territorial males visited more farms than non-territorial females ($p = 0.012$, Fig. 6.f). Details on statistics are provided in Table S1.

Territory location and use of the feeding station

High-ranked females bred closer to the feeding station (Spearman rank correlation, $r = -0.77$, $p = 0.002$, $n = 13$, including birds without GPS loggers $r = -0.59$, $p = 0.0001$, $n = 36$, Fig. 7.a), with distance from the territory to the feeding station being negatively correlated with time spent at the central feeding station ($F_{1,18.1} = 11.10$, $\beta = 0.60 \pm 0.18$, $p = 0.004$). In males, there was no relationship between dominance rank and distance between territory and the central feeding station (Spearman rank correlation, GPS-birds: $r = -0.23$, $p = 0.55$, $n = 9$; including birds without GPS-logger: $r = -0.28$, $p = 0.18$, $n = 25$, Fig. 7.b). Distance from the territory to the feeding station also tended to be negatively correlated with time spent at the feeding station ($p = 0.06$). Overall, flight distances relative to the feeding station were much larger in subdominant territorial females ($p < 0.001$), except during summer months (month squared × dominance rank: $p < 0.001$, Fig. 4.e). In males, social status was unrelated to flight distance to the central feeding station ($p = 0.31$, Fig. 5.e).

Discussion

We found strong evidence for level-specific associations between individual resource use and mobility, providing novel insights into the use of human-provided carrion by social avian scavengers. Our detailed quantification of individual rank order differences revealed different effects of social status on resource preference in breeding males and females, illustrating the potential complex social mechanisms underpinning individual resource use patterns

Resource preferences and individual movement behaviour

While feeding stations may have a profound impact on the foraging dynamics of local vulture populations (Monsarrat et al., 2013), studies investigating individual-level responses to these feeding practices are almost non-existent (Fluhr et al., 2017; García-Heras et al., 2013). We found that competitive superior individuals (females, the larger sex in this and most raptor species) made consistent use of the feeding station throughout the year. By contrast, subdominant individuals (males in particular) favoured farms as their main source of food, most likely because of reduced competition at these sites due to the unpredictable nature of food supply. These results demonstrate for the first time the asymmetric use of this widely used conservation tool in vultures, and point towards a major role of feeding stations in driving patterns of resource partitioning within populations.

Importantly, vultures preferring farms did not necessarily have larger home-ranges compared to birds feeding mostly at the central feeding station, despite both traits being individually repeatable. By contrast, ranging behaviour and flight activity varied plastically within individuals as a function of the use of the central feeding station. This shows that all individuals may temporally increase their use of predictable food, indicating that the feeding station may serve an important function as a food insurance (see also Oro et al., 2008). Patterns of within-individual plasticity between resource use and ranging behaviour were most pronounced in birds breeding far away from the feeding station (mostly foraging at farms) making large-scale flights to the central feeding station. Thus, instead of searching for unpredictable carcasses at farms (or over wider natural areas), these vultures may frequently leave their habitually exploited home range to visit the central feeding station (i.e. sometimes even including birds breeding on Lanzarote, Sanz-Aguilar et al., 2015). The temporal nature of these movements may be explained by birds facing various trade-offs: they may choose to forage at predictable feeding site in order to reduce food searching efforts, but face potentially higher levels of competition for food at this site compared to farms, while the energetic costs associated with large-scale movements to this site may be substantial. Indeed, the movement behaviour of vultures on Fuerteventura may be importantly shaped by “alisios” winds , the dominant northeast trade winds (with an average speed of 20 km/h) that are particularly strong during spring and summer (Johnson and Stevens, 2000). In addition, time-displacement constraints may be particularly important for single-prey loaders such as Egyptian vultures, notably during chick rearing (May-July). Overall, these patterns point towards differences in foraging costs associated with territory distance to the feeding station, which at least in females seems associated with social status (see below)

The important role of spatial constraints, and central-place foraging task in particular, in shaping resource use patterns is further illustrated by the strong seasonal plasticity in the use of the feeding station. Outside the breeding season, all tracked individuals, except dominant and non-territorial males, spent more time at the central feeding station and hence, decreased their flight distance relative to this site. Large-scale and straight-line movements to predictable feeding sites seem to be general among Egyptian vultures, and has been previously observed in mainland Spain (López-López et al., 2014). However, as we showed here, these movements may be part of a much more complex foraging and spatial dynamics, highly influenced by the existence of a single, predictable feeding station.

Social mechanism underlying individual resource preference

While it is recognized that social status shapes individual foraging decisions, we are currently not aware of other studies showing the existence of consistent, year-round differences in status-dependent resource specialisation in relation to resource distribution and predictability. Furthermore, although dominance status plays an important role in determining carcass and predictable resource exploitation in obligate scavengers (Bosè et al., 2012; Duriez et al., 2012; Prior and Weatherhead, 1991; Wallace and Temple, 1987), sex- and individual-rank order differences in resource use have been very rarely quantified in vultures (Donázar et al., 1999). As such, a key finding of our study is that effects of social rank on resource use were reversed within territorial males and females, thus, showing that rank-specific foraging trade-offs can be complex, and shape resource preferences differently within each sex.

In territorial females, resource preferences depended on the distance of the territory to the feeding station, with dominant birds breeding at closer distances and spending more time at this resource, and low-ranked birds breeding further away and, consequently, relying more on farms. This suggests that the location of territories with respect to predictable food may be the main mechanism shaping status-dependent resource use in this sex. More specifically, securing a territory close to the feeding station may be beneficial in terms of knowledge on the occurrence of food dumps, and reduced time-displacement costs during chick rearing, while at the same time, dominant birds have instant access to food provided at this site since they are able to push most other birds away from food. In contrast, high-ranked territorial males spent consistently more time at farms throughout the year, while low-ranked territorial males spent little time at both farms and feeding station while breeding, suggesting they may generally rely more on natural food resources (Gangoso et al., 2009b). Outside the breeding season, the absence of central place foraging tasks, as well as the probable lower availability of food, may drive low-ranked males to exploit predictable food at the central feeding stations, despite a high cost-benefit ratio of resource acquisition due to their low social position. As opposed to females, the despotic distribution of territories in males may be determined by the presence of high quality food dumps near farms (i.e., frequent supply of livestock) instead of distance to the feeding station. However, future studies should unravel the differential cost associated with foraging for natural vs. semi-unpredicatble resources and the role of farms in determing territory quality to fully understand rank-specific foraging trade-offs in males.

A complementary scenario may be that subdominant territorial males can specifically visit the feeding station to improve their social rank and/or to search for new partners (Blanco and Tella, 1999; Heinrich and Marzluff, 1991). In fact, after breeding, large gatherings at the feeding station sometimes reaching up to 100 individuals, suggests that this site may also serve a function as a social meeting place (van Overveld et al. in prep).

Furthermore, competitive asymmetries among individuals may not be the only individual factor explaining differences in resource use. First, the observed sex-specific resource preferences may also be linked to asymmetries in foraging-roles between males and females, which is common in sex-dimorphic birds of prey (Newton, 1979) and avian scavengers (Donázar et al., 1999). Consequently, sex-asymmetries in resource preference may not be the result of resource competition per se, but rather the result of a more general difference in foraging niche partitioning (Krüger, 2005), in which the sexes perceive the value of resources differently depending on levels of competition. Second, although non-territorial, adult males visited more farms (compared to females), this difference may have resulted from the large-scale explorative movements made by these males during the breeding season. These movements, peaking around the egg-laying phase, seem to be aimed at collecting information about potential future recruitment sites (Valone and Templeton, 2002) more than being the result of social competition. Finally, younger birds preferred the feeding station over farms which, given the overall low social position of young birds, suggests that this preference for a more competitive environment seems better explained by their poor explorative skills and limited environmental knowledge (Sanz-Aguilar et al., 2015). Probably, this age-effect also accounts for the high variance observed in resource preference in non-territorial males.

Ecological and applied implications of surplus food

Predictable feeding sites may attract a large number of birds typically consisting of a mixture of individuals facing different foraging trade-offs, including permanent (dominant and non-territorial females, young inexperienced birds), and temporal visitors (subdominant females breeding far away from these feeding sites and males). Apart from individual traits explaining resource use patterns, our findings point towards a major role of spatial constraints in shaping the use of predictable food resources. Sex-differences in competitive abilities and/or foraging roles may create scenarios whereby males and females may perceive the value of territories differently regarding the location of predictable food, leading to complex patterns of resource partitioning and specialization. Overall, these results show that feeding stations may have a substantial impact on the social dynamics of local vulture populations, an issue that has so far received limited attention (Cortés-Avizanda et al., 2016). Future work, preferably by using food manipulation experiments, should unravel the exact influence of predictable food on sex-specific settlement patterns.

Future analyses should reveal the extent to which the differential use of predictable food may influence survival rates and reproductive output, and may change the selective pressures operating within populations. Strong negative effects on fitness may potentially arise if feeding stations are supplied with carcasses from intensive livestock farms rich in veterinary drugs (Blanco et al., 2017) or conversely, when feeding stations are situated in highly poisoned areas and are intended to serve as a poison-free place. For animals with a strong male- or female-based social structure, as is the case in many vulture species, feeding stations have the potential for driving asymmetric patterns of individual and/or sex-specific mortality within populations (see also Sanz-Aguilar et al., 2017).

Lastly, the strong decrease in the use of the central feeding station during the breeding season (by dominant territorial and non-territorial females) suggest that vultures may switch to alternative carrion resource to feed their young and/or may generally include more natural carrion resources in their diet in periods of high abundance of such prey items (Monsarrat et al., 2013). More detailed studies are needed to deepen out the effectiveness of surplus food in relation to the dietary breath of different vulture species, which may help to further fine-tune conservation efforts.

To summarize, our results show that the food predictability and distribution may be an important driver underlying resource specialisation in vultures, whereby competition for predictable surplus food may drive individual resource preferences. In this way, predictable food may importantly affect both the foraging and social dynamics of local vulture populations. However, our results also evidence that other poorly known sex-specific mechanisms are at play, opening new research avenues. Overall, our study highlights the need to take into account social rank differences when studying patterns of individual resource specialization in highly social species.

Acknowledgements

We thank Ana Trujillano, Carmen Díez, Marcos Mallo, Walo Moreno, Juan Ramírez, and Julio Roldán for their invaluable work in monitoring the ‘’Guirre’’ population on the Canary Islands. We also thank David F. Westneat for help SAS codings. TVO received funding from the European Union’s Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No ”SocForVul 659008”. The long-term monitoring of the vulture population has been funded by the projects REN 2000–1556 GLO, CGL2004-00270/BOS, CGL2009-12753-C02-02, CGL2012-40013-C02-01, and CGL2015-66966-C2-1-2-R (Spanish Ministry of Economy and Competitiveness and EU/FEDER). Further support was provided by, the Cabildo Insular de Fuerteventura and the Dirección General de Protección de la Naturaleza (Viceconsejería de Medio Ambiente, Canarian Government).

Ethic statements

Capture, banding and monitoring of Egyptian vultures were conducted under permits and following the protocols approved by the Cabildo Insular de Fuerteventura and the Dirección General de Protección de la Naturaleza (Viceconsejería de Medio Ambiente, Canarian Government) and following the protocols approved by the Ethic Committee of CSIC (CEBA-EBD-12-56), in accordance with the approved guidelines.

Author Contributions

T.V.O., N.J.D, M.G.A and J.A.D developed research questions. T.V.O. and L.G. conducted fieldwork and T.V.O. collected dominance data. T.V.O. carried out the statistical analyses with input from N.J.D., T.V.O wrote the manuscript with editorial input from co-authors (J.A.D., D.S., L.G., N.J.D., M.G.A, W.B., M.R.). All authors gave final approval for publication.

Figure 1. Overview of Fuerteventura showing the availability of semi-predictable resources (farms, black dots, n = 319), and predictable resources (two feeding stations at approximately 40 km distance (red stars) and garbage dump (red dot)). The grey dots represent the territories of GPS-logged territorial birds (11 females and 9 males) and the white dots all occupied territories in 2016 (n = 60).

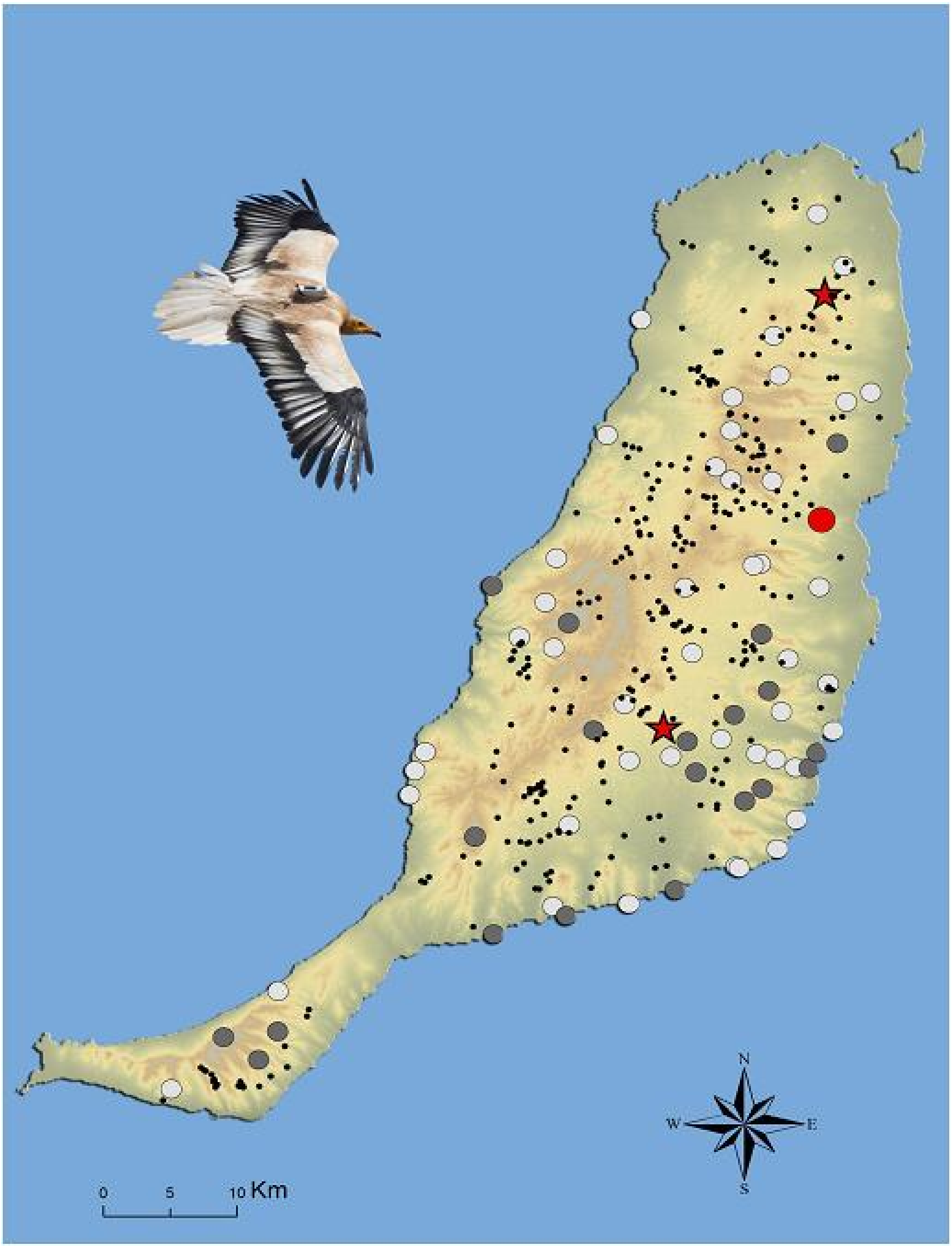

Figure 2. Within- and among-individual correlations between mobility parameters (home range size and flight activity) and time spent at the central feeding station (X-axis) in Egyptian vultures for (**a**) territorial females, (**b**) territorial males, (**c**) non-territorial females and, (**d**) non-territorial males, tracked between October 2015 and September 2016. (**a.1-d.1**) among-individual correlations (n = 45 individual means), (**a.2-d.2 and a.3-d.3**) within-individual correlation (n = 486 months). The plot of the among-individual correlation is visualized as the correlation between means of each individual trait; the within-individual correlation is visualized as the correlation between the deviations of each monthly observation from a focal individual's mean for each trait.

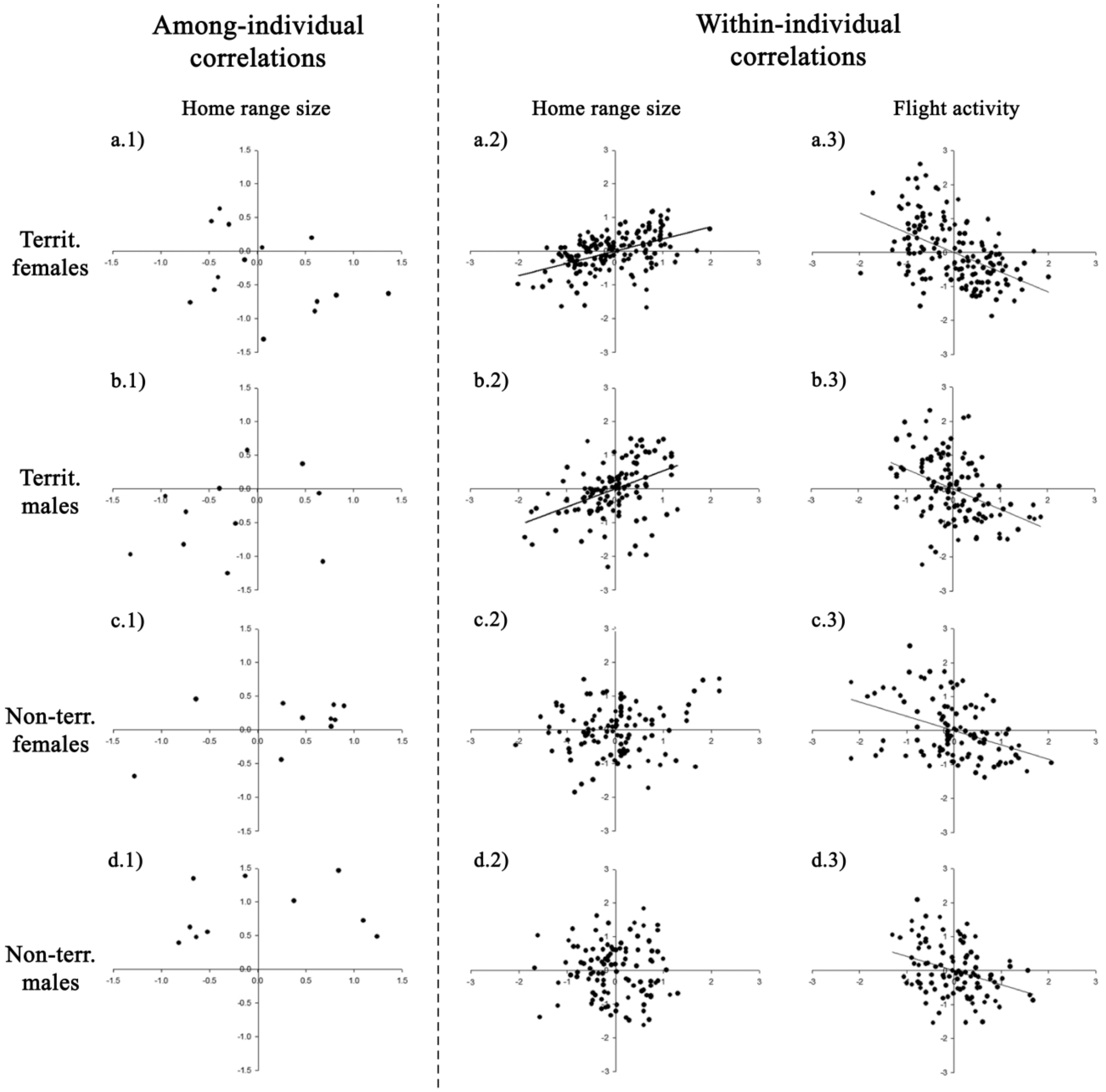

Figure 3. Differences in a) dominance rank (high values indicating high ranks) and b) resource preference (ratio time spent at feeding stations:time spent at farms (scaled by the standard deviation and mean-centred) for 40 Egyptian vultures fitted with GPS loggers categorized according to sex and territorial status (TF: territorial females, NTF: non-territorial females, TM: territorial males, NTM: non-territorial males).

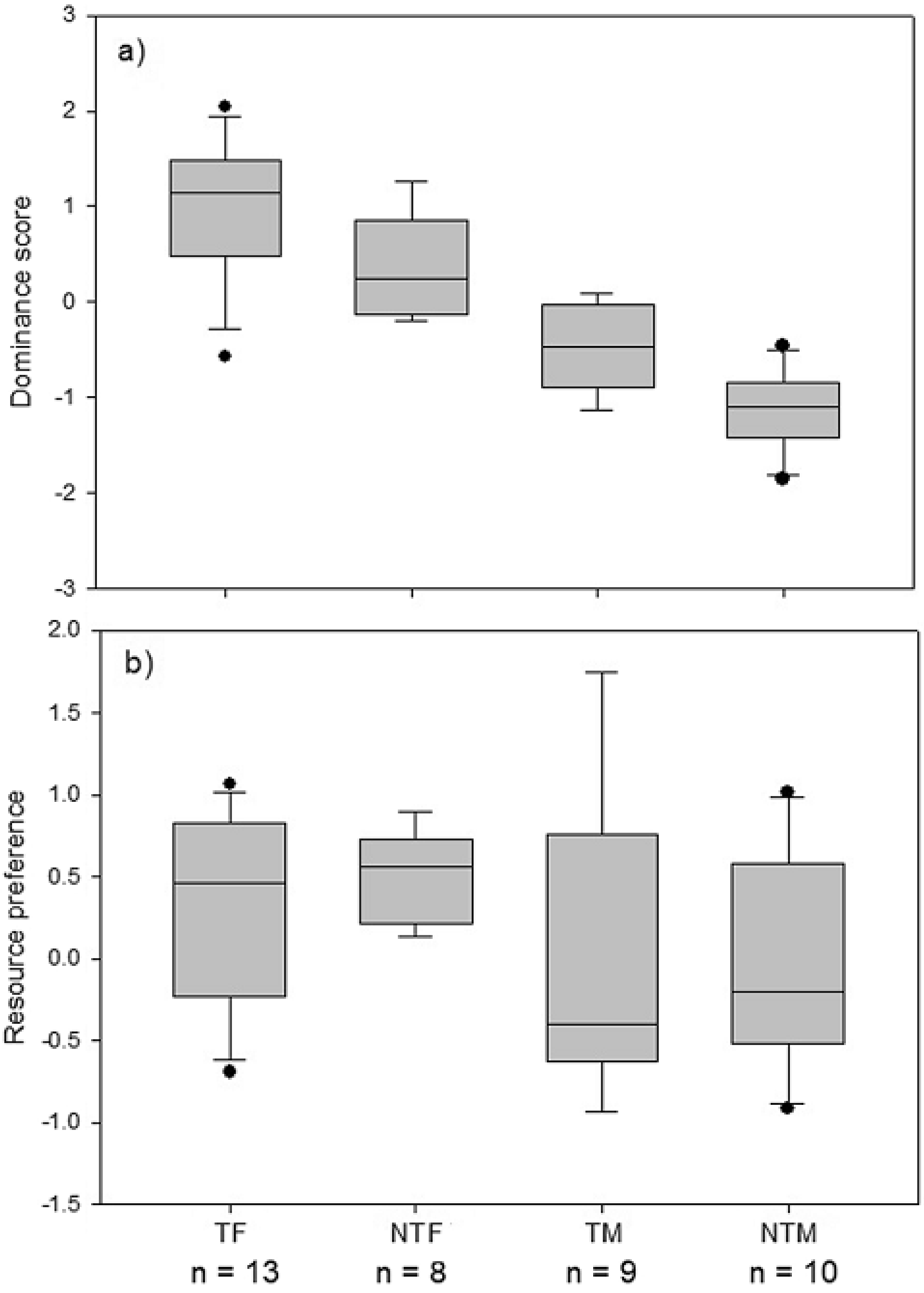

Figure 4. Overview of monthly variation in a) time spent at the central feeding station, and b) farms (all pooled), c) home range size (95% Kernel Density Estimate, KDE), d) flight activity (number of hours flying), e) flight distance from the central feeding station, and f) the total number of farms visited. Data for territorial female Egyptian vultures tracked with GPS-loggers on Fuerteventura between October 2015 and September 2016. For illustrative purposes, individuals were categorized according to dominance status (dominant above and subdominant below the median), but included as a continuous variable in statistical models. Note that the breeding activities of vultures occur between January and July (with the peak in egg-laying occurring in March)

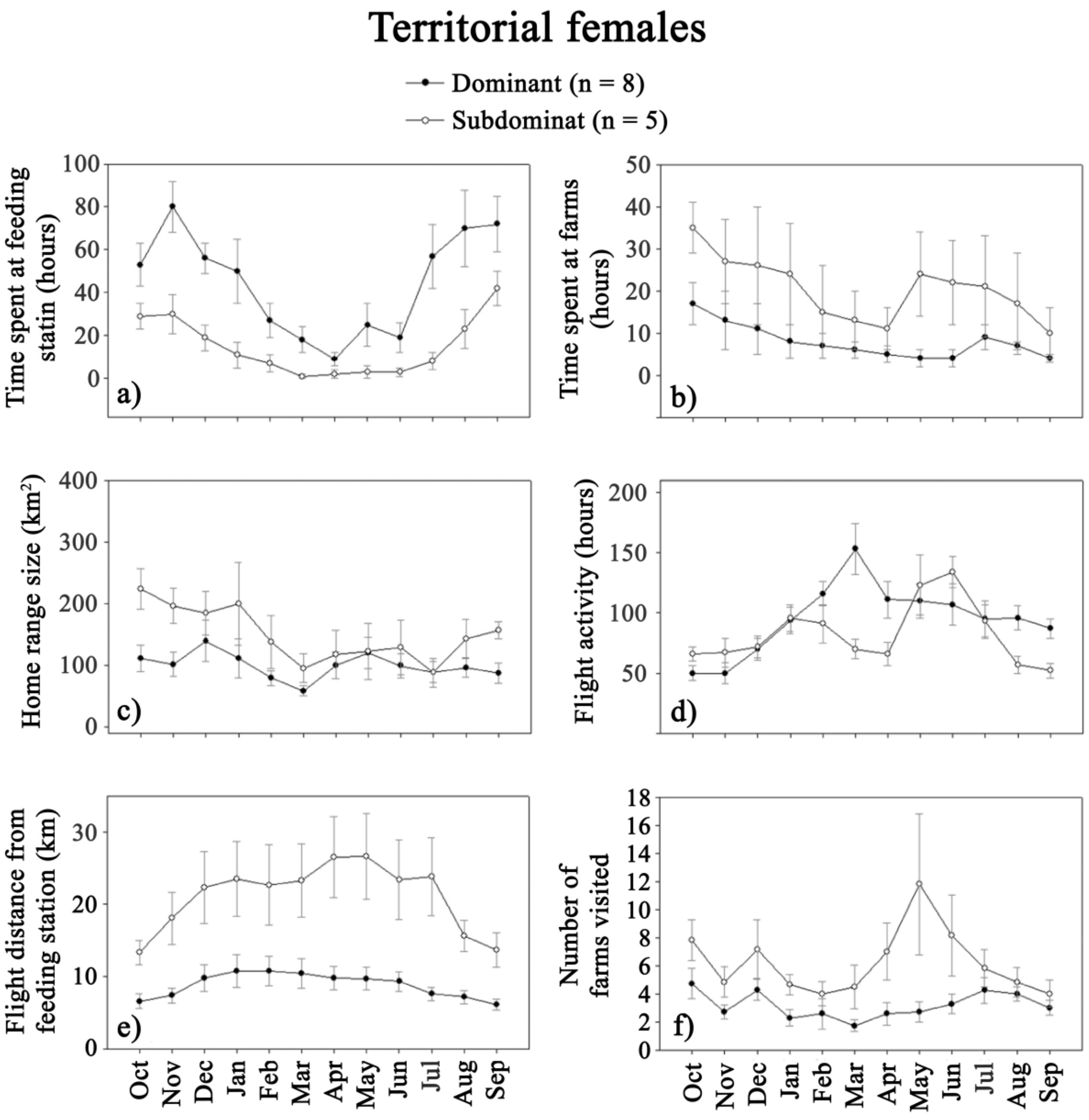

Figure 5. Overview of monthly variation in a) time spent at the central feeding station, and b) farms (all pooled), c) home range size (95% Kernel Density Estimate, KDE), d) flight activity (number of hours flying), e) flight distance from the central feeding station, and f) the total number of farms visited. Data for territorial male Egyptian vultures tracked with GPS-loggers on Fuerteventura between October 2015 and September 2016. For illustrative purposes, individuals were categorized according to dominance status (dominant above and subdominant below the median), but included as a continuous variable in statistical models. Note that the breeding activities of vultures occur between January and July (with the peak in egg-laying occurring in March)

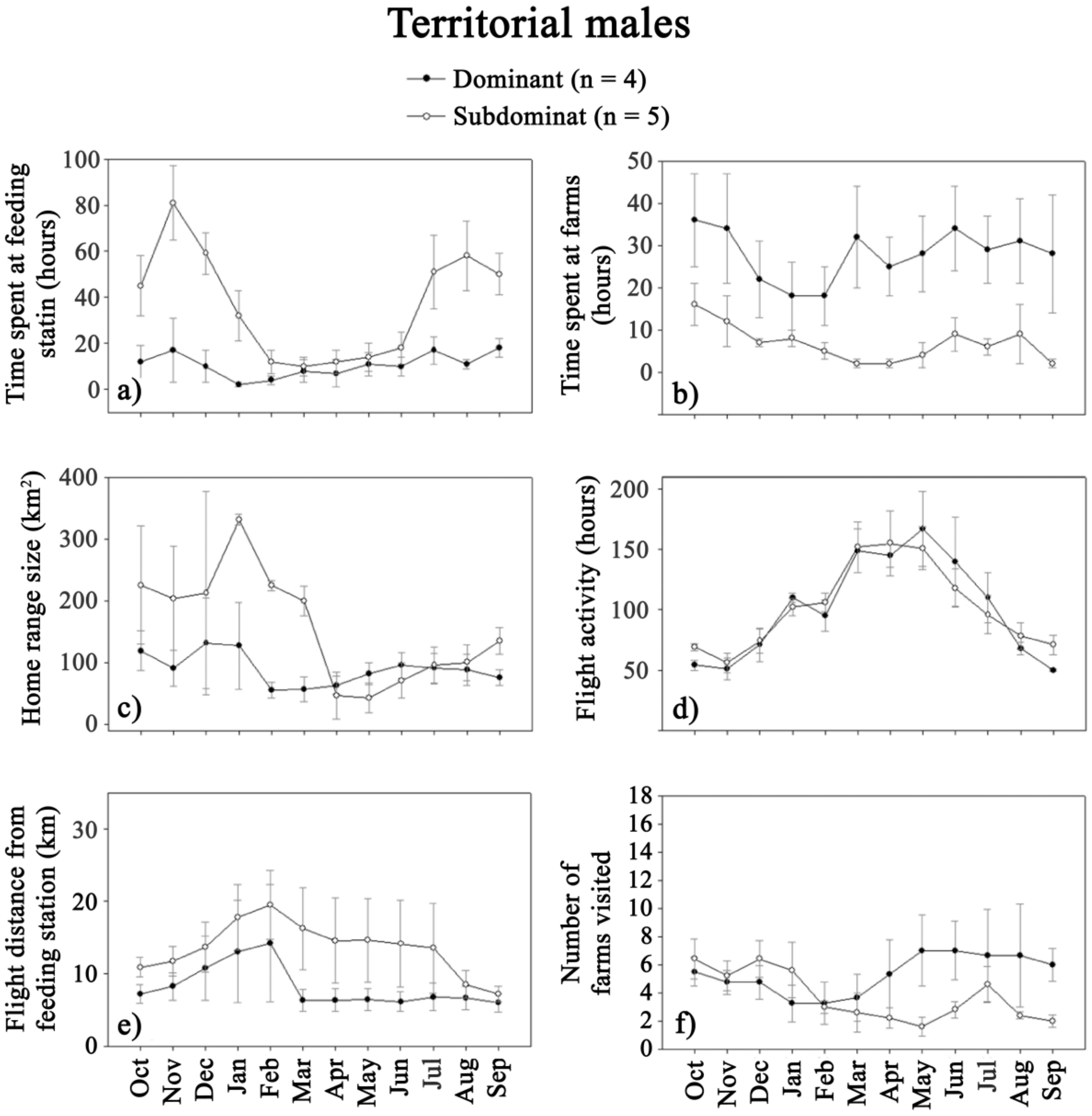

Figure 6. Overview of monthly variation in a) time spent at the central feeding station, and b) farms (all pooled), c) home range size (95% Kernel Density Estimate, KDE), d) flight activity (number of hours flying), e) flight distance from the central feeding station, and f) the total number of farms visited. Data for non-territorial Egyptian vultures tracked with GPS-loggers on Fuerteventura between October 2015 and September 2016. In non-territorial males and females no effects of dominance was present. Note that the breeding activities of vultures occur between January and July (with the peak in egg-laying occurring in March)

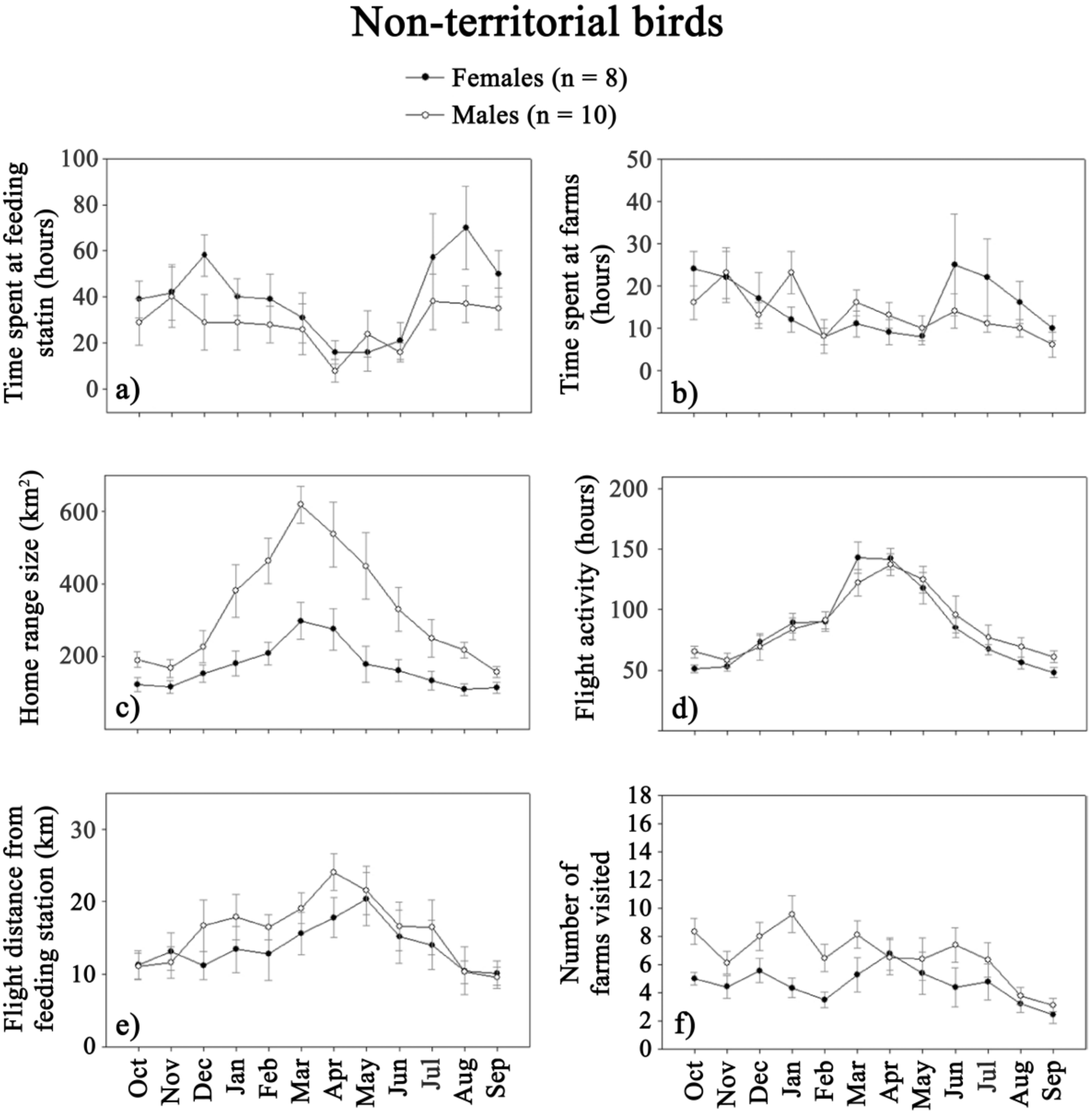

Figure 7. Relationship between dominance rank and distance from the breeding territory to the central feeding station (km) for male and female Egyptian vultures on Fuerteventura in 2016. Black dots represent birds fitted with GPS-loggers (13 females and 9 males) and crosses birds with known dominance rank (36 females and 25 males). The relationship in females is significant (Spearman rank correlation, r = -0.77, p = 0.002, and r = -0.59, p = 0.0001, respectively), while non-significant in males (p = 0. 55 and p = 0.18 respectively).

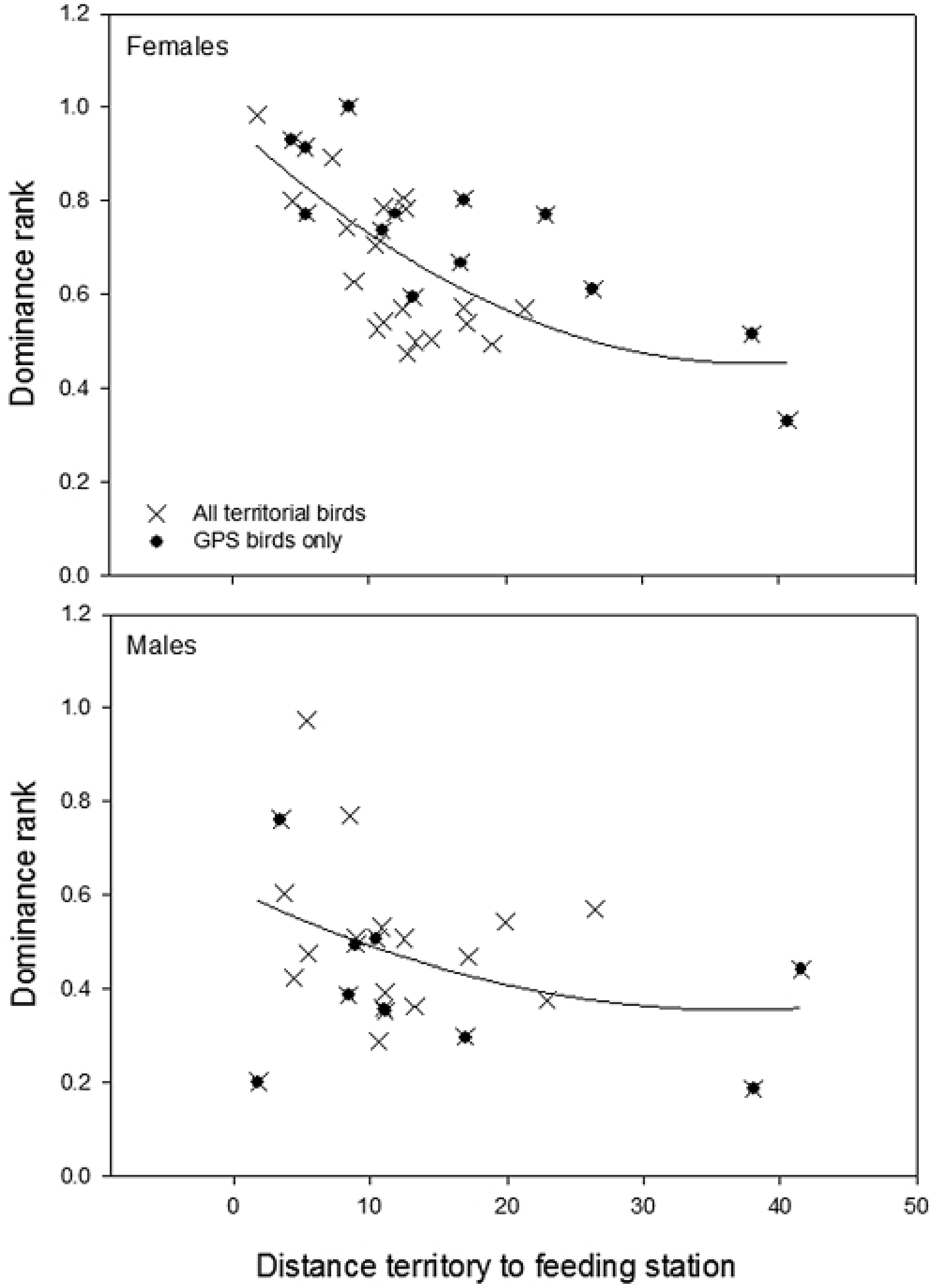

Table 1. Estimated within- and among-individual covariances (Cov.) and correlations between mobility parameters (home range size (logKDE95), and flight activity (time spent flying)), resource use (time spent at farms and at the central feeding station, square-root transformed), and resource preference (ratio time spent at the feeding station:farms, arctangent transformed) of Egyptian vultures on Fuerteventura extracted from a bivariate mixed model with no covariates. Significant correlations ($p < 0.05$) are printed in bold.

	Activity		Home range		Farms		Feeding station	
	Cov. ± S.E.	r	Cov. ± S.E.	r	Cov. ± S.E.	r	Cov. ± S.E.	r
a) Within-individual correlation								
Home range	0.03 ± 0.03	0.10						
Farms	0.05 ± 0.03	-0.10	0.04 ± 0.03	0.07				
Feeding station	**-0.30 ± 0.04**	**-0.42**	**0.15 ± 0.03**	**0.27**	0.01 ± 0.03	0.01		
Resource preference	**-0.16 ± 0.03**	**-0.24**	**0.11 ± 0.03**	**0.21**	**-0.20 ± 0.03**	-0.37	**0.39 ± 0.10**	0.77
b) Between-individual correlation								
Home range	0.03 ± 0.03	0.08						
Farms	-0.02 ± 0.05	-0.05	-0.04 ± 0.07	-0.05				
Feeding station	0.01 ± 0.05	0.02	0.04 ± 0.07	0.09	-0.10 ± 0.07	-0.23		
Resource preference	0.02 ± 0.05	0.05	0.06 ± 0.07	0.14	**-0.27 ± 0.09**	-0.60	**0.42 ± 0.03**	0.87

Table 2. Results of GLMM on seasonal effects and individual attributes affecting monthly resource preference (ratio time spent at the feeding station:farms, arctangent transformed), home range size (logKDE95) and flight activity (time spent flying, square-root transformed) of 45 Egyptian vultures tracked with GPS-loggers on Fuerteventura (Spain). All transformed response variables were scaled and centred. Repeatability (R) was calculated as the among-individual variance divided by the sum of the among-individual and the residual (within-individual) variance, and its significance tested by comparing models with and without the random effect of bird ID using a likelihood ratio test.

	a) Resource preference			a) Home range size			c) Activity		
Fixed effects	β (SE)	$F_{NUMdf, DENdf}$	*P*	β (SE)	$F_{NUMdf, DENdf}$	*P*	β (SE)	$F_{NUMdf, DENdf}$	*P*
Intercept	-0.52 (0.23)		0.031	-0.73 (0.25)		0.005	1.31 (0.23)		0.000
Sex	-0.28 (0.33)	$2.65_{1,58.2}$	0.110	0.25 (0.36)	$0.95_{1,55.7}$	0.330	-0.96 (0.33)	$4.94_{1,51.9}$	**0.031**
Age	-0.27 (0.09)	$9.33_{1,32}$	**0.045**	0.05 (0.10)	$0.27_{1,32.8}$	0.610	0.10 (0.09)	$1.17_{1,31.5}$	0.290
Territorial status	-0.80 (0.33)	$0.02_{1,51.4}$	0.880	2.21 (0.35)	$46.67_{1,49.6}$	**0.000**	-0.06 (0.33)	$0.40_{1,46.4}$	0.530
Dominance rank	-0.68 (0.31)	$0.19_{1, 52.8}$	0.670	-0.03 (0.33)	$0.04_{1,50.8}$	0.840	0.47 (0.33)	$4.22_{1,47.5}$	**0.046**
Month	0.08 (0.03)	$6.29_{1, 393}$	**0.013**	-0.12 (0.03)	$12.67_{1,392}$	**0.000**	0.12 (0.03)	$14.80_{1, 391}$	**0.000**
Sex*dominance rank	1.53 (0.37)	$17.48_{1, 53.9}$	**0.000**	0.01 (0.34)	$0.00_{1, 51.8}$	0.950	-0.15 (0.37)	$0.17_{1, 48.4}$	0.680
Sex*territorial status		$15.55_{1, 53.9}$	**0.000**		$7.08_{1, 51.7}$	**0.010**		$0.84_{1, 48.4}$	0.360
Month²	0.17 (0.11)	$15.34_{1, 389}$	**0.000**	0.23 (0.11)	$1.69_{1, 389}$	0.190	-1.02 (0.10)	$126.7_{1, 388}$	**0.000**
Month²* sex*dominance rank		$6.80_{2, 387}$	**0.001**		$4.15_{2, 387}$	**0.017**		$4.28_{2, 386}$	**0.015**
Month²* sex*territorial status		$8.38_{3, 387}$	**0.000**		$25.14_{3, 387}$	**0.000**		$3.19_{3, 386}$	**0.024**
Random effects	σ² (SE)	Z	P	σ² (SE)	Z	P	σ² (SE)	Z	P
Individual	0.18 (0.06)	3.2	0.001	0.22 (0.07)	3.35	0.000	0.21 (0.06)	3.33	0.000
Residual	0.46 (0.03)	13.81	0.000	0.47 (0.03)	13.82	0.000	0.40 (0.03)	13.79	0.000
Adjusted repeatability	*R*	χ^2	P	*R*	χ^2	P	*R*	χ^2	P
	0.28	64.7	0.000	0.32	82.3	0.000	0.34	85.8	0.000
Null-model	σ² (SE)	Z	P	σ² (SE)	Z	P	σ² (SE)	Z	P
Individual	0.47 (0.11)	4.23	0.000	0.43 (0.10)	4.18	0.000	0.18 (0.06)	3.2	0.001
Residual	0.53 (0.04)	14.86	0.000	0.56 (0.04)	14.87	0.000	0.83 (0.06)	14.85	0.000
Non-adjusted repeatability	*R*	χ^2	P	*R*	χ^2	P	*R*	χ^2	P
	0.47	209.1	0.000	0.43	184.8	0.000	0.18	39.8	0.000

Supplementary material

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Figure S1. Frequency distribution of groundspeed measured by the two GPS-devices (Eobs and UvA-Bits). A threshold groundspeed of 3 m/s was used to distinguish between flight and non-flight behaviour. Running analyses with different thresholds for ground speed (2-5 m/s did not change the results, data not shown)

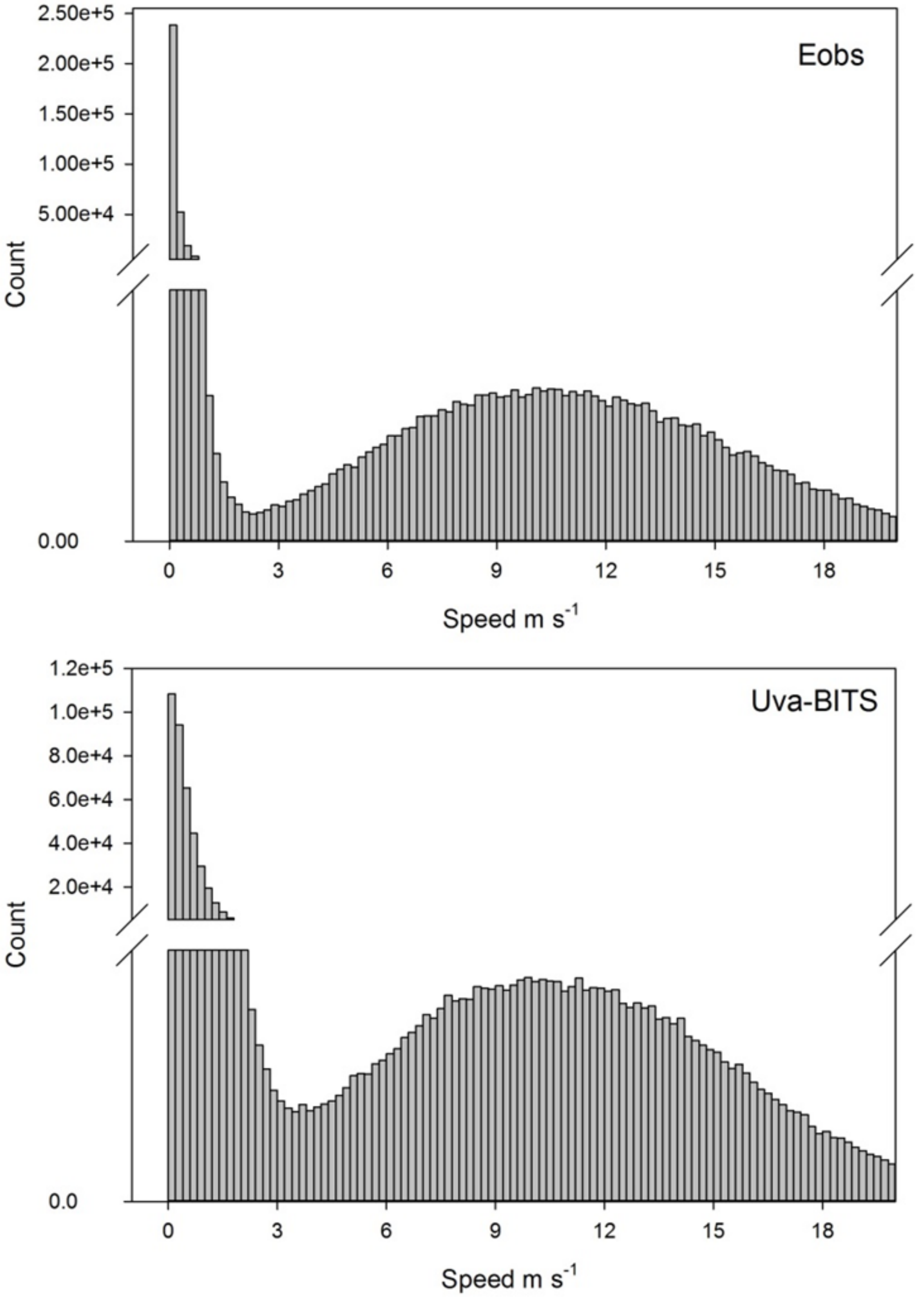


Figure S2. Average monthly time-budgets of GPS-logged Egyptian vultures (n = 45) on Fuerteventura between October 2015 and September 2016. Both the use of semi-predictable resources (farms) and predictable resources (feeding station) is strongly reduced during the breeding season (January-July). The high percentage of time with no signal between March and May is due to birds incubating eggs on nest in caves or on cliffs with bad reception. Note the clear preference for the central feeding station and to lesser extent farms, while the feeding station in the north and the garbage dump are ignored by most birds. Also note that the remaining time occupied with non-flight behaviour mostly covers time spent resting, but may also include time spent consuming carcasses of wild animals (natural food resources).

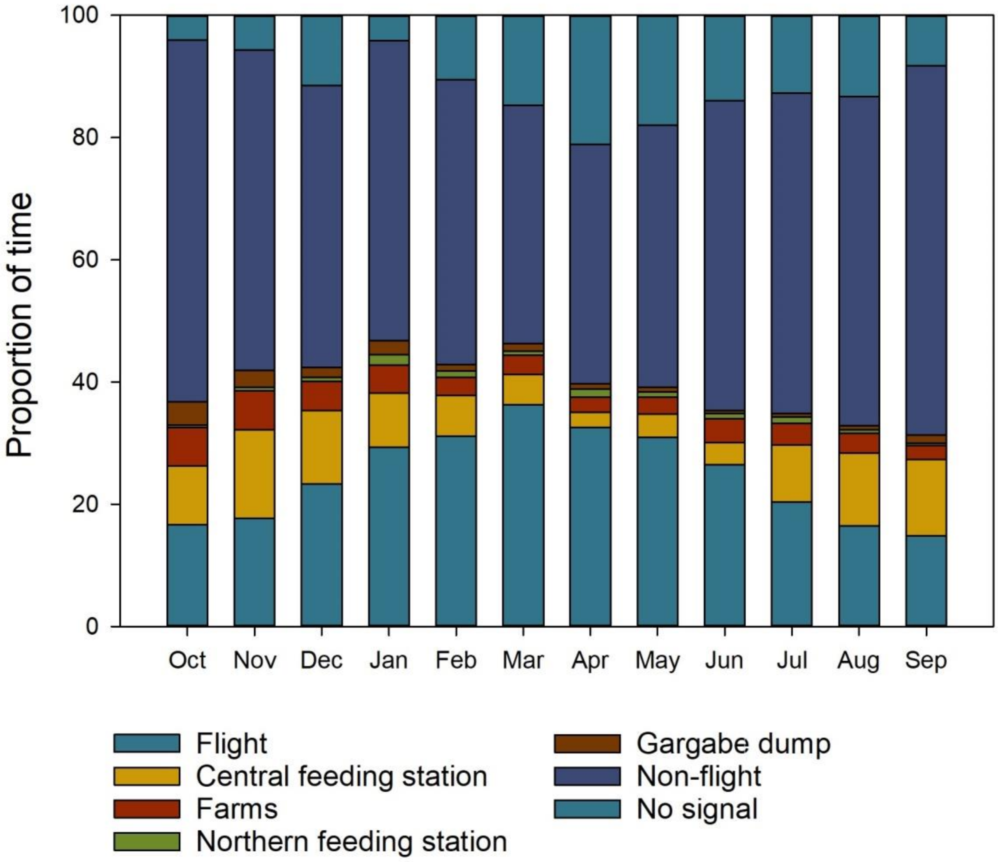
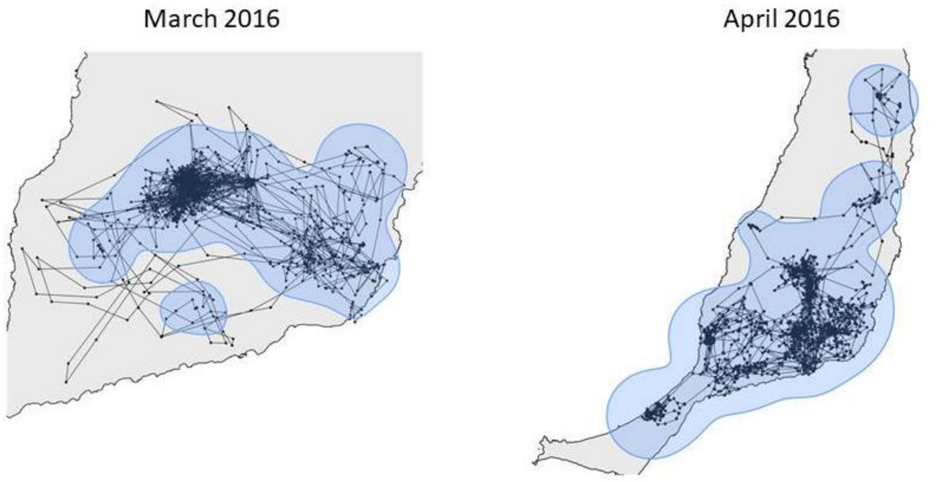


Figure S3. Examples showing over-smoothing of home-range sizes (device 6018, unpaired female) using a reference smoothing factor (H_ref). Default (reference) smoothing factor estimation is typically not reliable when ranging behaviours shows a multi-model distribution. Automatic calculation of a smoothing factor through the least-square cross validation algorithm did not work because of the high resolution of data resulting in small distances between GPS fixes.



March 2016

April 2016

H_ref = 1283.3m ; 95%KDE = 280.2 km²

H_ref = 3350.3m ; 95%KDE = 1441.3 km²

Figure S4. Examples showing home-range sizes based on different manually chosen smoothing parameters, using fixed kernel contour method ('classic method', adehabitHR package, R version 3.03) and Brownian Bridge Movement Models (BBMM, with a maximum time lag of 60 min., using the BBMM package, R version 3.0). Both methods produced highly similar 95% kernel density estimates (95%KDE). While BBMM are intended to integrate time spent at locations and to take into account autocorrelations (by determining movements paths), time lag variation may cause little change to KDE measurements based on classic kernel contour methods when using data re-sampled at specific time-intervals (in our case 10 min.). In addition, Fuerteventura is a small island with little barriers. Movements paths of Egyptian vultures typically tend to largely overlap, since birds spend considerable time in certain areas (multimodal distribution of locations). Movements in-between these areas may be too fast (given relatively high flights speeds of Egyptian vultures) to become included in home range estimates.

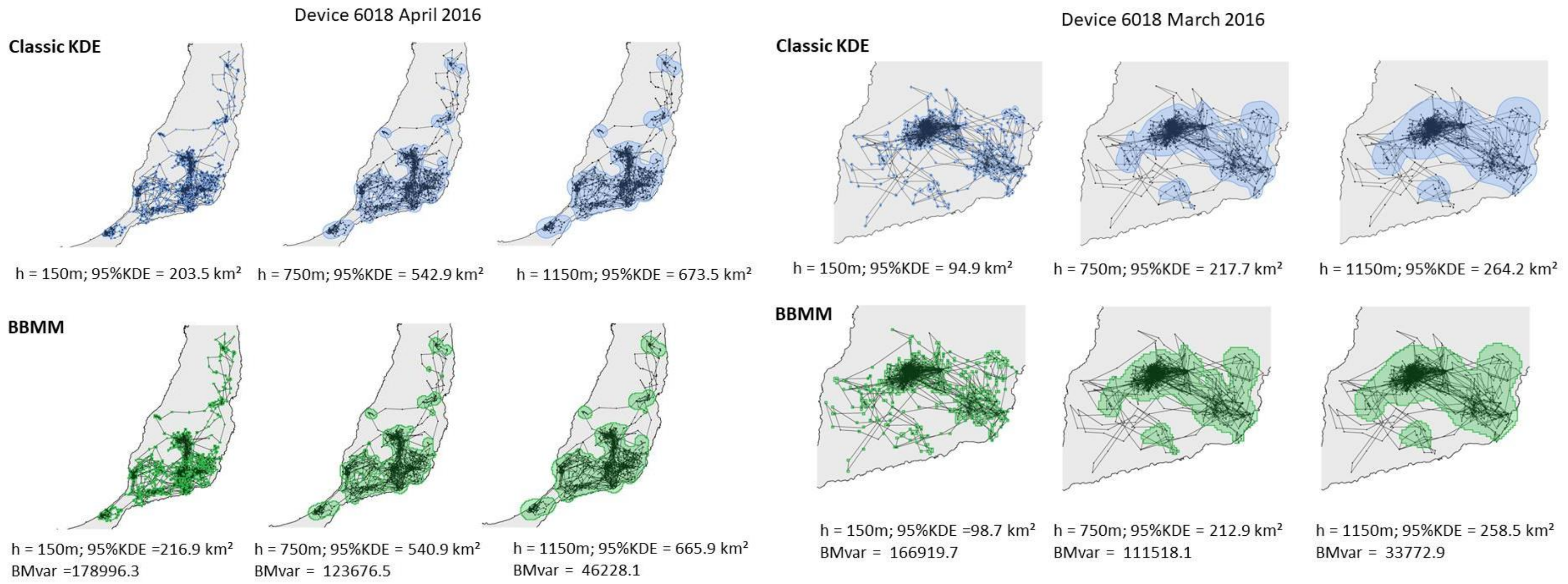


Figure S5. Correlations between monthly home ranges (95%KDE) using the fixed kernel contour method (‘clas’, with h = 750, used in our analyses, on the x-axes), and 95%KDE calculated with different smoothing factors using a similar method and Brownian Bridge Movement Models (BBMM) (on the y-axes). Numbers in graph correspond the smoothing factor (h) in meters (href = 2528.9). All Pearson correlation coefficients > 0.86, p < .0001, n = 486 individual-months per graph.

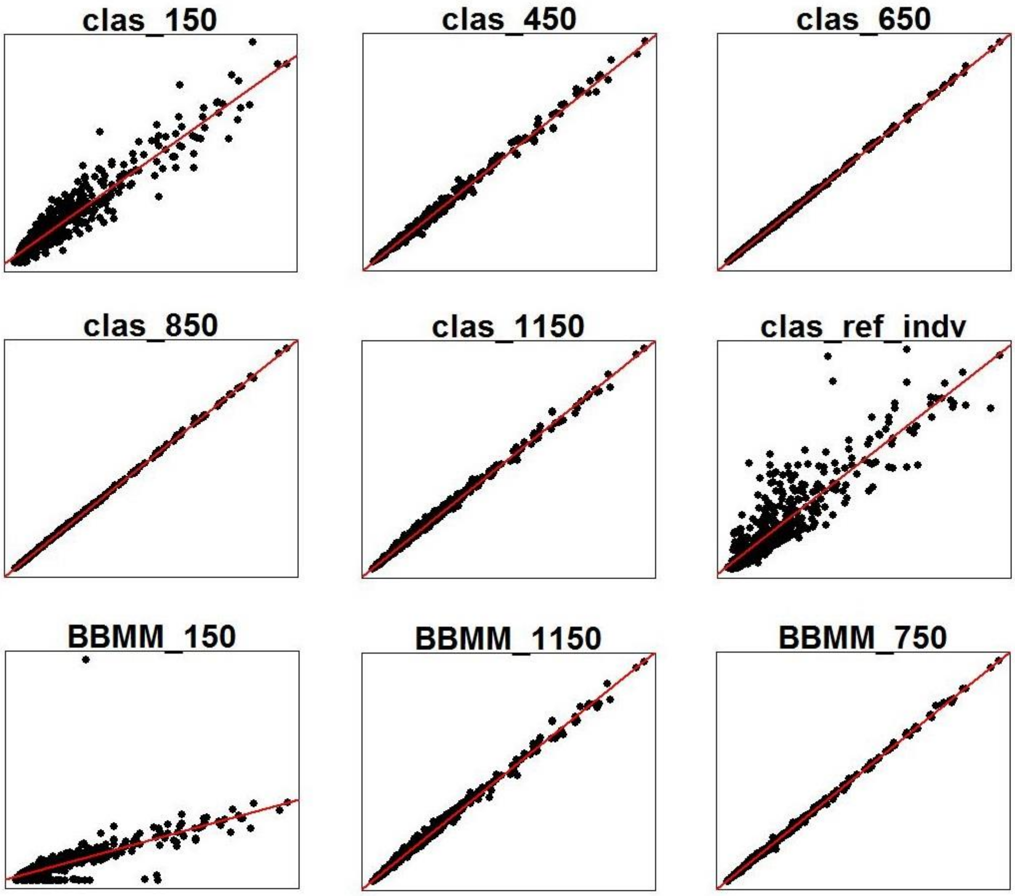


Figure S6. Relationship between the number of displacements scored for each individual (n = 141, > 20 displacements) and the dominance score (David's score), corrected for chance. A weak, but significant, positive correlation exists between the number of interactions and dominance score (Pearson correlation: r = 0.32, p = 0.001), which is due to dominant birds visiting the feeding station more frequently (see results).

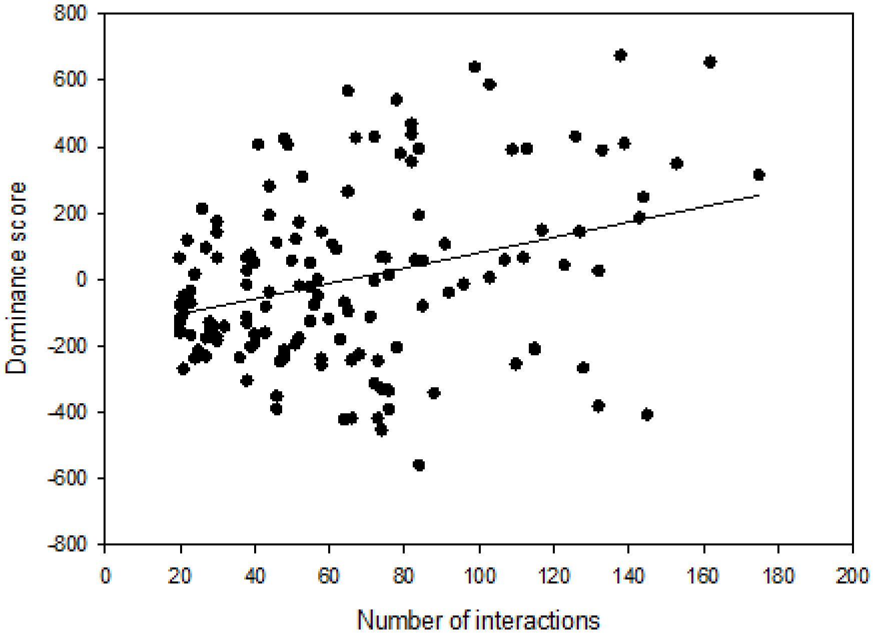
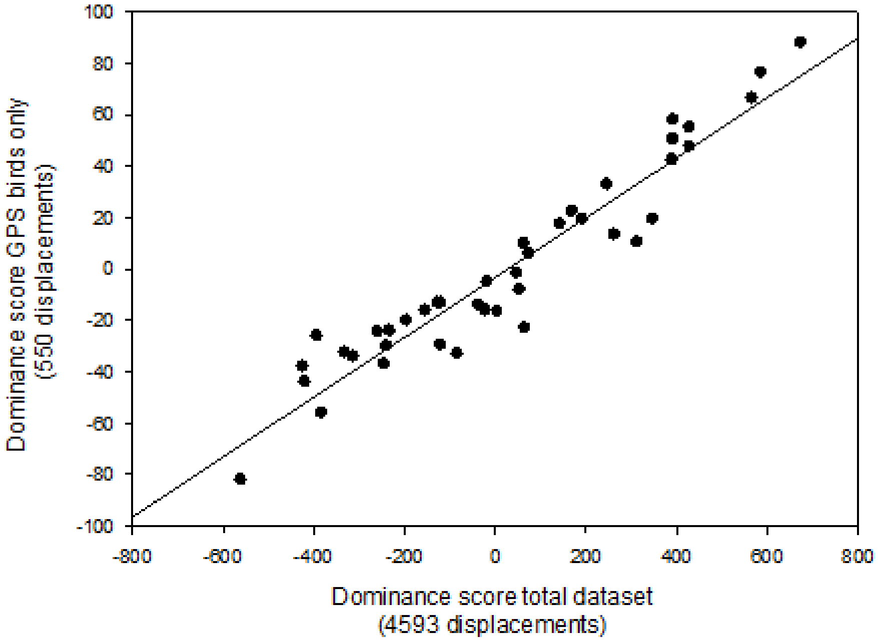


Figure S7. Relationship between unstandardized David's score calculated using either all interactions between 141 birds in the total datasets (4593 displacements) and scores calculated using interactions between GPS birds only (550 displacements) (Pearson correlation: r = 0.95, p <.0001)



Text S1. The structure of dominance relations

To examine whether the dominance relationships were linear we calculated the 'adjusted linearity index h'(de Vries, 1995), using the 'Compete' package in R (Curley, 2016). This index ranges from 0 (non-linear) to 1 (highly linear). To determine the statistical significance of h', we tested whether this index differed significantly from the expected value for random dominance relations by running 10000 randomizations (corrected for unknown relationships by randomly filling in null dyads). Landau's linearity indices h′ for both the total and GPS dataset were low (h′ = 0.07 and h′ = 0.14, respectively), although significant (p = 0.0001, p = 0.0017). The low h′ indexes are most likely due to the high number of null dyads in the datasets leading to a bias in these estimates (Shizuka and McDonald, 2013). We therefore also calculated the directional consistency index (DCI) (Van Hooff and Wensing, 1987), which provides a measure for assessing how frequent a type of behaviour occurred in its more frequent direction relative to the total number of times it occurred (using the equation DCI = (H - L)/(H + L), where H is the total number of times the behaviour occurred in the direction of the higher frequency and L is the number of times in the less frequent direction). DCI scores were high in both datasets (DCI = 0.957 and DCI = 0.945 respectively), indicating a relatively strong linearity in hierarchy.

Text S2. Monthly variation in resource use

Average monthly flight activity was generally low during the non-breeding season (July-December) and substantially increased during the breeding season (January-June) (18.2% ± 7.0 SD, n = 250 and 31.1% ± 10.3, n = 236 respectively). Average monthly time spent at the central feeding station was lower during the breeding season compared to the non-breeding season (18.25h ± 23:02 SD, n = 236 and 42:16h ± 35:25 SD, n = 250, respectively). This difference was due to a lower (absolute) number of visits (14.4 ± 16.9 SD, n = 236 vs. 26.3 ± 21.1 SD, n = 250), shorter visiting bouts (01:15h ± 00:46 SD, n = 185 vs. 01:38h ± 00:46 SD, n = 226) and fewer individuals visiting this feeding site (30.8 ± 3.0 SD, n = 6 vs. 37.7 ± 1.8 SD, n = 6) during breeding. Foraging activities were also more dispersed during the breeding season compared to the non-breeding season (i.e., average monthly flight distance from central feeding station: 16.1 km ± 10.0 SD, n = 236 vs. and 11.8 km ± 9.7 SD, n = 250, respectively).

Average monthly time spent at farms was slightly lower during the breeding season compared to the non-breeding season (12:23h ± 14.29 SD, n = 236 and 15.54h ± 17:56 SD, n = 250, respectively). Visiting bouts at farms were shorter during the breeding season (00:59h ± 00:41 SD, n = 218 vs. 01:30h ± 01:14 SD, n = 242) while visiting rates were slightly higher (12.3 ± 11.8SE, n = 236 vs. 10.6 ± 10.1SD, n = 250, respectively). Farms visited during the breeding season were located further away from the central feeding station compared to the farms visited during the non-breeding season (average monthly distance: 16.7km ± 11.3 SD, n = 222 and 11.8km ± 9.8 SD, n = 246, respectively). The average monthly number of farms visited (per individual) did not differ between the breeding and non-breeding season (4.8 ± 4.0 SD, n = 236 and 4.6 ± 2.9 SD, n = 250 respectively).

Table S1. Results of GLMM on seasonal effects and individual attributes affecting monthly time spent at the central feeding station (square-root transformed), time spent at farms (square-root transformed), home range size (logKDE95), flight acivity (time spent flying, square-root transformed) and number of farms visited (square-root transformed) for territorial males (9 individuals, 101 months), territorial females (13 individuals, 142 months) and non-territorial birds (18 individuals (10 males and 8 females), 209 months). All transformed response variables were scaled by the standard deviation and mean-centred. “Distance” as “Dist” and “Dominance” as “Dom.”.

		Territorial females			Territorial males			Non-territorial birds		
Dependent variable	Fixed effects	β (SE)	$F_{\text{NUMdf, DENdf}}$	*P*	β (SE)	$F_{\text{NUMdf, DENdf}}$	*P*	β (SE)	$F_{\text{NUMdf, DENdf}}$	*P*
Time at central feeding station										
	Sex	n/a	n/a	n/a	n/a	n/a	n/a	0.23 (0.37)	$0.39_{1,24.5}$	0.540
	Dom. rank	0.82 (0.23)	$12.49_{1,16.8}$	**0.003**	-0.02 (0.46)	$0.00_{1,7.83}$	0.970	n/a	n/a	n/a
	Dist territory	-0.60 (0.18)	$11.10_{1,18.1}$	**0.004***	-0.35 (0.16)	$4.77_{1,8.42}$	0.060	n/a	n/a	n/a
	Month	-0.10 (0.05)	$3.55_{1,128}$	0.060	0.02 (0.06)	$0.09_{1,89}$	0.770	-0.02 (0.05)	$0.11_{1,191}$	0.740
	Month^2	0.93 (0.11)	$75.95_{1,127}$	**0.000**	0.25 (0.11)	$5.22_{1,88.1}$	**0.025**	0.27 (0.07)	$17.66_{1,189}$	**0.000**
	Month^2*Dom. rank	-0.26 (0.09)	$7.74_{1,128}$	**0.006**	-0.60 (0.16)	$13.14_{1,88.1}$	**0.001**	n/a	n/a	n/a
	Month^2*Dist territory	0.20 (0.07)	$8.30_{1,140}$	**0.005***	0.22 (0.06)	$14.07_{1,88.1}$	**0.000**	n/a	n/a	n/a
	Month^2*sex	n/a	n/a	n/a	n/a	n/a	n/a	0.06 (0.13)	$0.19_{1,189}$	0.660
		* Significant when entered in the model without Dom. rank								
Time at farms										
	Sex	n/a	n/a	n/a	n/a	n/a	n/a	-0.32 (0.27)	$1.35_{1,33.8}$	0.250
	Dom. rank	-0.13 (0.20)	$0.46_{1,11.3}$	0.51	1.51 (0.53)	$7.98_{1,6.48}$	**0.028**	n/a	n/a	n/a
	Month	-0.23 (0.05)	$18.61_{1,130}$	**0.000**	-0.19 (0.06)	$10.16_{1,90.7}$	**0.002**	-0.20 (0.05)	$13.76_{1,194}$	**0.000**
	Month^2	0.16 (0.07)	$5.93_{1,129}$	**0.016**	0.24 (0.07)	$10.54_{1,89.6}$	**0.002**	-0.04 (0.10)	$2.90_{1,192}$	0.090
	Month^2*Dom. rank	0.09 (0.10)	$0.79_{1,128}$	0.380	0.21 (0.18)	$1.76_{1,88.5}$	0.19	n/a	n/a	n/a
	Month^2*sex	n/a	n/a	n/a	n/a	n/a	n/a	-0.06 (0.29)	$1.32_{1,192}$	0.220

		Territorial females			Territorial males			Non-territorial birds		
Dependent variable	Fixed effects	β (SE)	$F_{NUMdf, DENdf}$	*P*	β (SE)	$F_{NUMdf, DENdf}$	*P*	β (SE)	$F_{NUMdf, DENdf}$	*P*
Home range size										
	Sex	n/a	n/a	n/a	n/a	n/a	n/a	-0.74 (0.20)	$14.21_{1,18.5}$	**0.001**
	Dom. rank	0.16 (0.26)	$0.38_{1,14.5}$	0.550	0.37 (0.54)	$0.47_{1,10.3}$	0.510	n/a	n/a	n/a
	Month	-0.13 (0.04)	$8.86_{1,128}$	**0.004**	-0.31 (0.08)	$14.51_{1,90.9}$	**0.000**	-0.01 (0.05)	$0.08_{1,196}$	0.77
	Month^2	0.56 (0.10)	$33.46_{1,127}$	**0.000**	0.13 (0.15)	$0.65_{1,89.1}$	0.420	-0.50 (0.06)	$68.4_{1,193}$	**0.000**
	Month^2*Dom. rank	-0.38 (0.08)	$20.09_{1,127}$	**0.000**	-0.47 (0.24)	$3.88_{1,89}$	**0.052**	n/a	n/a	n/a
	Month^2*sex	n/a	n/a	n/a	n/a	n/a	n/a	0.19 (0.12)	$2.45_{1,192}$	0.120
Flight activity										
	Sex	n/a	n/a	n/a	n/a	n/a	n/a	-0.11 (0.22)	$0.29_{1,17.9}$	0.590
	Dom. rank	0.46 (0.26)	$3.18_{1,16.4}$	0.090	0.45 (0.36)	$1.61_{1,13.2}$	0.230	n/a	n/a	n/a
	Month	0.10 (0.06)	$2.67_{1,127}$	0.100	0.23 (0.07)	$13.01_{1,91.8}$	**0.001**	0.01 (0.04)	$5.59_{1,193}$	**0.019**
	Month^2	-0.58 (0.13)	$18.75_{1,126}$	**0.000**	-1.05 (0.12)	$71.67_{1,89.4}$	**0.000**	-0.78 (0.05)	$252.25_{1,191}$	**0.000**
	Month^2*Dom. rank	-0.19 (0.11)	$2.55_{1,127}$	0.110	-0.32 (0.19)	$2.86_{1,89.3}$	0.090	n/a	n/a	n/a
	Month^2*sex	n/a	n/a	n/a	n/a	n/a	n/a		$4.64_{1,190}$	**0.033**
Total number of farms										
	Sex	n/a	n/a	n/a	n/a	n/a	n/a	-0.67 (0.25)	$7.00_{1,39.6}$	**0.012**
	Dom. rank	-0.84 (0.32)	$6.50_{1,15.9}$	**0.022**	0.77 (0.49)	$2.45_{1,9.45}$	0.150	n/a	n/a	n/a
	Month	-0.02 (0.07)	$0.09_{1,128}$	0.770	-0.20 (0.08)	$6.91_{1,90.4}$	**0.010**	-0.27 (0.06)	$23.23_{1,196}$	**0.000**
	Month^2	-0.22 (0.14)	$2.32_{1,127}$	0.130	0.23 (0.14)	$2.68_{1,88.4}$	0.110	-0.21 (0.07)	$8.75_{1,193}$	**0.004**
	Month^2*Dom. rank	0.32 (0.12)	$6.93_{1,128}$	**0.010**	-0.07 (0.22)	$0.10_{1,88.3}$	0.750	n/a	n/a	n/a
	Month^2*sex	n/a	n/a	n/a	n/a	n/a	n/a		$0.11_{1,193}$	0.740

Chapter 3

Individual- and farm-dependent drivers of vultures visits to livestock exploitations based on GPS data

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Chapter 4

Probing into farmers' perceptions of a globally endangered ecosystem service provider

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Abstract

Society's perception of ecosystem services is key in conservation, particularly for endangered species providing services linked to human activities. Misperceptions may lead to wildlife-human conflicts with the risk of disappearance of the species involved.

We contrasted farmers' perceptions with highly accurate quantitative data of an endangered vulture species that provides ecosystem services. We combined surveys of 59 farmers with data from 46 GPS-tagged Canarian Egyptian vultures (*Neophron percnopterus majorensis* endemic to the Spanish Canary Islands) to disentangle factors influencing consistency between farmers' awareness of vulture occurrence on their properties and vulture behavior.

Egyptian vultures were perceived as the main providers of scavenging services and the most beneficial avian scavenger. Consistency between farmers' perceptions (surveys) and vulture use of their farms (GPS data) was higher in the morning, in older males, and at farms with lower livestock numbers, located near vulture communal roosts, and visited more frequently by vultures.

Our results underline the potential influence of modern livestock husbandry in disconnecting people from ecosystems, and how appreciation could be even lower for scarce or threatened ecosystem service providers.

Keywords: Canary Islands; Egyptian vultures; GPS tracking; local ecological knowledge; social perception; biodiversity conservation

Introduction

The importance of maintaining biodiversity to support the provision of ecosystem services and its relation to human well-being is broadly recognized (e.g. Díaz et al., 2015; MA, 2005). Ecosystem services are defined as the benefits that people obtain from ecosystems (Díaz et al., 2015) and include provisioning (e.g. food and water), regulating (e.g. climate regulation, water purification or disease and pest control) and cultural services (e.g. recreation, reflection, cognitive development). Research on ecosystem services has focused on quantifying biophysical or economic value (de Oliveira and Berkes, 2014; Martín-López and Montes, 2015; Martín-López et al., 2012; Sekercioglu et al., 2016), but increasing attention is being paid to efficiency, the interrelationships with human activities, and the role played by populations or species delivering the service, the so-called "ecosystem service providers" (Kremen, 2005; Luck et al., 2009; MA, 2005; Moleón et al., 2014; Whelan et al., 2008).

The importance of maintaining ecosystem services from a socio-ecological perspective has not been recognized until very recently (Bennett et al., 2016; Martín-López and Montes, 2015). Bearing in mind that humans are a crucial piece of many ecosystems, the need to avoid the disconnection of ecosystems from human societies is acknowledged (Bennett et al., 2016; Cowling et al., 2008; Martín-López and Montes, 2015; Olea and Mateo-Tomás, 2009). Consequently, society's perception of ecosystem services is a key issue for conservation (Ban et al., 2013; Morgan-Brown et al., 2010).

Most studies on society's perception of ecosystem services have focused on coarse approximations of their recognition and relative importance, knowledge of the concept of ecosystem services, and the personal features determining differences in perception between individuals (Hartter et al., 2014; Lewan and Söderqvist, 2002; Martín-López et al., 2012; Muhamad et al., 2014). Less attention has been devoted to the appreciation of the ecosystem service providers (Pfeiffer et al., 2015). This is not a trivial issue because a misperception about the role of organisms interacting with stakeholders may determine the emergence of wildlife-human conflicts (Everard et al., 2017) with the subsequent risk of disappearance of the organisms providing such services (Allen, 1893).

Obligate (i.e. vultures) and facultative (e.g. corvids, mammalian carnivores or raptors) scavengers provide crucial regulating services through carcass removal, such as nutrient cycling and disease and pest control (Moleón et al., 2014; Morales-Reyes et al., 2015; Ogada et al., 2012a; Sekercioglu et al., 2016; Whelan et al., 2008; Wilson and Wolkovich, 2011), but they also provide important cultural services (Gangoso et al., 2013; Whelan et al., 2008). For these reasons, scavengers have been perceived as beneficial to humans for millennia (Moleón et al., 2014; Whelan et al., 2008). Unfortunately, populations of avian scavengers, and vultures in particular, have diminished worldwide over the last several decades due to non-natural mortality (Koenig, 2006; Ogada et al., 2012a).

Another very important and widespread factor contributing to population decreases is the loss of traditional livestock farming practices leading to a diminishing number of carcasses available for scavengers (Donázar et al., 2009a, 1996a; Olea and Mateo-Tomás, 2009). This reduction may be, in turn, accentuated by the dissociation between farmers and ecosystems with a loss of local ecological knowledge (i.e. the cumulative body of knowledge, practices, and beliefs regarding the relationships of living things to their environment, hereafter, LEK; Díaz et al., 2015), and a lower appreciation of ecosystem services provided by scavengers (Morales-Reyes et al., 2018a). This may hinder conservation efforts against harmful practices like indirect poisoning with baits aimed to kill predators and the use of veterinary drugs that are highly toxic to vultures feeding upon carcasses of medicated animals (Margalida et al., 2014b, 2013a).

Here, we investigated whether Canarian Egyptian vultures (*Neophron percnopterus majorensis*) are acknowledged by local farmers as ecosystem service providers. We then assessed whether farmers are aware of the presence and abundance of vultures foraging on their properties while disentangling factors influencing these perceptions. For the latter, we took advantage of two different studies: (1) one about the use of farms by GPS-tagged vultures and (2) another about the knowledge of this use by farmers on these farms. The study was conducted on Fuerteventura, where a population of this globally endangered species still survives (Birdlife International, 2017). There, Egyptian vultures rely on traditional goat farming under a mix of intensive and extensive regimes (Gangoso et al., 2006). Livestock practices, however, are progressively intensifying so that small traditional farms are disappearing while large farms with mechanized systems are becoming more frequent (García-Martínez et al., 2009). Within this scenario, we specifically predict that the probability of matching farmers' LEK and foraging patterns of GPS-tagged vultures would be greater in: 1) older or more experienced farmers, because presumably both lead to higher LEK (Gómez-Baggethun et al., 2010; Oteros-Rozas et al., 2013); 2) male compared to female farmers since it has been found that men are associated with a higher LEK in Mediterranean Europe (Oteros-Rozas et al., 2013); 3) larger farms (greater numbers of livestock) because of a greater availability of carcasses; and 4) farms and their surroundings that are visited by a greater number of vultures.

Materials and methods

Study area

The Canary Islands are situated in the northeast Atlantic Ocean, between 27º 37’ and 29º 25’ N, and 13º 20’ and 18º10’ W. Fuerteventura (1659.7 km^2) is the most south-easterly island. The landscape is dominated by grass and scrublands with an almost total absence of woodland (Rodríguez Delgado et al., 2000). Agricultural land occupies only 16.75% of the territory (Molina, 2002) of which only 0.3% is usually cultivated (Cabildo de Fuerteventura, 2007). Farming is based on livestock (goats and, to a lesser extent, sheep; Gangoso et al., 2006). From 1970 onwards, the number of heads increased from 20.000 to 100.000 in 2013 but has decreased in recent years (Canarian Government, 2017). There were officially 404, 345 and 301 owners of goats and/or sheep in 2013, 2014 and 2015, respectively. Unlike in other Spanish regions, carcass disposal remains banned in the Canary Islands because of sanitary regulations imposed by the European Union after the outbreak of bovine spongiform encephalopathy in 2001(Donázar et al., 2009b). Officially, remains resulting from natural death and sacrifices of the oldest animals are regularly collected by a specialized company and buried in a garbage dump. Farmers pay an insurance to cover such carcass-collecting service. However, field observations and farmers themselves revealed that carcasses are often abandoned despite the ban (M. García-Alfonso, unpublished data). However, information on carcass disposal is scarce because farmers are usually reticent to provide details on this illegal practice (see Results section).

As there are no large scavenger species, such as griffon vultures, on the island, abandoned carcasses usually last several days in the field until total consumption. Moreover, Egyptian vultures may feed on old small remnants scattered across the disposal sites (authors, pers. obs.), so their presence on the farms is not restricted to the day on which carcasses are disposed.

Study species and basic population monitoring

The Canarian Egyptian vulture is an endemic subspecies inhabiting the eastern islands of the archipelago, where it is sedentary. It is a medium-sized vulture (around 2.5 kg) nesting in cliff cavities of variable size. Breeding pairs are territorial but large aggregations of birds may be found at communal roosts and feeding places such as garbage dumps, artificial feeding stations and livestock farms (Cramp and Simmons, 1980; Donázar, 2004, 1993). This vulture feeds on carcasses of small and medium-sized animals that are shared with the other three endemic subspecies of facultative scavengers: common buzzards (*Buteo buteo insularum*), common ravens (*Corvus corax canariensis*) and yellow-legged gulls (*Larus michahellis atlantis*) (see García-Heras et al., 2013). The species significantly declined during the 20th century due to the incidence of non-natural mortality, mainly accidents with power lines and indirect poisoning (Donázar et al., 2002b; Gangoso and Palacios, 2002; Gangoso et al., 2009a). Currently, the Canarian Egyptian vulture survives only in Fuerteventura and Lanzarote with the bulk of the population concentrated in the former (Agudo et al., 2010). Similar negative population trends are found worldwide and consequently, the species is considered as globally "endangered" (Birdlife International, 2017).

Canarian Egyptian vultures have been intensively monitored since 1998. Territories are regularly visited to determine population size and breeding success, with 54 breeding pairs found in Fuerteventura and 5 in Lanzarote in 2014. Moreover, known locations often used for communal roosting at night (mainly power lines, see Donázar et al., 2002) are also regularly monitored. Intensive marking schemes (metal and plastic rings) have resulted in about 90% of the population being individually identifiable as of 2014.

Vulture capture and tagging

From June 2013 to September 2015, we trapped 46 Canarian Egyptian vultures (22 males and 24 females, whose ages ranged from fledgling to 14 years old) with cannon-nets and tagged them with solar-powered GPS transmitters. This represents 16% of the current population. Two types of GPS-devices were used: 26 individuals were equipped with UvA-BiTS (Bouten et al., 2013), and 19 with E-obs devices (GmbH, Munich, Germany). Another individual successively carried a device of each class. Both types of devices have multiple onboard sensors providing geographical coordinates, altitude, speed and tridimensional movements of each individual according to a defined time interval. For the first tagged vultures (n = 22, Table S1), the time interval between locations varied from 3 seconds to 20 minutes due to initial tests of the devices. From 2015 onwards, all devices were programmed with time intervals between 1 and 5 minutes.

Devices were attached as backpacks using 0.84 and 1.12 cm wide Teflon harnesses. Total system weight was between 31 g (UvABiTS) and 54 g (E-obs), about 1.4- 2.4 % of the mean body mass respectively, which is below the limit recommended by previous studies to avoid negative effects (3%, Sergio et al., 2015). All procedures were subject to ethical review and were carried out in accordance with the approved guidelines set out by the Bioethics and Animal Welfare Committee (CEEA-EBD-CSIC). Vulture trapping and marking were approved by the Canarian Government.

Analyses included a total of 12,432,333 locations of 46 different vultures collected over 914 days between 1st July 2013 and 31st December 2015 (Figure S1). Mean (±SD) number of locations per individual was 270,268 (±351,651). Number of days with information per individual was 444 (±364) days (Table S1). We included GPS information from 18 months before to 18 months after the completion of the surveys, to better capture the general behavior of the vulture population.

Use of farms by vultures

Since carcasses resulting from the activity of the farms were not discharged at the farm buildings but rather in their vicinity, we first calculated the mean dumping distance from the buildings to the disposal sites. We tried to obtain such information through phone calls (n = 122, M. García-Alfonso unpublished data), but only 10 farmers were willing to reveal where they left the carcasses. We extrapolated this information (mean distance: 286 m, 95% confidence interval 180 - 393 m) to all farms surveyed (section 2.5). We used these lower and upper confidence limits to establish two buffer areas around the farm buildings and selected all GPS fixes within these distances. Accordingly, two sets of analyses were performed. To determine the presence of vultures foraging at farms, we selected stationary GPS fixes by establishing a maximum altitude of 25 m and a maximum instantaneous speed of 2 m/s (Klaassen et al., 2017; Schlaich et al., 2016). After filtering the data set, we retained 6,472,416 stationary locations.

Local ecological knowledge

We conducted 59 face-to-face surveys through questionnaires with farmers in July 2014 (Table S2). The sampling strategy was systematically divided into three main stages. First, we randomly selected an initial set of farmers of extensive livestock farming systems from the Spanish General Register of Livestock Farms. Second, we acquired the contact information of farmers from the local sanitary authorities. Third, we conducted the surveys with farmers on or near their farms. The sample size was representative of the total population of farmers in the study area (see Morales-Reyes et al., 2018a) for details and Figure 1). All farmers were informed that their participation was voluntary and anonymous. We used the questionnaire to collect information regarding two topics: (i) perception of the capacity of Canarian Egyptian vultures to provide ecosystem services relative to the other three scavenger species (buzzards, ravens and gulls), and (ii) farmers' awareness of the presence and number of Canarian Egyptian vultures in his/her farm or its surroundings.

First, to evaluate the farmers' perceptions about the capacity of Egyptian vultures and the other scavengers to provide ecosystem services, according to Morales-Reyes et al., 2018a, we used two variables: (1) *Ecosystem service provider (ESP) index:* average farmer's perception of each one of the four avian scavenger species habitually found at carcasses. We used a five-point scale from very harmful to very beneficial, asking the respondents to explain their answers (n = 59); (2) *Scavenging services [%]:* percentage of farmers that selected each species as a provider of scavenging services (i.e. carcass consumption) either in the first, second or third ranking of importance (n = 59).

Secondly, to determine factors influencing the consistency between farmers' awareness of Egyptian vulture presence and GPS data, we used the following information from the surveys: (1) occurrence of vultures perceived by farmers on their farms (n = 55), (2) number of goats and sheep on the farms (n = 55), (3) number of vultures detected simultaneously by farmers on their farms (n = 22), and (4) period of the day (i.e. morning, midday and/or afternoon) when vultures were observed by farmers on their farms (n = 21). Farmers' answers were considered as a representation of their global experience on farms in the medium-term instead of specific observations in a specific period of time (see Table S3 for specific questions answered).

Statistical analyses

We used the Kruskal-Wallis test ($\alpha = 0.05$) to identify differences in farmers' perceptions of the capacity of avian species to provide ecosystem services (*ESP index*), and Pearson's chi-squared test ($\alpha = 0.05$) to determine differences in the perception of species as providers of scavenging services in particular (*Scavenging services [%]*).

For determining factors influencing consistency between awareness of vulture occurrence and GPS data, we selected three response variables: (1) Presence of vultures (*Presence*). Awareness was considered consistent (value = 1) when the response of the farmers matched the GPS data (i.e. farmers answered that they detected vultures and there was at least one GPS location associated with their farms, or farmers did not detect vultures and no GPS locations were associated with their farms); and inconsistent for the other two possibilities (value = 0). (2) Period of the day with the presence of vultures (*TimeSlots*). Awareness was considered consistent (value = 1) when farmers answered that they detected the presence of vultures at a certain time of day (morning, midday and/or afternoon) and there was at least one GPS location associated with their farm during this time period, or they did not detect vultures and there were no GPS locations; and inconsistent for the other two possibilities (value = 0). (3) The number of vultures perceived by the farmers at their farms (*Number*). We used the mean value when the farmer gave a range of numbers of vultures.

The explanatory variables were divided into four groups (Table 1): (1) four variables representing vulture behavior (i.e. vulture visits); (2) three associated with farmers; (3) one associated with time; and (4) eight related to characteristics of the farms. Before modeling, collinearity between explanatory variables was tested (Graham, 2003). We never included in the same model pairs of variables with a correlation coefficient higher than |0.5| (Spearman) or a p-value higher than 0.05 (Mann-Whitney U). All the variables were included in the modeling procedures except for the explanatory variable *Hour,* which was only fitted to the response variable *TimeSlots.* We standardized all variables (except *Gender* and *Hour*) by subtracting the mean of each variable and dividing the resulting value by its standard deviation. Since explanatory variables had a non-normal distribution, data were analyzed in a Generalized Linear (Mixed) Model framework (Bolker et al., 2009). *Presence* was modeled by means of Generalized Linear Models (GLMs), with binomial error distribution and logit link function. For *TimeSlots*, we used Generalized Linear Mixed Models (GLMMs) with binomial error distribution and logit link function, where farmer was included as a random factor to avoid pseudoreplication since the response variable *TimeSlots* involved three values per farm (morning, midday and afternoon). Moreover, the four "vulture visits" variables were calculated for each period of the day.

For each of the two first response variables (i.e. *Presence* and *TimeSlots*), we performed two sets of models corresponding to values of explanatory variables ("vulture visits") within the two buffers established by lower and upper limits of the confidence interval of the distances from carcass disposal sites to the farms (180 and 393 m, see above), thus implying a total of four sets of models. Models were fitted with a maximum of four variables simultaneously to avoid overparameterization. The number of candidate models per set differed because collinearity was different for each buffer (Tables S4 and S5). Model selection was made on the basis of the Akaike's Information Criterion corrected for small samples size (AICc) (Sugiura, 1978). We discarded models including uninformative parameters, i.e. parameters whose 85% confidence interval overlapped with 0 (Arnold, 2010; Burnham and Anderson, 2002). In addition, when top-positioned models were redundant, i.e. two or more models included fixed effects with a similar biological interpretation, only one of them was retained, e. g. the four variables related to vulture visits or connectivity index variables with corresponding distance variables (Table 1). Models differing less than two AICc points from the top-ranked models (i.e. the one with the lowest AICc) were considered statistically equivalent, and thus model averaging was applied to deal with model selection uncertainty (Burnham and Anderson, 2002). We tested for overdispersion and determined the explained deviance in the selected subsets of models.

We used Spearman's correlation to test the relationship between the number of vultures that farmers observed on their farms (*Number*) and the four "vulture visits" explanatory variables (Table 1).

We used R statistical software (R Core Team, 2016) with the stats package for GLM and confidence intervals, lme4 (Bates et al., 2015) for the GLMM analysis, AICcmodavg (Mazerolle, 2016) for model ranking and MuMIn for model averaging and for calculating overdispersion and explained deviance in GLMMs (Barton, 2016).

Results

Farmers perceived Egyptian vultures as the most beneficial avian scavengers, followed by common buzzards, yellow-legged gulls and common ravens (Kruskal-Wallis test, χ^2 = 125.7, $p < 0.001$; Figure 2a). Reasons given by farmers for considering Egyptian vultures as beneficial (n = 56) were: vultures are scavengers (n = 48), vultures do not produce damage (n = 2), vultures are necessary (n = 1), vultures are predators (n = 1), and no reason (n = 5). Moreover, Egyptian vultures were significantly perceived as the main providers of scavenging services followed by common ravens (Pearson's chi-squared test, χ^2 = 117.6, $p < 0.001$; Figure 2b).

Surveys (see section 2.5) revealed an average number of 119 (range 2 - 425) livestock casualties per farm and year, with larger farms showing a higher number of deaths (Spearman's rho = 0.49, $p < 0.01$, n = 50). Farmers indicated whether they abandoned the carcasses always (n = 4), sometimes (n = 29), or never (n = 25). Some farmers also revealed that large farms benefited more from the official carcass-collecting service, to the extent that some owners of small farms indicated that they do not receive this service at all.

Overall, about 60% of farmers' perceptions about the visits of vultures on their farms were consistent with GPS data (Table 2). In 40% of the surveys, there was consistency between the presence of GPS tagged-vultures on the farms and positive answers by farmers regarding the occurrence of vultures (Table 2). On the contrary, between 35 and 42% of them (depending on the radius considered) did not perceive the presence of the birds even though the GPS-tagged vultures certainly visited their farms. Absences of GPS data were always consistent with the farmer's perception of absence (i.e. no farmers indicated that vultures were visiting their farm when no GPS-tagged vultures made visits).

Concerning the consistency of the presence of vultures (*Presence*), we obtained similar evidence at both spatial scales (180 and 393 m): there were both an effect of gender of the farmer and the number of days with visits of vultures (Table S4). Thus, the probability of this consistency was higher for males and for those farms visited more frequently by GPS-tagged vultures (Table 3). Two additional variables were influential at the smallest radius (Table S4): farmers' awareness was more consistent with GPS data for those farms with a smaller number of livestock and located near communal roosts used by vultures at night (Table 3; Figure 3). The percentage of explained deviance was 20.3 and 11.2% for 180 m and 390 m radii, respectively.

The consistency in awareness in relation to the period of the vulture visits (*TimeSlots*) decreased from morning to afternoon with the number of livestock at farms and with the distance to communal roosts (Table 4 and S5). Moreover, at 180 m radius, farmers' responses were more consistent with GPS data for those farms receiving visits of more vultures, while at the 393 m radius we found an additional positive relationship with the age of the farmer (Table 4 and S5). The percentage of explained deviance was 41.8% and 35.0% for 180 m and 390 m radii, respectively.

Regarding the number of vultures detected by the farmers (*Number*), we did not find significant relationships with the four variables measuring "vulture visits" (Spearman’s rho between -0.04 and 0.15; p> 0.06 in all the cases).

Discussion

To our knowledge, this is the first study comparing stakeholder awareness of the presence and abundance of ecosystem service providers with highly accurate quantitative field data measuring the spatial distribution of these providers. Since our results revealed that farmers largely perceived the Egyptian vulture as beneficial due to their scavenging habits, this approach helps us understand how stakeholders directly perceive the potential benefit they obtain from the service suppliers. Our findings showed that farmers that did not receive vulture visits at their farms never detected their presence, but half of the farmers receiving visits of vultures did not notice them, which could lead to an underestimation of actual services. Some increase in misperceptions when vultures visited the farms was apparent when the buffer of observations around the farm increased (Table 2), which is consistent with a less precise perception of those birds moving outside the activity zone and sight of the farmers.

Since GPS-tagged vultures are only a fraction (15%) of total vultures inhabiting the island, it could be argued that we obtained only a partial view of the probability of the presence of vultures on the farms. Thus, some farms visited by Egyptian vultures would appear in our analyses as non-visited, leading to an increase of false absences. Nevertheless, all farmers detecting vultures at their farms received visits of GPS-tagged individuals, which indicates that we achieved a representative sample for the purposes of this study. Additionally, it should be taken into account that we used GPS data recorded in the same period of the surveys to accumulate medium-term data on the occurrence of vultures on the farms. Thus, temporal biases were minimized.

The fact that the vast majority of farmers perceived vultures as highly beneficial and acknowledged their scavenging services is probably due to the persistence in the study area of traditional extensive livestock farming systems (see Morales-Reyes et al., 2018a). In fact, Fuerteventura, along with other oceanic islands, is one of the few places in the world where vultures and human activities are still deeply connected and where cultural ecosystem services associated with the charismatic Egyptian vultures still survive (Gangoso et al., 2013, 2006). However, misperceptions among farmers receiving vulture visits suggest that the actual benefits received at their holdings are somewhat undervalued. Thus, acquiring informed knowledge on the factors affecting awareness accuracy may be key to understanding the social dimension of vulture conservation.

The highest consistency between GPS data and farmer awareness of vulture presence was found in older men, a finding that is likely related to historical and cultural factors. Although we only examined a very specific aspect of LEK, this result would agree with recent studies conducted in rural areas of Spain, that found that men have a higher traditional ecological knowledge than women, and that LEK increases with age (Gómez-Baggethun et al., 2010; Oteros-Rozas et al., 2013). Other studies, however, depicted different scenarios in which women and younger people perceived regulating services (e.g. those provided by vultures through the removal of carcasses) as more important, with provisioning services perceived as more important by men and older people (Briceño et al., 2016; Martín-López et al., 2012). In this sense, it has been shown that regulating services are perceived to a lesser degree than provisioning services, which are more directly detected since they are more readily observable (de Oliveira and Berkes, 2014; MA, 2005; Muhamad et al., 2014). The apparent contradiction between our results and previous research regarding older males perceiving a regulating service, such as carcass removal, more accurately may result from the fact that vultures are easily observable, unlike most regulating services that are intangible (e.g. air purification or climate regulation), and thus they are as detectable by people as a provisioning service (Martín-López et al., 2012). Moreover, the effect of age could be related to the high abundance of Egyptian vultures in the past (Donázar et al., 2002b), and thus older people would be much more familiar with the species and its detection. In the same way, it is also possible that female farmers were less common in the past due to cultural reasons and that this has affected our results. Finally, it cannot be discarded that age and/or sex asymmetries in the time spent by owners on farms may have influenced our results, but unfortunately these data were not available.

As would be expected, farmer awareness about the presence of vultures was more consistent with data from GPS-tracked birds when they frequently visited the farm. Thus, a major presence of vultures, either on the farm or in its surroundings, clearly increases the concordance between farmer perceptions and GPS data. Therefore, adjustment of perception of an ecosystem service to data obtained from GPS-tagged birds seems to depend on the frequency of the service as well as the number of providers. In the same way, locations of the farms regarding the distribution of vultures over the island influenced farmers' perceptions. Perception was more consistent with GPS data when farms were closer to roosting places, increasing the probability of observing vultures in the surroundings of the farms. Consequently, more contact with vultures, even outside the farms, could imply a greater knowledge and ease of recognition of the species (Roque De Pinho et al., 2014), motivating a major predisposition to recognizing vulture presence on farms.

More attention should be paid to the negative relationship between farm size and the probability of consistent perception. This result may seem counterintuitive considering our initial prediction of increasing "consistency" because more livestock should imply more carcasses and, consequently, a higher frequency of visits of vultures (Mateo-Tomás and Olea, 2010). However, it can be argued that the sanitary regulations imposed by the European Union after the outbreak of bovine spongiform encephalopathy in 2001 may play a role in our results (Donázar et al., 2009b; Margalida et al., 2010; Moleón et al., 2014). Despite the fact that the abandonment of livestock carcasses is still banned in Fuerteventura, some owners of small farms indicated that they rarely or never received carcass collection services. Therefore, the availability of carcasses can certainly be lower on large farms where illegal dumping of large amounts of carrion can be problematic (M. García-Alfonso unpublished data). Nonetheless, this only partially explains our results because the GPS-tagged vultures still visited large farms without detection by the farmers. Owners of large farms often hire help from outside the family (Navarro-Ríos et al., 2011) and probably spend less time in outdoor activities (including the disposal of carcasses and other livestock remains), which would be carried out by employees. Thus, although some carcasses and remains are probably still abandoned to vultures on large farms, their presence would not be known by the owners. In agreement with this, previous studies have reported that farmers with smaller livestock numbers had a more positive perception of the ecosystem services provided by scavengers (Morales-Reyes et al., 2018a).

Finally, the finding that farmers had an awareness more consistent with GPS data during the morning than during the afternoon may be a reflection of their daily duties, i.e. milking and feeding activities, which are carried out in early hours, while vulture behavior was monitored throughout the day. This suggests that local people perceive the environment at different times compared to scientific studies performed collecting information throughout the day (see Knapp et al., 2013; Morales-Reyes et al., 2018b).

Concluding remarks

Because humans are part of ecosystems (Cowling et al., 2008; Olea and Mateo-Tomás, 2009), a dissociation between nature and human society may lead to the loss of ecosystem services. Here, we show that LEK of older farmers working on small farms was more consistent with GPS data in relation to the ecosystem services provided by vultures on their property. LEK is important to balance resource use with conservation and manage natural resources sustainably (Eshuis and Stuiver, 2005; Knapp et al., 2013). In the Mediterranean area, farmers' LEK and a greater appreciation of ecosystem services is clearly derived from the maintenance of traditional livestock farming practices, such as transhumance (e.g. Morales-Reyes et al., 2018a; Oteros-Rozas et al., 2013), but these practices are disappearing in many regions of the world due to industrialization and globalization. They persist in rural areas but are likely to continue declining (Gómez-Baggethun et al., 2010). In agreement with previous studies in different contexts (Gómez-Baggethun et al., 2010; Kai et al., 2014; Turner and Turner, 2008) but contrary to a recent study on farmers' LEK (Morales-Reyes et al., 2018b), our results indicate the deterioration or loss of LEK, apparently associated with increased farm size and mechanization resulting from the intensification of livestock practices, which is occurring across Europe (García-Martínez et al., 2009). Thus, even if the service providers continue to supply the service, the farmers no longer perceive it as such.

Our results add a new dimension to previous studies claiming the importance of traditional livestock farming practices in the conservation of scavengers (Liberatori and Penteriani, 2001; Mateo-Tomás and Olea, 2010; Morales-Reyes et al., 2018a; Olea and Mateo-Tomás, 2009) and provide evidence of the importance of management of livestock and associated practices from both the farmer and policymaker perspective.

Our study also shows that the stakeholders' perception of the ecosystem services provided is dependent on the spatial distribution of the population of the providing species, as well as its abundance. A higher frequency of visits and greater proximity to dense population nuclei, such as the communal roosts where most of the island's population of vultures is concentrated (see Donázar et al., 2002), implied a greater probability of consistency between farmer awareness and data from GPS-tagged vultures. To assess the individual knowledge of stakeholders it is therefore necessary to incorporate accurate information about the distribution and abundance of the species as well as on the movement of individuals. This result not only presents interesting perspectives to explain why there are strong local asymmetries among stakeholders' perceptions receiving apparently similar ecosystem services (Morales-Reyes et al., 2018a), but could have other important implications. Despite perceiving vultures as beneficial due to their scavenging behavior, half of the farmers were not aware of receiving the service, and thus a decline in animal populations, along with a disconnection from nature presumably resulting from the loss of traditional practices, could change perceptions in the long-term towards a misperception of their benefits.

In summary, our findings indicate that studies aimed at understanding how the local community perceives animals operating as ecosystem service providers should include multiple dimensions. While personal features of stakeholders, such as gender or age, are widely recognized as important aspects, other socio-cultural factors associated with changes in traditional practices and the resulting loss of LEK are less understood. Our study highlights the potential role of modern livestock husbandry in disconnecting people from the benefits provided by wild animals, and how all of these aspects act in concert with the distribution, abundance, and frequency of the ecosystem service provider itself, such that the service may be even more underappreciated for scarce or threatened organisms.

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Figure 1. Spatial information used for studying farmer's perception of vultures and awareness of their presence in Fuerteventura as contrasted with information provided by GPS-tagged birds. Surveyed farms: location of farms where the 59 face-to-face surveys were done. Other farms: location of non-surveyed farms with goats and/or sheep in Fuerteventura between 2013 and 2015. Predictable feeding sources: location of the three more predictable places in terms of food for vultures. Capture site: location of the cannon net used for capturing vultures and tagging them with GPS devices.

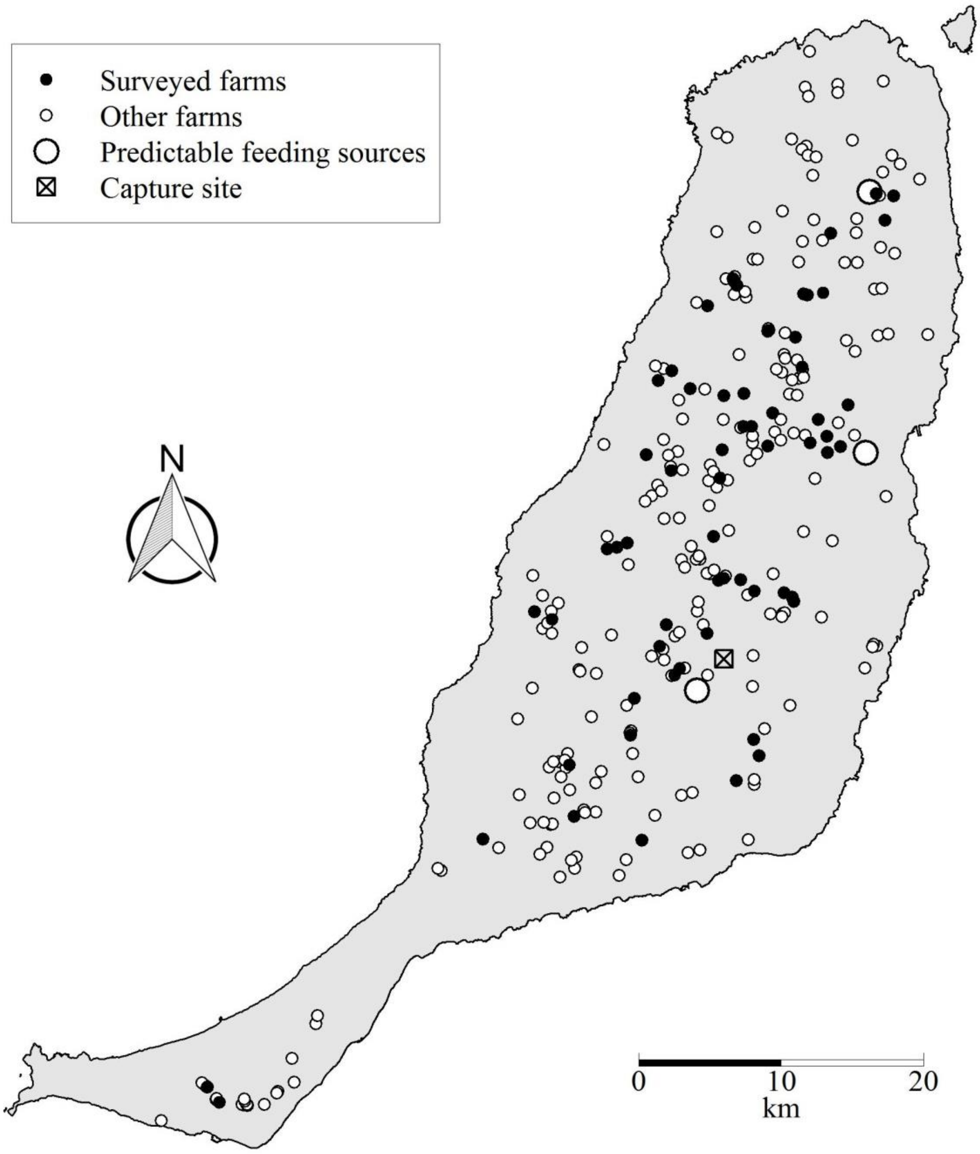

Figure 2. Perception of capacity of scavenger species to provide scavenging services. (a) Farmers' perceptions of scavengers as ecosystem services providers (*ESP index*) by species. Bars and whiskers indicate the mean value of *ESP index* ± SD. (b) Percentage of farmers that perceived the provision of scavenging services (*Scavenging services [%]*)by species. The different grade of colors in (b) show whether these species were ranked first (darkest color), second (middle) or third (lightest) as providers. (Species drawings: © Juan Varela, from left to right: *Neophron percnopterus majorensis*, *Buteo buteo insularum*, *Corvus corax canariensis,* and *Larus michahellis atlantis*).

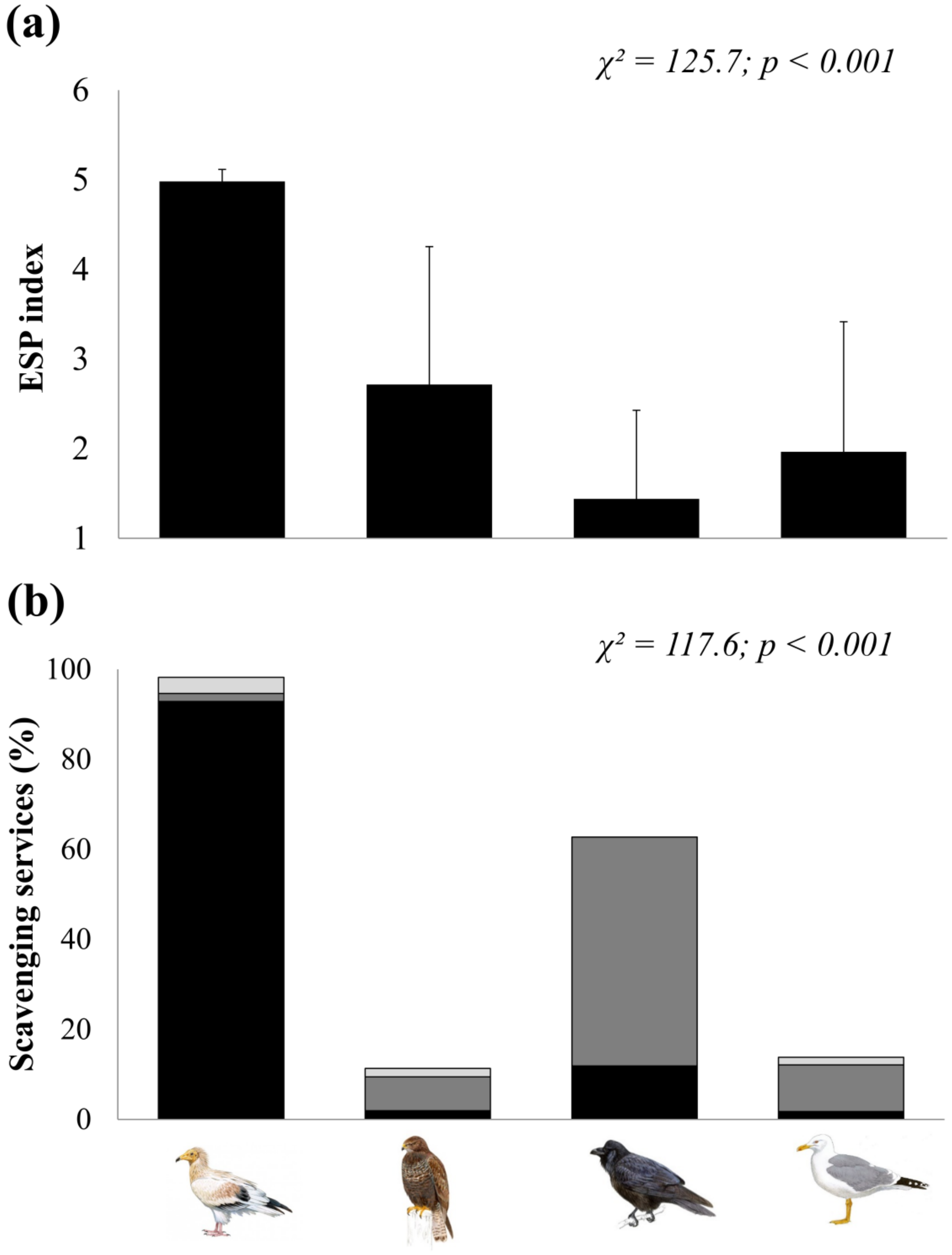

Figure 3. Effects of farm size (number of goats and sheep: *Goat Sheep*) and distance to the nearest communal roost (*Dist Roost*) on the probability of consistency between data of GPS-tagged vultures and farmers' awareness of presence of Egyptian vultures (*Presence*) in their farms. We considered 180 m around the farm as the buffer to determine presence of GPS-tagged vultures.

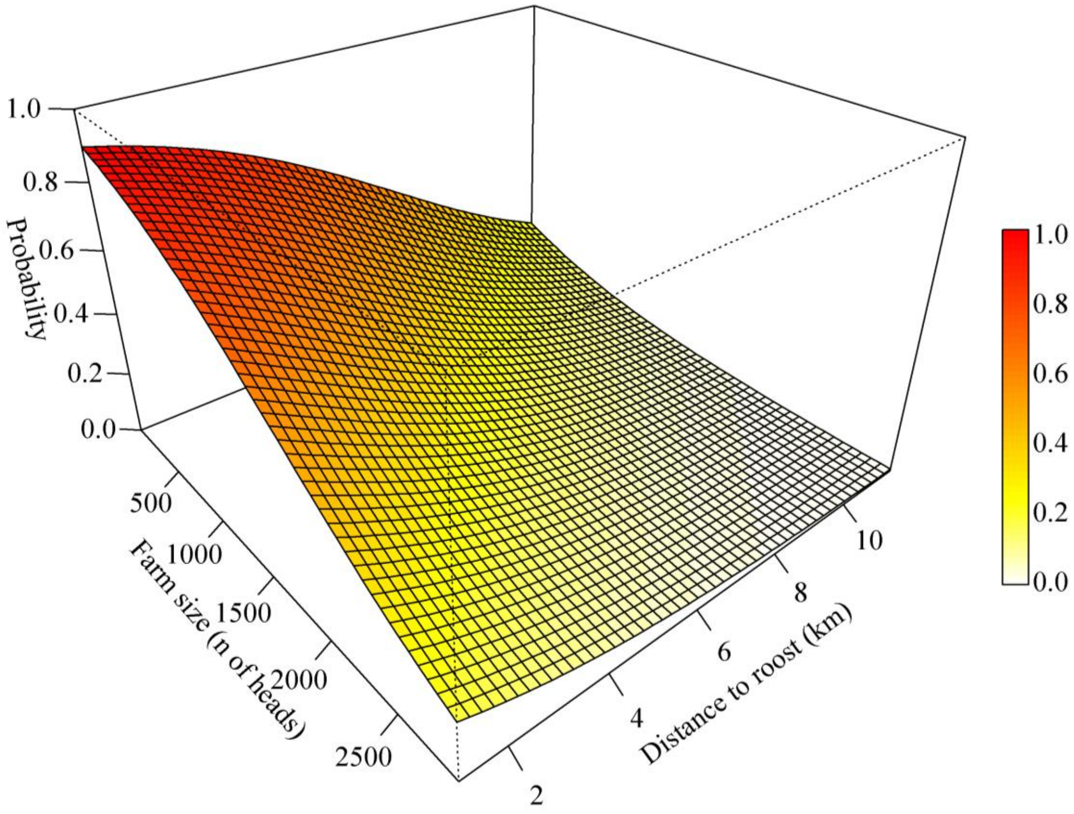

Table 1. Explanatory variables used to analyze farmers' perceptions about Canarian Egyptian vultures in Fuerteventura. Four sets of models were performed using two response variables *Presence* and *TimeSlots* calculated according to two radii 180 and 393 meters. All variables where initially included in model performing except *Hour* used just in *TimeSlots* models.

Variable	**Description**
Vulture visits	
Num days[a]	Number of days with at least one position of vultures associated with the farm.
Max indvs simult[a]	Maximum number of vultures detected at the same time in the farm.
Max indvs day[a]	Maximum number of different vultures detected per day in the farm.
Max indvs month[a]	Maximum number of different vultures detected per month in the farm.
Farmer	
Gender	Gender of the surveyed farmer.
Age	Age of the surveyed farmer (years).
Experience	Number of years working as a farmer.
Time	
Hour	Division of the day in morning (sunrise – 12:00), midday (12:00 – 16:00) and afternoon (16:00 – sunset). Times were selected according to popular Spanish delimitation of midday.
Farm	
Goat Sheep[b]	Number of goats and sheep per farm.
Dist mAFS[c]	Distance to the main artificial feeding station (center of the island)(km)
Index AFS[c]	Index of connectivity to artificial feeding stations (AFS) and garbage dump.
Index Roost[c]	Index of connectivity to roosting places.
Index Terr[c]	Index of connectivity to vultures' territories.
Dist AFS	Distance to the nearest artificial feeding stations (AFS) or garbage dump (km).
Dist Roost	Distance to the nearest roosting place (km).
Dist Terr	Distance to the nearest vultures' territory (km).

[a]) Calculated from GPS tracking of the whole day for the probability of presence (*Presence*) and of each period of the day for the probability of presence disaggregated by time slot (*TimeSlots*).

[b]) Total number of livestock, on the basis of livestock censuses (see Methods).

[c]) Index of connectivity calculated following the formula of Hanski (1998): $S_i = \Sigma_{j \neq i} \exp(-\alpha d_{ij}) N_j$. For distance $d_{ij,}$ we used the Euclidian distance in kilometers. N_j was only included for *Dist Roost* (mean number of vultures on each roosting place obtained from field data).

Table 2. Farmers' perceptions in relation to the presence in the farm of GPS-tagged Egyptian vultures. Values represent percentage of farmers' answers (n = 55) at two different buffer radii.

		Radius (m)	
Perception	**Presence of vultures**	**180**	**393**
Yes	**Yes**	40.0	40.0
Yes	**No**	0.0	0.0
No	**Yes**	34.5	41.8
No	**No**	25.5	18.2

Table 3. Estimates and standard errors (SE) resulting from model averaging of selected models of *Presence* for two radii around the farm. See Table 1 for a full description of each explanatory variable. 85% confidence intervals of the estimates are also shown (7.5% and 92.5% limits). Relative importance (RI) of each variable calculated as sum of the Akaike weights over all of the models in which the term appears. The reference level for factor *Gender* is 'Male'.

Variable	**Estimate**	**SE**	**7.5%**	**92.5%**	**RI**
Radius 180 m					
(Intercept)	2.665	0.931	1.329	4.027	
Goat Sheep	-0.001	0.001	-0.002	-0.000	1
Dist Roost	-0.341	0.166	-0.584	-0.100	1
Num days	0.007	0.008	0.000	0.023	0.619
Gender					0.619
Gender Female	-1.480	1.557	-4.318	-0.466	
Radius 393 m					
(Intercept)	0.007	0.337	-0.480	0.493	
Num days	0.012	0.005	0.005	0.021	
Gender Female	-2.558	1.386	-4.938	-0.801	

Table 4. Estimates and standard errors (SEs) resulting from model averaging of selected models of *TimeSlots* for two radiuses around the farm. See Table 1 for a full description of each explanatory variable. 85% confidence intervals of the estimates are also shown (7.5% and 92.5%). Relative importance (RI) of each variable calculated as sum of the Akaike weights over all of the models in which the term appears. The reference level for factor *Hour* is 'morning'.

Variables	**Estimates**	**SE**	**7.5.%**	**92.5.%**	**RI**
Radius 180 m					
(Intercept)	0.386	0.544	-0.407	1.180	
Goat Sheep	-0.206	0.374	-1.225	-0.124	0.305
Max indvs day	0.344	0.490	0.07	1.433	0.457
Dist Roost	-0.211	0.380	-1.239	-0.144	0.305
Hour					1
Hour midday	0.702	0.741	-0.378	1.783	
Hour afternoon	-1.170	0.749	-2.263	-0.076	
Radius 393 m					
(Intercept)	0.861	0.569	0.031	1.691	
Age	0.154	0.302	0.006	1.017	0.301
Goat Sheep	-0.471	0.475	-1.314	-0.174	0.632
Dist Roost	-0.379	0.417	-1.152	-0.048	0.632
Hour					1
Hour midday	0.268	0.734	-0.803	1.339	
Hour afternoon	-1.708	0.795	-2.869	-0.548	

Supplementary material

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Table S1. Information about GPS locations used for analyzing the probability of consistency between data of GPS-tagged vultures and farmers' awareness of vulture presence at their farms. PVC: individual identifier. Locations: number of GPS-fixes retained after removing non-stationary locations, i.e. locations with speed higher than 2 m/s and altitude higher than 25 meters. Days: number of days with information on stationary locations. Min date: date of the first location for each individual. Max date: date of the last location for each individual. Locations total: total number of locations, including stationary and non-stationary. Days total: total number of days, including stationary and non-stationary locations.

PVC	locations	days	min date	max date	locations total	days total
225	326726	914	2013-07-01	2015-12-31	591679	914
226	325525	914	2013-07-01	2015-12-31	578904	914
228	588846	914	2013-07-01	2015-12-31	1234537	914
22C	375463	912	2013-07-01	2015-12-31	632599	912
22T	395452	914	2013-07-01	2015-12-31	680585	914
22W	67602	137	2013-07-01	2013-11-14	109045	137
22X	378273	914	2013-07-01	2015-12-31	720759	914
237	314246	912	2013-07-01	2015-12-31	553926	912
2X1	415875	914	2013-07-01	2015-12-31	795628	914
2X2	509825	912	2013-07-01	2015-12-31	1027161	912
2X3	273701	844	2013-07-01	2015-12-30	465455	914
2X4	219430	914	2013-07-01	2015-12-31	405831	914
2X5	621664	905	2013-07-01	2015-12-31	1177793	905
3FC	237965	914	2013-07-01	2015-12-31	468382	914
3FF	212434	893	2013-07-01	2015-12-31	364119	893
3NP	549832	791	2013-10-23	2015-12-31	942524	791
231	238637	797	2013-10-26	2015-12-31	483968	797
234	66407	583	2014-05-28	2015-12-31	141662	583
371	62930	583	2014-05-28	2015-12-31	119133	583
224	52736	580	2014-05-31	2015-12-31	98786	580
341	66970	580	2014-05-31	2015-12-31	116251	580
2XV	43590	578	2014-06-02	2015-12-31	65050	578
2XM	24863	221	2015-05-23	2015-12-31	45355	221
3PU	22837	222	2015-05-23	2015-12-31	43497	222

PVC	locations	days	min date	max date	locations total	days total
3PX	20474	222	2015-05-23	2015-12-31	39677	222
2XC	26248	221	2015-05-25	2015-12-31	47636	221
3FA	19610	221	2015-05-25	2015-12-31	45052	221
221	1322	89	2015-09-16	2015-12-31	26645	107
222	1030	90	2015-09-16	2015-12-31	27837	107
255	719	81	2015-09-16	2015-12-29	31135	107
370	1074	94	2015-09-16	2015-12-31	28306	107
3AC	797	76	2015-09-16	2015-12-29	29090	107
3XV	804	100	2015-09-16	2015-12-31	18232	107
254	775	87	2015-09-17	2015-12-31	30217	107
40H	686	82	2015-09-19	2015-12-30	18245	105
22M	726	76	2015-09-20	2015-12-29	21723	104
22P	519	74	2015-09-20	2015-12-31	24562	104
2XX	1131	84	2015-09-20	2015-12-31	26344	104
40C	569	78	2015-09-20	2015-12-31	26482	105
40F	59	19	2015-09-20	2015-11-06	3065	56
20H	700	79	2015-09-22	2015-12-31	13815	102
2XJ	475	59	2015-09-22	2015-12-30	18467	102
2XL	966	78	2015-09-22	2015-12-31	23453	102
257	607	82	2015-09-23	2015-12-31	28610	101
3AU	705	74	2015-09-23	2015-12-31	28954	102
40J	591	80	2015-09-23	2015-12-31	12157	102

Table S2. Demographic information of the surveyed farmers' on Fuerteventura. Surveys evaluated farmers' perception of Canarian Egyptian Vultures and awareness of their presence in their own farms. Position: charge of the farmer in the farm. Sex: sex of the surveyed farmer (Male or Female). N: total number of surveyed farmers. N (GPS analyses): number of surveyed farmers' answers included for comparison with vultures GPS data.

Position	Sex	Range of age	N	N (GPS analyses)
Manager	M	< 30	2	2
Manager	M	30-40	2	2
Owner	F	> 60	1	1
Owner	F	30-40	1	1
Owner	F	40-50	4	4
Owner	F	50-60	2	1
Owner	M	< 30	1	1
Owner	M	> 60	6	6
Owner	M	30-40	9	8
Owner	M	40-50	10	9
Owner	M	50-60	19	18
Shepherd	M	40-50	1	1
Shepherd	M	50-60	1	1

Table S3. Variables used to evaluate farmers' perception about Canarian Egyptian vultures on Fuerteventura and to analyze consistency between farmers' awareness of vulture presence and GPS data. Question in surveys column shows question asked to farmers during face-to-face surveys.

Variable	**Question in surveys**
ESP index	Among the species that you see, could you evaluate how much beneficial or harmful are they for you? Evaluate them between 1 (very harmful) and 5 (very beneficial). Why do you consider each one beneficial or harmful?
Scavenging services [%]	Among the species that you see eating carcasses at your farm, which of them do you think that participate more in removing such carcasses? Could you sort the species according to their importance in the disposal of carrion?
Presence	Do Egyptian vultures visit your farm? Yes No
TimeSlots	What time do Egyptian vultures usually visit your farm?: Morning Midday Afternoon
Number	How many Egyptian vultures do you usually see in your farm?

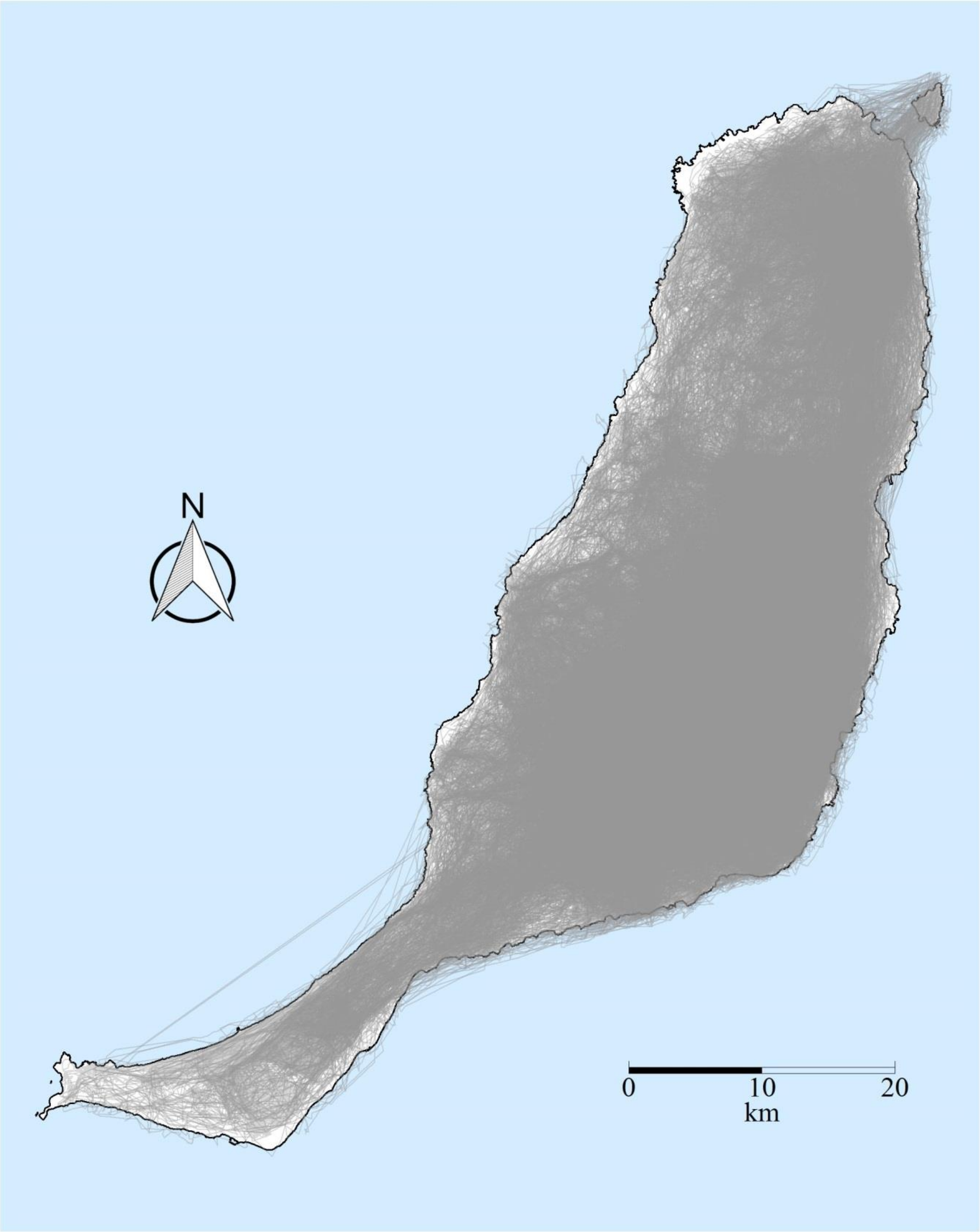
Table S4. Top-ranked candidate models for the probability of consistency between data of GPS-tagged vultures and farmers' awareness of vulture presence (*Presence*) at their farms. Models selected for model averaging are shown in bold. Models including uninformative parameters and correlated variables were removed. Delta AICc: difference in AICc between each model and the best model (lowest AICc). AICcWt: AICc weights. Cum.Wt: Cumulative weights. Radius: threshold distances around the farms. K: number of parameters. ModelLik: likelihood of each model.

Model	AICc	Delta AICc	AICcWt	Cum.Wt	Variable	K	ModelLik
Radius 180 m							
772	**67.645**	**0**	**0.286**	**0.286**	**Goat Sheep + Dist Roost + Num days + Gender**	**5**	**1**
38	**68.613**	**0.968**	**0.176**	**0.462**	**Goat Sheep + Dist Roost**	**3**	**0.616**
647	69.694	2.049	0.103	0.565	Goat Sheep + Dist Main AFS + Dist Roost + Num days	5	0.359
242	69.96	2.315	0.09	0.655	Goat Sheep + Num days + Gender	4	0.314
108	70.28	2.635	0.077	0.731	Num days + Gender	3	0.268
418	70.342	2.697	0.074	0.806	Dist Roost + Num days + Gender	4	0.26
2	71.799	4.154	0.036	0.841	Goat Sheep	2	0.125
40	71.898	4.253	0.034	0.876	Goat Sheep + Num days	3	0.119
105	72.438	4.793	0.026	0.902	Dist Roost + Gender	3	0.091
12	72.631	4.986	0.024	0.925	Dist Roost	2	0.083
892	72.897	5.252	0.021	0.946	Dist Main AFS + Dist Roost + Dist Terr + Num days	5	0.072
0	72.98	5.335	0.02	0.966	1	1	0.069
292	73.008	5.363	0.02	0.985	Dist Main AFS + Dist Roost + Dist Terr	4	0.068
293	73.598	5.953	0.015	1	Dist Main AFS + Dist Roost + Num days	4	0.051
Radius 393 m							
97	**72.603**	**0**	**0.700**	**0.700**	**Num days + Gender**	**3**	**1**
14	75.14	2.537	0.197	0.897	Num days	2	0.281
0	76.842	4.239	0.084	0.981	1	1	0.12
248	79.792	7.189	0.019	1	Dist AFS + Dist Roost + Dist Terr	4	0.027

Table S5. Top-ranked candidate models for the probability of consistency between data of GPS-tagged vultures and farmers' awareness of vulture presence in each time slot (*TimeSlots*). Models selected for model averaging are shown in bold. Models including uninformative parameters and correlated variables were removed. Delta AICc: difference in AICc between each model and the best model, (lowest AICc). AICcWt: AICc weights. Cum.Wt: Cumulative weights. Radius: threshold distances around the farms. K: number of parameters. ModelLik: likelihood of each model.

Model	AICc	Delta AICc	AICcWt	Cum.Wt	Variable	K	ModelLik
Radius 180 m							
95	**86.51**	**0**	**0.363**	**0.363**	**Max indvs day + Hour + (1|Farm ID)**	**5**	**1**
263	**87.317**	**0.808**	**0.242**	**0.605**	**Goat Sheep + Dist Roost + Hour + (1|Farm ID)**	**6**	**0.668**
16	**87.821**	**1.311**	**0.188**	**0.793**	**Hour + (1|Farm ID)**	**4**	**0.519**
48	89.194	2.684	0.095	0.888	Dist Main AFS + Max indvs day + (1|Farm ID)	4	0.261
40	89.909	3.399	0.066	0.954	Goat Sheep + Dist Roost + (1|Farm ID)	4	0.183
0	90.66	4.151	0.046	1	(1|Farm ID)	2	0.126
Radius 393 m							
16	**85.828**	**0**	**0.321**	**0.321**	**Hour + (1|Farm ID)**	**4**	**1**
263	**86.033**	**0.206**	**0.289**	**0.610**	**Goat Sheep + Dist Roost + Hour + (1|Farm ID)**	**6**	**0.902**
525	**86.231**	**0.404**	**0.262**	**0.872**	**Age + Goat Sheep + Dist Roost + Hour + (1|Farm ID)**	**7**	**0.817**
40	89.814	3.986	0.044	0.916	Goat Sheep + Dist Roost + (1|Farm ID)	4	0.136
0	89.873	4.045	0.042	0.958	(1|Farm ID)	2	0.132
128	89.916	4.088	0.042	1	Age + Goat Sheep + Dist Roost + (1|Farm ID)	5	0.129

Figure S1. Movements of GPS-tagged Canarian Egyptian vultures (N = 46) over Fuerteventura used for analyzing the probability of consistency between GPS data and farmers' awareness of vulture presence at their farms.



General discussion

The study of animal movement has a major role in knowing essential aspects for animal conservation, but has proved difficult so far particularly in very mobile organisms. This is the case of vultures, which have evolved to perform large-scale movements routinely, covering vast areas with relatively little energy expenditure. In addition, other features of vultures' lifestyles add complexity to the study of how they move to cope with spatial and temporal variations in the distribution and abundance of resources. Vultures are highly social and long-lived vertebrates with delayed sexual maturity, so intricate social relationships and environmental knowledge is expected to develop over long lifespans in which they exhibit two clearly differentiated lifestyles, before and after recruitment as breeders. This is especially true for territorial breeders, such as Egyptian vultures, that pass from a communal pre-adult stage spanning several years to an adult stage in which they defend exclusive breeding territories. Moreover, as the most endangered avian functional guild (Ogada et al., 2016, 2012a; Sekercioglu et al., 2016), vulture populations and so their ecological functions and the ecosystem services they provide require conservation actions (Badia-Boher et al., 2019; Johnson and Hackett, 2016; Margalida et al., 2014a). All these particularities make vultures interesting study models both from basic and applied perspectives, and indeed they have been subject of a large body of research in recent decades (DeVault et al., 2016; Donázar et al., 2009a; Duriez et al., 2014; Margalida et al., 2014a; Moleón et al., 2014). Nonetheless, some aspects associated with vulture movement, which are essential to making informed management and conservation decisions, remain highly unknown. Understanding how vultures exploit the environment according to individual traits through their different life-history stages, the spatiotemporal structure of the population, and the distribution of resources, is a key part for the comprehension of their behaviour and an indispensable step to face conservation challenges effectively.

In order to shed light on these issues, this thesis combine GPS technology, 20-years of population monitoring data, and detailed environmental information to investigate how Canarian Egyptian vultures interact with human facilities used for feeding, resting and roosting, and to assess human perception of their presence and importance as ecosystem service providers. Particularly, we increased our understanding about drivers of electrocution risk by reducing typical biases of previous studies. We expanded what is known about how the emerging scenario of changing predictability on feeding resources is affecting vultures foraging and social dynamics. Ultimately, we examined livestock farmers' perception about vultures as ecosystem service providers, and disentangled the factors influencing the consistency between the use that vultures make of farms detected with GPS and the farmers' awareness of that use.

Spatial and/or temporal concentration of otherwise naturally unpredictable food has strong ecological effects in populations, communities and ecosystems due to induced changes in animal behaviours and distribution (Cortés-Avizanda et al., 2016; Gilroy and Sutherland, 2007; González et al., 2006; López-Bao et al., 2010; Monsarrat et al., 2013; Mundy et al., 1992; Schoech et al., 2008; Selva et al., 2017; Zuberogoitia et al., 2013). Our findings indicate that an uneven predictability of feeding resources deeply influences the Canarian Egyptian vultures' movement behaviour. In Fuerteventura there are three highly predictable feeding places, the garbage dump and two supplementary feeding stations. The older feeding station, located in the center of the island, not only provides abundant and predictable food, but also seems to act as an important social meeting point which modulates how vultures make use of other resources: in its surroundings, electric pylons were used more intensively and farms were more visited. This point resulted greatly attractive for less experienced, non-breeding individuals which benefited from food predictability. In the case of breeding birds, the more dominant females (the larger sex) preferred to feed on this predictable feeding source than in less predictable points such as farms, to the extent that they tend to settle in nearby territories. In addition, the territorial subdominant males, which apparently relied more on wild preys during the breeding season, used with greater intensity the feeding station during the non-breeding season, probably due to a lower availability of wild carcasses, a release from the spatial constraint imposed by reproductive tasks, and/or to improve their social rank in the population. All these findings indicate that the spatio-temporal distribution of food resources in this insular system determined that birds exploited the landscape in a complex manner. Important ecological and conservation consequences arise because the value of territories and hence their propensity to be occupied seem to be determined by their location regarding the supplementary feeding stations, as has been suggested for continental Egyptian vultures (Grande et al., 2009; Oppel et al., 2017) and other species (García and Margalida, 2009). Underlying mechanisms of settlement are however poorly known and other factors, such as previous knowledge of prospected areas (Chaine et al., 2013; Haughland and Larsen, 2004; see Serrano, 2018 for raptors) and conspecific attraction (Blanco and Tella, 1999; Carrete et al., 2007; Krause and Ruxton, 2002), could be playing a pivotal role.

Livestock farms are predictable in space but not so in time (semi-predictable feeding resources) and are distributed all over the island, which imply lower levels of competition for food in comparison with the feeding station. Farms with larger herd and where livestock carcass disposal is higher were more attractive for vultures, as it could be expected due to their major temporal predictability. In the same direction, electric pylons located in areas with a higher amount of carcasses were more intensively used. Within territorial individuals, we found that farms where in general more used by younger individuals, so a lower experience seems again to be shaping the use of more predictable feeding resources. When considering dominance hierarchies and sex asymmetries within breeders, we found that subdominant females and dominant males preferred visiting farms than the main feeding station during the whole year. Besides the lower competition at farms as compared to the feeding station, some kind of resource partitioning between sexes, or sex-specific preferences for certain resources or social foraging behaviour, seems to occur. Whereas these females had their territories far away from the main feeding station because dominant ones monopolized appropriate locations in it vicinity, dominant males had their territories spread over the island, suggesting that, in the case of males, preferred territories did not depend on the distance from highly predictable feeding resources but on the distance from semi-predictable ones. In this way, the spatial distribution and predictability of feeding resources and the sex-dependent social rank effect seem to be driving the spatial distribution of territories. At the same time, the use of pylons and farms is conditioned by the distribution of territories, but in opposite ways for breeders and non-breeders. While territorial individuals preferred visiting farms and using pylons both closer to their territories, non-breeders avoid using these resources in the proximity of established pairs, probably due to owners' defence of the area. All these results show the close interdependence between the spatiotemporal distribution of resources and space use by birds, with a dynamic feedback in which food resources not only modulate the abundance of birds and the use of pylons, but also the distribution of territories which in turn determine a differential use of pylons and food resources by the different fractions of the population.

Those vultures which were successful at breeding were less prone to use farms than unsuccessful individuals. This suggests that vultures could be exploiting wild preys and/or looking for specific nutrients for chicks' growth during the breeding period, when natural resources are more abundant (Carrete and Donázar, 2005; Hiraldo et al., 1979; Reynolds et al., 2004; Richardson et al., 1986). In this line, non-territorial and dominant territorial females, which mainly focused their activity at the feeding station, showed a lower use of this point during the breeding season. Likewise, subdominant territorial males, which were also more attached to the feeding station during the non-breeding season, neither foraged at farms nor at the feeding station during the breeding season probably because they also rely more on wild carcasses. All these results suggest that resources that becomes locally abundant, such as carcasses from wild mammals, birds and reptiles (García-Heras et al., 2013; Medina, 1999), may have an important role on space use and vultures' diet. In conclusion, the fact that even the most dominant individuals changed their behaviour when facing that rise of feeding resources could indicate an interest on specifics nutrients, or a general preference for resources where competition is lower.

Social perception is an essential factor for species conservation, which has been especially relevant for the recovery of Canarian Egyptian vultures (Badia-Boher et al., 2019). Our results suggest that social groups directly affected by beneficial species as ecosystem services providers increase their awareness of the existence of benefits when such species are more abundant, not only providing higher services but also being generally easier to observe. Nevertheless, human disconnection from nature, which could be happening due to intensification of livestock husbandry practices, reduces awareness despite the presence and abundance of the target species. That increasing disconnection reflected in the loss of ecological knowledge in local societies has multiple reasons (Turner and Turner, 2008). The effect that we found, likely associated with the modernization of livestock practices, seems to be related to one of them, the development derived from cultural homogenization and rapid modernization (Benz et al., 2000; Case et al., 2005; Kai et al., 2014) Such loss of links with nature joined to the decline of biodiversity and animal populations might end up being a conservation problem ought to the social belief that certain species are not worth conserving.

To summarize, we demonstrate that vultures show complex patterns of movement and resource use related to intrinsic individual factors and extrinsic environmental cues, and how these patterns influence and are in turn influenced by the spatial distribution and structure of the population. We also exemplify the importance of studying movement behaviour and ecology in long-lived animals by considering individual traits and specific life-history stages, which may ultimately define how the different fractions of the population are affected by human activities. Considering populations with uniform criteria when implementing management strategies and mitigation measures could lead to a reduction in the effectiveness of conservation actions or even involve negative effects.

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Conclusions

1 The intensity of use of electric pylons by vultures both during day and night, was driven by the distance to road and the distribution of feeding resources and breeding territories. Vulture used more those pylons far from roads and located in areas with high availability of livestock carrion. Also, pylons in the proximity of the main feeding station (a social meeting point with predictable food resources) were used more intensively, mainly during the non-breeding season. Moreover, pylons close to breeding territories were less used probably because owners excluded conspecifics. Mortality by electrocution was closely related to intensity of use. Taking into account this sole factor, if mitigation measures were applied on 6 % of pylons the mortality by electrocution could be reduced in about 50 %.

2 Differences in the use of feeding resources in territorial birds suggest a foraging niche partitioning based on sex and rank, with more dominant females preferring the main feeding station and subdominant ones preferring farms, whereas more dominant males preferred also farms and subdominant ones seemed to exploit more natural food resources. The later increased the use of the main feeding station during the non-breeding season presumably for improving their social rank or due to lower abundance of wild preys. This complex behavioural network requires further analyses for shedding light on its genesis trough the cost-benefit trade-off experienced by each individual population segment. In conclusion, food predictability and distribution drove resource specialization in vultures. We found a differential use of predictable food exists regarding to sex, social rank, territorial status, and breeding season. Thus, degree of food predictability may importantly affect both the foraging and social dynamics of local populations of vultures.

3 Number of vultures and visits to farms increased with higher availability of carrion and higher distances to roads and urban areas. Visits decreased with the proximity to breeding territories, likely due to owners' defence from intruders which would explain the stronger effect during breeding season. Additionally, because of the strong attractive effects of highly predictable feeding places, the number of vultures decreased away from them. Individual characteristics of territorial birds influenced visiting rates of farms, so visits were lower for: (i) older birds, mainly far from their territories, thanks to their better foraging skills and experience; (ii) successful breeders, probably because they rely on wild prey with specific

nutrients for chicks; and (iii) females, suggesting again some kind of resource partitioning of food preferences. In conclusion, the presence of vultures at farms (semi-predictable feeding places), was influenced by the season (breeding vs non-breeding), the availability of trophic resources, and the distance to road and urban areas. The spatial distribution of territories, highly predictable feeding points, and individual characteristics also play a role. This reveals the need for multifaceted management of food resources as they are unequally consumed by different fractions of the population at places of variable predictability.

4 Egyptian vultures were perceived as the main providers of scavenging services and the most beneficial avian scavenger. Consistency between farmers' perceptions and vulture use of their farms (evaluated respectively by surveys and GPS data) was higher in the morning, in older male farmers, and at farms with lower livestock numbers, located near vulture communal roosts, and visited more frequently by vultures. Our results underline the potential influence of modern livestock husbandry in disconnecting people from ecosystems. This together with the effect of distribution, abundance, and frequency of the ecosystem service provider over perception, indicates that even if the service is still provided, it will be underappreciated in the case of organisms getting scarce.

5 The study of movement ecology of vultures using GPS technology may improve our understanding about social and behavioural aspects crucial for their conservation. We highlight the importance of considering individual traits and specific life-history stages, which may ultimately define how the different fractions of the population are affected by human activities. Considering populations with uniform criteria when implementing management strategies and mitigation measures could lead to a reduction in the effectiveness of conservation actions or even involve negative effects.