Efectos ecológicos de la heterogeneidad espacial y predecibilidad en la distribución de los recursos: carroñas y gremios de carroñeros

The ecological and conservation effects of food resource predictability: carcasses and vertebrate communities

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Tesis doctoral

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A mi familia

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RESUMEN

Efectos ecológicos de la heterogeneidad espacial y predecibilidad en la distribución de los recursos: carroñas y gremios de carroñeros

La variabilidad en la distribución y abundancia de los recursos tróficos puede afectar a la organización espacial de los vertebrados. Sin embargo, aún es escaso el conocimiento que tenemos sobre el efecto de la heterogeneidad de los recursos en el funcionamiento de las poblaciones y las comunidades. Los recursos pulsados se definen como episodios ocasionales de gran abundancia de alimento concentrados en el espacio y el tiempo. Los gremios de carroñeros se estructuran en torno a un ejemplo paradigmático de recurso pulsado: las carroñas. Las carroñas aparecen de manera impredecible en el espacio y el tiempo en condiciones naturales, y son explotados por multitud de especies desde bacterias hasta buitres. Sin embargo, las actividades humanas (incluidos los esfuerzos de gestión) puede hacer previsibles los recursos en su distribución espacial y temporal y por lo tanto pueden afectar a los gremios. Los principales objetivos de esta tesis fueron: 1) explorar el papel del azar como motor de los procesos de facilitación dentro de un gremio de carroñeros y 2) detectar las consecuencias ecológicas y de conservación que tiene el hacer predecible espacio-temporalmente el alimento en las estaciones de alimentación suplementaria (muladares). Hemos encontrado que la aleatoriedad de las carroñas favorece la diversidad del gremio de carroñeros y promueve la existencia de procesos de facilitación intragremiales. Por otra parte, a través de un enfoque transcontinental encontramos que las aves carroñeras migrantes cambian sus patrones de distribución espacial entre las zonas de cría (en Europa) y las zonas de invernada (en África) de manera acorde con el grado de concentración de la comida. Por otra parte, el solapamiento de la dieta fue mayor en Europa, donde los recursos son escasos y previsibles. La disponibilidad de carroñas de larga duración (como las que se encuentran en los muladares) se detectó que promovían la concentración de carroñeros facultativos incrementando el riesgo de predación sobre los vertebrados que viven en los alrededores de estas áreas. Así, el efecto de los pulsos de carroñas puede afectar a otros niveles tróficos. La concentración de carroñas se está promoviendo actualmente por parte de la Unión Europea mediante restrictivas normas sanitarias. Hemos encontrado que esta tendencia está provocando la co-ocurrencia de especies de carroñeros en los muladares, causando un gran solapamiento de su dieta que anteriormente estaba segregada. Por último, sobre la base del análisis de observaciones realizadas en los muladares proponemos un diseño apropiado y el manejo adaptativo de los mismos. En este sentido ofrecemos varias directrices para el manejo de la cantidad de alimento, las horas de vertido, los sitios para disponerlos…. Así, se evitaría la monopolización de los recursos en estas estaciones de alimentación suplementaria por parte la especies dominante: los buitres leonados (*Gyps fulvus*), favoreciendo de este modo a aquellas especies carroñeras más amenazadas y menos competitivas.

Palabras claves: carroñas como recursos pulsados, carroñeros migrantes, manejo adaptativo, predecible-aleatorio, procesos ecológicos intragremio, respuesta en el comportamiente de alimentación, riesgo de depredación.

ABSTRACT

The ecological and conservation effects of food resource predictability: carcasses and vertebrate communities

Variability in the distribution and abundance of food resources can shape the spatial organization of vertebrates. However, knowledge on the effect of resource heterogeneities on the functioning of populations and communities remains still scarce. Pulse resources are defined as occasional episodes of food abundance in space and time. Scavenger guilds are structured around a paradigmatic example of pulse resources: the carcasses. Carcasses appear randomly in space and time under natural conditions and are exploited by a myriad of species from bacteria to vultures. However, human activities (including well-intentioned management efforts) may confer predictability to food resources in their spatial and temporal distribution thus potentially affecting scavenger guilds. The main aims of this thesis were: 1) to explore the role of randomness as motor of intra-guild facilitatory processes and 2) to detect both ecological and conservation consequences when food resources become predictable both in space and time in supplementary feeding stations. We found that carcass randomness favoured the diversity of scavenger assemblages and promoted the existence of intraguild facilitatory processes. Moreover, through a transcontinental approach we detected that migrant avian scavengers change spatial distribution patterns between the European breeding areas and the African wintering grounds following variations in the clumping of resources. Moreover, diet overlap was higher in Europe where the resources are scarce and predictable. The availability of long-lasting carcasses (as those found in vulture restaurants) determines concentrations of facultative scavengers that may prey on non-scavenger vertebrates living in the vicinity of these areas. Thus the effect of carcass pulses may permeate to other trophic levels. Clumping of carrion resources is being currently promoted in the European Union by restrictive sanitary regulations. We found that this trend is provoking co-occurrence of scavengers at the few remaining feeding places and diet overlap between scavenger species formerly showing diet segregation. Finally, on the basis of analyses of observations performed at vulture restaurants we propose an appropriated design and adaptive management of vulture restaurants. In this sense we provide several guidelines for management of the quantity of food supplies, hours, and sites aimed to avoid the monopolization of the supplementary feeding resources by the dominant griffon vultures (*Gyps fulvus*) thus favouring to the most endangered scavenger species.

Keywords: adaptive management, behavioural-foraging response, intraguild ecological processes, migrant scavengers, predictable-random, pulsed-carrion-resource, risk predation.

LISTA DE PUBLICACIONES ORIGINALES

Esta tesis se basa en seis artículos originales y tres publicaciones divulgativas. La autora ha contribuido significativamente en la planificación, recopilación de datos, modelado y análisis, así como la escritura de todos los artículos.

Introducción: BOX 1. Donázar, J.A., Cortés-Avizanda A. and Carrete, M. (2009) The role of trophic resource predictability in the structure of scavenger guilds. En: Donázar, J.A., Margalida, A. & Campión, D. (Ed.). Vultures, feeding stations and sanitary legislation: a conflict and its consequences from the perspective of conservation biology. Sociedad de Ciencias Aranzadi, Donostia. Munibe: ISSN 1698-3807; 29.

BOX 2. Selva, N & Cortés-Avizanda A. (2009) The effects of carcasses and carrion dumps sites on communities and ecosystems En: Donázar, J. A., Margalida, A. & Campión, D. (Ed.). Vultures, feeding stations and sanitary legislation: a conflict and its consequences from the perspective of conservation biology. Sociedad de Ciencias Aranzadi, Donostia. Munibe: ISSN 1698-3807; 29.

BOX 3. Cortés-Avizanda A. (2008 published in 2010) Pros and Cons of vulture restaurants. *Endangered Species UPDATE*, 25 (1): 19-22 Invited paper.

Capítulo I. Cortés-Avizanda, A., Jovani, R., Carrete, M., & Donázar, J.A. Chance promotes species diversity and coexistence: a field experiment on the facilitatory processes within an avian scavenger guild. (Unpublished manuscript)

Capítulo II. Cortés-Avizanda, A., Almaraz, P., Carrete, M., Sánchez-Zapata, J.A., Delgado, A., Hiraldo, F. & Donázar, J.A. Spatial and trophic responses of two transaharian migrant species to changes in resource distribution: a transcontinental approach. (Unpublished manuscript)

Capítulo III. Cortés-Avizanda, A., Carrete, M., Serrano, D., & Donázar, J.A. 2009. Carcasses increase the probability of predation of ground nesting birds: a caveat regarding the conservation value of vulture restaurants. *Animal Conservation*, 12: 85-88.

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Capítulo V. Donázar, J.A., Cortés-Avizanda, A. & Carrete, M. 2010. Dietary shifts in two vultures after the demise of supplementary feeding stations: consequences of the EU sanitary legislation. *European Journal of Wildlife Research*, 56: 613–621

Capítulo VI. Cortés-Avizanda, A., Carrete, M., & Donázar, J.A. 2010. Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. *Biological Conservation*, 143: 1707-1715.

INTRODUCTION

Resources have been addressed by ecologists as a commodity required by an organism for maintenance, growth, and reproduction (Ricklefs 2000). They also have long recognized how the structure and dynamics of ecological systems are controlled, at least in part, through resource availability.

It has been stressed that resources play a primary role in the functioning of ecosystems affecting the distribution and abundance of populations and community structure, but also ultimately triggering bottom-up and top-down forces within the ecological networks (Hairston *et al.* 1960, Carpenter *et al.* 1985, Polis & Strong 1996, Brett & Goldman 1997, Begon *et al.* 2006).

Heterogeneity in spatial and temporal patterns plays a key role in the availability of resources influencing the sustain of communities (Fuhlendorf *et al.* 2006; Bissonette & Storck 2007), modelling interespecific relationship and eventually favouring the coexistence of species by allowing the differential use of variable patches with variable resource availability (Brown *et al.* 1994; Wauters *et al.* 2002; Carrete *et al.* 2005; Groom *et al.* 2006, Stephens *et al.* 2007). Therefore, questions regarding distributions and dynamics of organisms within a spatial context are at the centre of evolutionary and ecological research (Hanski 1999) aimed at identifying demographic constraints to population viability or recovery (Groom 2006).

The functional and ecological response to food source distribution and its effects on animal distribution and/or activity have always largely attracted the attention of ecologists (see, e.g. MacArthur & Pianka 1966; Macdonald 1983; Carr & Macdonald 1986; Maher & Lott 2000; Ostfeld & Keesing 2000, Sinclair et al 2006). In this sense, it has recently been suggested that another important component of resource availability is the random distribution over the temporal dimension. Bissonette and Storck (2007) argued that the temporal discontinuities in resource availability are a critical concept to incorporate in our research studies because the homogeneous distribution over time could influence the animal population responses and then be relevant for understanding the dynamics within ecosystems and communities (see below).

Although the role of food resource availability on the social organization and population structure in vertebrates has been well described (MacArthur and Pianka 1996, Macdonald 1981, 1983, Johnson *et al.* 2002; Krause & Ruxton, 2002; Revilla 2002, 2003; Eide *et al.* 2004; Begon *et al.* 2006) only theoretical backgrounds state how heterogeneous environments may facilitate the coexistence of species within assemblages (Chesson, 2000; 2001) whereas empirical information is still very scarce and limited to the description of, for example, certain effects of clumped resources such as monopolization and dominances in a context of invasion of species (Sexton 1990, Petren & Case 1996, Kiesecker *et al.* 2001, see below). Moreover, as we will highlight in this thesis, the availability of "sudden" or "pulsed" resources do not only affect the behavioural responses of feeders but may also induce spatial changes in the local densities of consumers, and may even indirectly affect other trophic levels and/or the viability of other neighbouring populations not directly related with the exploitation of the resource. Hence, when resources present a certain degree of predictability and/or extend in time the effects might become more evident and may trigger top-down and bottom-up regulation processes, at least at local scales permeating through food webs and affecting different trophic levels.

FROM RANDOM TO PREDICTABLE DISTRIBUTION OF FOOD RESOURCES: EFFECTS ON GUILD FUNCTIONING

Chance may alter the natural course of any ecosystem and/or could become the motor that maintains interespecific relationships, favouring the assemblage of species and ultimately even increasing diversity within communities (Tokeshi 1999, Siepielski et al 2010). Therefore, the loss of randomness in nature (e.g. in the availability of food resources) and/or the potential transformation into a predictable food resource via current human activities, are expected to have a significant impact on the structure and functioning of communities and ultimately affect the future viability of species. However, this fact is even more complex: the interactions among the species that comprise a community are not only negative (competition) but can also be positive (facilitation). The negative effect of interactions has been frequently described in the literature, for example, when the presence of one species alters the number, distribution or affects the reproduction of other species (Begon *et al.* 2006; Sinclair *et al.* 2006). Nevertheless, the role of positive interactions in a context of variable resource predictability remains almost unexplored.

Within this framework, it seems desirable to gain an insight of the ways in which randomness acts as the specific mechanism governing and supporting ecological processes related to the interspecific relationships, not only with those concerning competitive interactions but also with facilitatory processes which may play decisive roles permitting the access to food resources (see below).

Considering the scenario from the other side, we need to learn of the ecological effects of clumping of resources. Different study models have converged to address a basic prediction: when food becomes available in a clumped and abundant manner, species aggregated around it (Wilmers *et al.* 2003a; Carrete *et al.* 2006a; Begon *et al.* 2006). Aggregations of individuals may occur around local abundance of resources when intraspecific territoriality is relaxed, even if becoming social and/or living in groups do not provide a clear benefit (Maher & Lott, 2000, Johnson *et al.* 2002, Revilla & Palomares, 2002 and references therein). More specifically, Eide *et al.* (2004) advocate the potential importance of spatio-temporal predictability of prey on carnivore spatial organization. In this sense, and despite the great interest they may raise, information on these subjects is still scarce, whilst most published studies take a theoretical approach performed in limited size areas based on a monospecific approach (see von Schantz 1984; Carr & Macdonald1986; Eide *et al.* 2004). This may be of importance for migrant vertebrates that develop different stages of their life-cycles in very distant and diverse regions and are therefore forced to respond to changing environmental condition which may determine their individual fitness (Webster *et al.* 2002; Runge & Marra 2005, Norris & Taylor 2006 and references therein).

CARCASSES AS STUDY MODELS: THE LOSS OF A PULSED CHARACTER

Communities and ecosystems experience trophic resource pulses, defined as occasional events of rare, brief, and intense episodes of superabundance of food resources in space and time [reviewed in Yang *et al.* 2008; e.g.: the mast production of flowers, fruits, or seeds (Kelly 1994; Wolff 1996, Ostfeld *et al.* 1996, Curran and Leighton 2000, Mc Shea 2000); insect outbreaks (Carlton and Goldman 1984, Haney 1999, Yang 2004); large inputs of animal carcasses, dung, or urine (Rose and Polis 1998, Peek and Forseth 2003, Wilmers *et al.* 2003b, Yang 2006); eruptions of small mammal populations (Jaksic *et al.* 1997, Lithner and Jonsson 2002, Schmidt and Ostfeld 2003); synchronous coral spawning events (McCormick 2003)]. They are widespread phenomena in nature (see details review in Nowlin *et al.* 2008) and have important consequences for population dynamics and the structure of plant and animal communities (Ostfeld & Keesing 2000; Schmidt & Ostfeld 2008; Yang *et al.* 2008).

BOX 1 AVIAN SCAVENGERS IN THE OLD WORLD

Carrion are rare, discrete resources that are unequally distributed in space and require special skills to locate. Once discovered, further skills are needed to open tough skins, especially those of large mammals. Once the carcass is open, however, the extensive amount of food allows large numbers of individuals to benefit (Houston, 1973). Carcasses thus provide unique research conditions that permit the study of the potential evolution of coexisting species that are exploiting a discrete food resource. Specialization in scavenging habits seems to have evolved at least 50 million years ago during the Cenozoic Era. Although facultative scavenging has developed in different avian groups (Falconidae, Corvidae, Ciconidae) (Hertel 1994), only vultures are "true" scavengers, showing life-history strategies based on the obligate exploitation of carcasses (Houston 1973; 1974) Evidence supporting competition as the main factor structuring Old World vulture guilds is based on behavioral and eco-morphological research (Altwel, 1963; Kruuk 1967; König 1974, 1976; Alvarez et al. 1976; Grubh 1978, Mundy et al. 1992).The co-occurrence of several vulture species at large mammal carcasses in East Africa and other regions led Cody (1974) to state that they appear to have evolved ways of coordinating their common use of carrion. Three different patterns of resource use could coexist, which might correlate with differences in skull morphology (König 1983; Hertel 1994). "Gulpers" (Gyps spp) are species feeding on softer muscles and viscera whereas "Ripper" (Torgos, Aegypius, Sarcogyps, Trigonoceps) consume mainly skin, tendons, and flesh adhering to bones and large pieces of meat around the cadaver. Finally, "Scrappers" (Neophron and Necrosyrtes) feed on small pieces from around the kill. In addition to these groups, the bearded vulture, (Gypaetus barbatus), has very specialized food habits, consuming bones of small and medium-sized vertebrates (Margalida et al. 2009). Bio-geographic changes in the composition of these guilds appear to follow an orderly process (Hiraldo 1980). They are richer (up to seven species coexisting concordantly) in regions of the world such as India and East Africa where the availability of wild ungulate carrion is (or has been, from the evolutionary point of view) greater. As the richness in the ungulate communities decreases toward the outskirts of the Mediterranean, Central Asia and South Africa, the guilds become impoverished in an non-random way so that each group mentioned above is reduced to a single representative. Thus, in the Mediterranean and the Middle East the guild is composed of only four species: griffon vulture, black vulture, Egyptian vulture and bearded vulture. Nevertheless, the majority of the evidence favouring an "organized" structure within the scavenger guilds comes from eco-morphological approximations that are usually independent of short-term ecological conditions such as food supply and season (Wiens 1977; Wiens & Rotenberry 1979). On the other hand, behavioural aspects are essential in describing guilds because they identify functional roles of these species that are not necessarily predetermined by morphology (Slatkin 1980).

Pulsed resources are generally exploited by either resident generalist species, which shift their diets in response to the pulse, or mobile specialist species that will travel large distances to take advantage of a resource that has suddenly become available (Ostfeld & Keesing 2000; Yang *et al.* 2008). Resource consumers may show numerical and/or functional responses, including changes in their behaviour and an increase in reproduction rates. Such an increase in the populations of resource consumers will inevitably modify their interactions with prey, predators, and competitor and parasite species. Pulses will not only affect the life strategies and behaviour of individual consumers, but will also provoke a numerical response at the population level and multiple indirect effects at community and ecosystem level including trophic cascades (Yang *et al.* 2008).

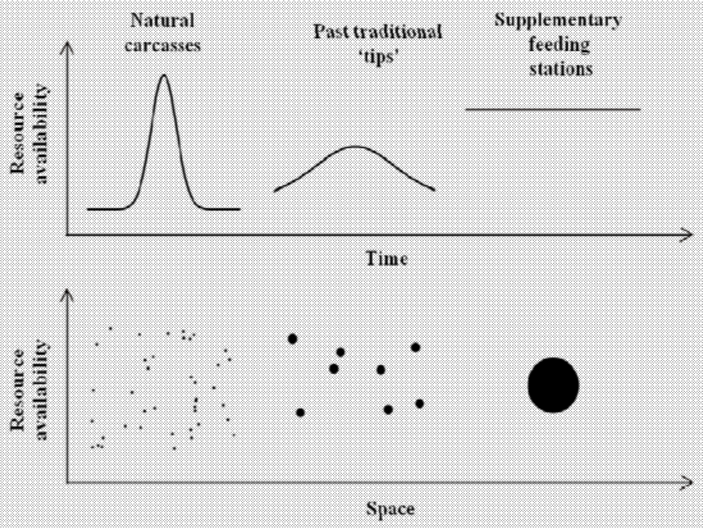
Currently, there is a growing interest on how pulsed resource availability and abundance could be modulated by environmental factors, in particular climatic change and the ecological effects that may be derived from these alterations. It is known that these episodic events with long inter-pulse intervals start to lose their rhythm eliciting significant consequences for many species (e.g. lemmings see for details Coulson & Malo 2008). Pulsed resources, however, may suffer profound alterations in the opposite way; that is, the disappearance of randomness (related to spatial and temporal components) and the increase in their predictability. These alterations can be also considered as a part of global change but have received very little attention among ecologists.

Within this framework, carcasses represent an optimal study model. They constitute a relevant and world-wide food resource receiving little attention from an ecological and conservation point of view (Selva 2004; Selva *et al.* 2005; Wilmers *et al.* 2003a,b; De Vault *et al.* 2003). Obviously, carrion resources are an important pulsed resource in nature because all animals die soon or later. Typical examples include mass mortality caused by epizootic outbreaks, beached whales, spawning salmon, and massive mortality of ungulates and aquatic vertebrates caused by adverse environmental conditions such as harsh winters and prolonged droughts, respectively (Valverde 1967; Houston 1979; Singer *et al.* 1989; Levy 1997, Wilmers *et al.* 2003a; Selva 2004). All these cases represent episodes of large availability of carrion, characterized by their low frequency, great intensity and short duration (Yang *et al.* 2008).

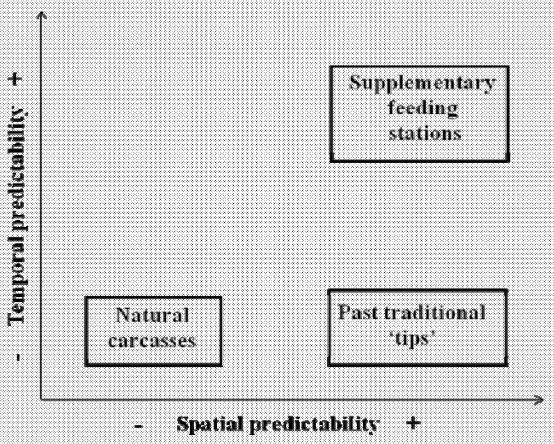
In any case, and regardless of the cause of death (either mass mortalities or solitary random e.g. a dead ungulate), a carcass represents kilograms to tones of easy–to-exploit food which become suddenly available and tend to be rapidly integrated into food webs by a myriad of species ranging from bacteria to vultures. In consequence, resource consumers may exhibit a numerical and/or functional response (see above).

BOX 2 SUPPLEMENTARY FEEDING STATIONS AND LEGISLATION

From an ecological point of view, we could define a gradient 'natural carrion' – 'traditional tips' – 'supplementary feeding station' so-called vulture restaurants. As mentioned above, if natural carrion represents a resource pulse, then in comparison traditional tips provide a less intense pulse of greater duration. At the other end of this gradient are the 'vulture restaurants', in which the essence of the resource as a pulse is lost and carrion availability becomes constant (figure below).



As well as this temporal gradient, there is also a spatial gradient in the distribution of the resource. Whilst in most natural terrestrial systems the distribution of carrion is random (Wilmers et al. 2003a; Selva 2004), at a current 'vulture-restaurant' the resource is concentrated in one place in an aggregated distribution. Today, this resource is no longer available in numerous sites, as was the case with 'traditional tips' in the past usually close to villages and farms, and is, instead, concentrated in a small number of supplementary feeding stations (vulture restaurants). These differences in the spatial-temporal distribution of carrion resources also imply a different degree of predictability: natural carrion is generally very unpredictable in terms of when and where; 'traditional tips', on the other hand, were spatially totally predictable and the regular supply to supplementary feeding stations makes them, moreover, temporally predictable (figure below)



After the outbreak of the so-called 'mad-cow' disease; the detection in humans of variant (vCJD) or new variant (nvCJD) Creutzfeldt-Jakob disease, acquired from cattle infected by bovine spongiform encephalopathy (BSE) in late 1990s, the European sanitary laws made obligatory the removal and cremation of all livestock carcasses (Regulation CE 1774/2002). Henceforth, all carcasses of domestic animals had to be collected from farms and transformed or destroyed in authorized plants; as a result many 'traditional tips' associated with stock farms closed down (Donázar et al., 2009a,b, Margalida et al. 2010). The implementation of this new law made ecologists and conservationist to worry about the possible consequences for avian scavenger populations (Tella, 2001). As consequence, several new regulations were redefined (i.e. EU1774/2002; EU322/2003; EU830/2005; CE 1069/2009) permitting carcasses to be left in the field to feed scavengers. In any case, legal constraints are still very important and the abandonment of dead animals is only possible under specific conditions and in specific locations. Thus, state and regional governments in Mediterranean countries are following a common strategy, whereby a few sites –supplementary feeding stations or ''vulture restaurants" – are supplied with carcass remains to feed scavengers (Donázar et al. 2009a, Margalida et al. 2010). However and following Piper (2006) recommendation we have to take into account that 1) carcasses disposed at vulture restaurants could not behave as a natural ones and 2) supplementary feeding programs must be implemented with a carefully understanding.

In this sense and up to now few researchers have relied on this new ecological scenario and dept on the study of aspects for improving of the effectiveness (see Donázar et al. 2010).

Carcasses thus have a large potential to shape the intra and interspecific interactions. Their availability may not only affect the life strategies and behaviour of individual consumers, but will also provoke scarcely explored indirect effects at the community level (Yang *et al.* 2008). As we state above, global change can deeply alter the pulsed/no-pulsed nature of food resources. However, we still possess a poor understanding of how the loss of non-pure episodically food resources can affect the functioning of ecosystems. With increasing ecosystem humanization, the pulsed character of carcasses is being lost. Humans have massively substituted wild ungulate populations by livestock. In consequence, carcass supply has (have) turned relatively predictable due to the increasing sedentariness in agro grazing activities (Donázar *et al.* 2010).

PREDICTABLE CARRION RESOURCES AT SUPPLEMENTARY FEEDING STATIONS

Food supplementation of free-living animal has become the most common tool in recovery programmes of populations of species in clear decline. This is an emergent hot topic both for conservation and basic ecology and merits a specific approach in a separate section. However, while in general supplementary feeding reduces the risk of starvation and may enhance reproductive performance (Newton 1998, Robb *et al.* 2008a) it has also been detected that these kind of wildlife management may result in population limitation (Carrete *et al.* 2006a, Robb *et al.* 2008b, Oro *et al.* 2008).

In the particular case of vultures and the rest of the Old World avian scavengers (BOX 1) the availability of carrion resources had tended to decrease progressively. Large predators' populations have declined, meaning a scarce availability of their kills, yet on the other hand, wild ungulate populations which are subject to hunting management are increasing and, thus, so is the number of their carcasses available to scavengers (Blázquez-Álvarez & Sanchez-Zapata 2009). Furthermore, carcasses originating from traditional extensive livestock, which were once left in situ or disposed at certain places close to villages and/or farms (i.e. 'tips' for dead animals, traditionally used in Mediterranean regions to discard carcasses BOX 3), are disappearing as a result of local economic changes and stricter sanitary legislation (Donázar 1993; Tella 2001; Donázar *et al.* 2009a, 2010; see above and BOX 2). This scarcity of carrion resources promoted the creation of vulture restaurants, i.e. supplementary feeding stations where carcasses became available in large quantities and in a predictable manner. This widespread conservation tool pretended to feed endangered scavenger species strictly dependent on this food resource. Up to day several research studies have revealed that vulture restaurants have some *Pros and Cons* (BOX 3). We must remember that supplementary feeding stations are not a natural way of disposing carcasses in the nature and therefore, as we will learn in this thesis, recovery programs that contemplate this particular conservation tool require a full understanding of the system with the help of scientific research.

BOX 3. *PROS AND CONS* OF VULTURE RESTAURANTS IN EUROPE

In Europe, the availability of food resources (i.e. carcasses) for scavengers has decreased during the latest decades mainly due to stricter sanitary legislation which, after the irruption of the BSE (Bovine spongiform encephalopathy), have lead to removal of all livestock carcasses and human hunter kills from the field. This is of great conservation concern because all European scavengers are protected species and some of them are in rapid population decline. Accordingly, European and regional administrations have supported the creation of "vulture restaurants" to provide scavengers with regular carcasses. Currently, these supplementary feeding stations have become the main food source for all avian scavengers which changes the spatio-temporal distribution of the food: before, carcasses were unpredictable both in space and time like other trophic pulse resources such as tree-masting or insect explosions which appear and are randomly distributed and unpredictable (Ostfeld and Keesing 2000; Rose and Polis 1998), and which suppose a "price" for the species or group of species that feed on it. Now, however, carcasses have become aggregated and predictable both in space and time. The proliferation of vulture restaurants may lead to positive and negative effects both on scavengers and other species in the ecosystems. Spain holds important Old world scavenger populations and, therefore Spain is the country where more vulture restaurants have been created. As consequence of this proliferation of vulture restaurants, several research studies have appeared in the literature describing a spectacular increase of the breeding population of one species i.e. the griffon vulture (Gyps fulvus) (ca. 10,500, resident) (Del Moral and Martí, 2001; authors' unpublished data) while other avian scavenger populations continue declining (BirdLife, 2004). In the case of the endangered Egyptian vulture (Neophron percnopterus), it has been reported that vulture restaurants help the maintenance of breeding pairs and even that the breeding success of neighbour pairs to these food sources was higher in comparison to other pairs in the Ebro valley (Grande et al. 2009); this conservation tool also permits the maintenance of large communal roosts during summer (Donázar et al. 1996; Grande et al. 2009). Indeed, vulture restaurants are currently a useful tool to support new individuals in the southern region of Spain (Cádiz, Andalucía) where the presence of the breeding pairs of Egyptian vultures is clearly declining (Benitez et al. 2009). However, the vulture restaurants' attempts to conserve the endangered population of bearded vultures (Gypaetus barbatus) in the Pyrenees have had undesirable responses: while the number of breeding pairs increased, the breeding success dropped dramatically. Research detected that the large assemblages of food prolonged in time aggregated the juveniles instead of being widespread. Bearded vultures are birds that do not live in groups so these concentrated individuals used to disturb the nearer breeding pairs. Moreover, because of this large availability of food, it has been detected that the number of new breeding pairs established near vulture restaurants increased too. In this scenario, the competitive interactions between all bearded vultures (juveniles and breeders) increased and vulture restaurants became stressful in this area for neighbouring breeding pairs that continuously defend their territories (Carrete et al. 2006a, b; Oro et al. 2008).

Nevertheless, few studies have investigated the indirect effects of the prolonged presence of facultative species at those sites with a continuous hyper-concentration of carrion resources. Facultative species consume carcasses less efficiently and more slowly than the specialists or strict carrion-eaters and most importantly, they do not feed only on carcasses but also rely on small prey. This question becomes especially important when the possible species affected are of conservation concern.

THESIS OUTLINE

The effects of the spatial distribution of resources on community structure and functioning form the conceptual framework of this thesis. I have investigated these issues both from an ecological and a conservationist perspective using carcasses as the study model. This thesis starts with the exploration of patterns of randomness of food resources in scavenger positive intraguild processes (Chapter I). Next, I examined their consequences on the spatial distribution of abundances and foraging strategies, always from a guild perspective (Chapter II). From this point on, the thesis examines the consequences of the clumping of food resources on communities of vertebrates ecologically independent from the exploitation of carcass resources (Chapters III & IV). Finally, the thesis concludes with the exploration of how species' diet variation and behaviour change at predictable resources - an interesting framework from which to ultimately obtain guidelines to improve conservation tools through adaptive management. (i.e. supplementary feeding stations; the so-called vulture restaurants) (Chapters V & VI).

FOOD PREDICTABILITY AND GUILD STRUCTURE AND FUNTIONING (CHAPTERS I-II)

As we state above, the role of chance in nature remains unstudied. However, trying to explain its influence on the maintenance of species coexistence arises as a hot topic within ecological research. Within avian scavengers both positive and competitive interactions take place (see references in Chapter I). Here, we try to deepen on the facilitatory processes involved in their coexistence when exploiting large ungulate carcasses that appear either at random (i.e. those freely available by chance in the field) or with a predictable pattern (i.e. disposed at supplementary feeding stations or so-called vulture restaurants). The main goal of the study was to investigate whether random food resources promote positive interespecific interactions permitting the coexistence of species and increasing the diversity of species (i.e. avian scavengers) within the guild.

On the other hand, distribution of food resources may also acquire importance for vertebrates that develop their life-cycles in very distant and diverse regions, often enforced to respond to changing environmental conditions that may be determinants of their individual fitness (Webster *et al.* 2002; Runge & Marra 2005; Norris & Taylor 2006 and references therein). In Chapter II, we analysed the spatial abundance distributions in relation to availability of feeding sources of two trans-Saharan avian scavengers: the black kite (*Milvus migrans*) and the Egyptian vulture (*Neophron percnopterus*) showing sympatric distributions on breeding (Europe) and wintering (Africa) grounds. Specifically, at the European summering regions, birds greatly rely on predictable resources such as garbage dumps and supplementary feeding stations. On the contrary, food availability in Africa is more variable: livestock is raised extensively but predictable resources exist in slaughterhouses in the vicinity of cities. Moreover, in sub-Saharan biomes, particular emerging phenomena such as the outbreaks of dessert locusts (S*chistocerca gregaria)* take place. The variability in the ecological scenarios that these two trans-Saharan migrant scavengers find may determine parallel or asymmetric responses in their distribution, abundance and ultimately different degrees of diet overlap.

CLUMPED RESOURCES AND NON-SCAVENGER COMMUNITIES (CHAPTERS III-IV)

Animal carcasses provide the primary food resource for guilds of scavengers composed not only of specialist but also of facultative carnivore and avian scavengers (Kristan & Boarman, 2003; Wilmers et al. 2003b). Under a scenario of food bonanzas, (i.e. large availability of carcasses for long period) facultative scavenger may also increase their predation pressure on populations of their main prey, a fact that could have further consequences on the population dynamics and structure of prey community. However, the effects of carrion resource on trophic levels other than scavengers have remained largely unexplored. Therefore, our departure hypothesis was that carrion pulses could have effects on different trophic levels- predators and herbivores- triggered by an increase in the predation risk at the vicinity of carcass sites. We performed some field experiments to investigate those effects. In a first step and taking as a study model a simple community of scavenger and ground-nesting birds in the Canary Islands we tested if predation risk on simulated nest of ground-nesting birds increased near carcasses, both randomly appeared and placed in predictable places (Chapter III). In other field experiment (Chapter IV) we examined the role of long-lasting carcasses abandon by hunters during winter in high-latitude regions where specialist carrion eaters are absent. Specifically, by means of snow-tracking and direct observations we investigated whether large ungulate carcasses elicit spatial responses in facultative scavengers and their prey.

EFECTS OF SUPLEMENTARY FEEDING ON THE INTERESPECIFIC INTERACTIONS WITHIN THE GUILD: GUIDELINES FOR OPTIMAL MANAGEMENT OF THIS CONSERVATION TOOL

(CHAPTERS V-VI)

The decline of traditional agro-grazing practices in Mediterranean regions together with the current, more restrictive, European sanitary legislation related to BSE that obliges to remove carcasses from the wild, have led to both a decrease in the availability of food for avian scavengers and a concentration of the resources in a few predictable places so-called "vulture restaurants" (Donázar *et al.* 2009a,b). However, despite the urgent conservation implications of this scenario (Donázar *et al.* 2009a) it is not known how the concentration of resources in predictable places can affect the interspecific relationships within the guild. In particular, as has been observed in other ecological scenarios (Petren & Case, 1996; Kiesecker *et al.* 2001 and references therein) clumped resources may be favouring dominant, here large body-size species, in detriment of smaller and more endangered species. In fact, the veracity of this scenario was already demonstrated by our previously reported findings (Chapter I): griffon vultures monopolize food resources at predictable places. In a further step we tried to deepen into how the accumulation of resources determines changes in the diets of scavengers and modulate trophic overlap (Chapter V). We selected a tandem of carrion eaters [the griffon (*Gyps fulvus*) and the Egyptian vulture (*Neophron percnopterus*) members of the same scavenger guild with clearly segregated diets (König 1983)]. The specific objective was to evaluate if the progressive disappearance of food resources linked to large ungulate carcasses (swine, sheep) has provoked asymmetric changes in the diet of the two scavengers. Specifically, we explored whether the trophic specialization of the griffon vulture would lead to few alterations in its diet following the decrease in food availability; on the contrary, the Egyptian vulture would respond according to these variations, increasing the consumption of alternative prey.

We finish this thesis with an applied study (Chapter VI). The concentration of carcasses in predictable places (vulture restaurants) is a globally-used management tool applied to the conservation and recovery of populations of endangered scavengers (Koening 2006; Swan *et al.* 2006). We lacked, however, of practical guidelines aimed to enhance an active and adaptive management of supplementary feeding places and resources devoted to the conservation target species. In our research, we specifically evaluated the use made by scavenger species of supplementary feeding stations that differ in their local characteristics and management (mainly in terms of time, quantity, and type of food provided). Taking into account the information available on the guild structure, the population size of scavengers in the study area (Ebro valley, northern Spain), and the foraging behaviour of each species, we tried to find out whether (1) large aggregations of griffon vultures, the largest and most abundant scavenger, would inhibit suitable conditions for intraguild facilitatory processes, reducing the abundance of other, smaller scavengers at these sites, and (2) which features, such as geographic location, and availability and type of food supplied at feeding stations, would favour the use by some species at the expense of others.

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CHAPTER I

Chance promotes species diversity and coexistence: a field experiment on the facilitatory processes within an avian scavenger guild

ABSTRACT

Randomness, *per se*, is understudied in ecological research. Scavenger guilds have evolved feeding upon unpredictable resources both in space and time (carcasses). Here, we address the role of resource randomness in the structure and functioning of an avian scavenger guild. We performed a large-scale field experiment where 58 carcasses where disposed (and continuously observed until complete feeding by scavengers) either in continuously active feeding places that have been operating during more than five years (predictable resources) or at random sites in the field. We found that random carcasses allowed facilitatory processes and lead to a higher diversity of species than predictable carcasses. Predictable resources disrupted intraguild facilitatory processes because the specialist dominant species (griffon vultures, *Gyps fulvus*) arrived earlier and monopolised food resources. Moreover, although species richness was similar at random and predictable sites the diversity of species that profited from carcasses frequently drop until 0 when in predictable carcasses. Supplementary feeding stations (i.e. predictable places) may become an ecological trap for some small scavengers because they occur in larger numbers but obtain less profit (food) than at random resources. This study provides the first field experimental evidence of the relevance of the randomness in the coexistence of a guild. Our findings open new insights on the role of predictability in the viability of populations and/or ecosystems functioning.

INTRODUCTION

Chance, *per se*, has a major role in ecology and evolution: from the tiny molecular scale (random gene mutation) to the organism level when, for instance, some finches arrive (by chance) to a pristine oceanic island (the “founder effect”), leading to an adaptive radiation by genetic drift (pure randomness, Futuyma 1998), or by non-random natural selection (Grant 1986). Surprisingly enough, when studying increasingly higher ecological scales (e.g. from individual behaviour to macroecological patterns), that is, when more and more randomness is incorporated into the studied phenomenon, easier is to visualize patterns (out of chance; Brown 1995, Solé & Bascompte 2006). Also, unexplained variance in a given ecological study is attributed to chance (annoying noise), and much of it is hoped to be due to unstudied variables or measure error, rather than to the real signature of chance alone. The underlying idea is that chance is the portion of nature that we still do not understand. Thus, the relevance of randomness, *per se*, uses to be underappreciated as a real motor promoting biodiversity.

The spatial and temporal availability of trophic resources poses an interesting and relevant study subject to understand the ecological role of chance when resource heterogeneity imply a source of randomness. Food distribution patterns drive the distribution, size, structure and social organization of animal populations (MacArthur & Pianka 1966; Macdonald 1981, 1983; Johnson *et al.* 2002; Chesson *et al.* 2001; Descamps-Julien & González 2005; Flöder *et al.* 2002; Ostfeld & Keesing 2000; Bissonette, & Storck 2007). More specifically, resource predictability has been found to shape foraging strategies, time of reproduction, breeding success, survival, behaviour, life-history trade-offs, and even large-scale long-term trends on the distribution of species (Robb *et al.* 2008; Overington *et al.* 2009; Dingemanse *et al.* 2010). In this sense, under a panoply of circumstances, including some mediated by human activities, resources may appear clumped available, thus increasing its spatial and temporal predictability. The study of the effects of such changes in resource availability on vertebrate populations has received increasing attention, especially at an intraspecific and intrapopulation level: it has been found to relax conspecific agonistic interactions creating large aggregation of individuals even when this may be not advantageous for individuals (Tokeshi 1999; Maher & Lott 2000; Johnson *et al.* 2002; Revilla & Palomares 2002; Eide *et al.* 2004).

However, our knowledge on the relevance of resource availability has not permeated into higher ecological levels. Despite heterogeneous environments are theoretically predicted to enhance the coexistence of species within assemblages (Chesson 2000; Chesson *et al.* 2001), empirical information is still very scarce. This is mainly skewed towards studies of clumped (i.e. predictable) resources favouring their monopolization by aggressive and dominant species, especially in the context of competition between pairs of native and invasive taxa (Sexton 1990; Petern & Case 1996; Kiesecker *et al.* 2001). However, the interactions among species that comprise a community are not just competitive but can also be positive (e.g. facilitatory processes; Bruno *et al.* 2003). How these interactions can be shaped by changes in the spatial and temporal distribution of resources is however still unknown.

Here, we explore through a large-scale field experiment the role of chance, *per se,* as a factor driving the coexistence of species in an avian scavenger guild. Avian scavengers group together a continuous of species from specialized consumers (obligate scavengers) to opportunistic-facultative scavengers (see Donázar *et al*. 2010 and references therein). Carcasses are pulsed resources with relatively high time-permanence whose consumption strongly shape relationships between potential consumers, from fungus and bacteria to arthropods and vertebrates (DeVault *et al.* 2003; Selva & Cortés-Avizanda 2009). Old-World avian scavenger guilds are characterized by complex interactions including facilitatory processes leading to optimal exploitation of food resources (Root 1967; Mundy 1982; Donázar 1993). Chance is almost intrinsic to exploiting carcasses because dead animals show up in the field unpredictably in space and time. By manipulating the degree of resource predictability we specifically investigated if the functionality of these ecological processes is favoured by randomness. We achieved this by placing large ungulate carcasses either randomly in the field (i.e. simulating a wild dead animal) or predictably at supplementary feeding stations (the so-called “vulture restaurants”). These are places where livestock farmers used to frequently dispose the carcasses, making carcasses predictable in space and time for the avian scavenger community (see Cortés-Avizanda *et al.* 2010 for details).

STUDY SYSTEM AND HYPOTHESES

The research was carried out in a 10,000 km^2 area located in northern Spain, lying between the Pyrenees, the Iberian mountains and the Ebro valley. This region holds one of the largest European populations of avian scavengers (Birdlife 2004; Cortés-Avizanda *et al.* 2010; Donázar *et al.* 2010) with three vulture specie: griffon (*Gyps fulvus*) Egyptian (*Neophron percnopterus*), and bearded (*Gypaetus barbatus*), and other scavengers with facultative foraging habits: red (*Milvus milvus*) and black kites (*Milvus migrans*) and common ravens (*Corvus corax*). All the species have well-represented populations all over the study area. In the study area conservationists started 25 years ago to create vulture restaurants to feed vultures (Iribarren 1971). We took advantage from that conservationist initiative to compare the consumption of carcasses in predictable places (vulture restaurants) vs. carcasses disposed randomly in the field. The Griffon vulture is the heaviest species (10.5 kg) and has become comparatively much more abundant possibly because of the vulture restaurants and lower human persecution (up to 2400 breeding pairs) than the remaining scavenger species (all <2kg) which, as a whole, have no more than 500 breeding pairs (see Cortés-Avizanda *et al.* 2010 and references therein). Old-world vultures are considered to conform a guild, that is a group of species which have co-evolved sharing a common resource (i.e. food) and develop special behavioural and morphological skills in order to take advantage from its exploitation (see Root 1967; Blondel 2003). This guild and associated facultative species is considered to be “competition-structured”; thus, groups of species with divergent eco-morphological characters are adapted to exploit different parts of the carcass (Kruuk 1967; König 1983; Hertel 1994; Hertel & Lehman 1998). But apart of this, within these assemblages positive interactions are decisive. Thus the success in the use of the resource is dependent from facilitatory processes running in opposed directions: small body size scavengers arriving earlier at carcass increase the probability of location of the resource by large vultures which, on their turn, when dismember the carcass increase the opportunities of access to food resources by small scavenger species (Kruuk 1967; König 1974, 1983).

In our study system, the only species able to open large ungulate carcasses is the griffon vulture so the facilitatory processes pivot around the arrival of individuals of this species. Recent changes in sanitary legislation, however, have determined that most of available resources for scavengers are concentrated in supplementary feeding stations where apparent increasing competition might arose between the dominant griffon vulture and the rest of smaller body-size species (Cortés-Avizanda *et al.* 2010) as has been also observed in other avian assemblages (Mönkkönen *et al.* 2004). This scenario, therefore, provides a unique opportunity to assess the role of chance of food resources on the structure and functioning of the scavenger guild.

Our departure hypothesis is that randomness in food resource disposition permits that the interespecific positive interactions occurs promoting the coexistence between species and consequently conferring higher diversity of species to communities and guilds. Specifically, we predict that: i) although random resources would attract lower numbers of scavengers would show higher diversity of consumers than clumped and predictable sources which despite maintain high species richness and abundances the diversity would decrease mainly because the gather of larger numbers of griffon vultures; ii) consequently, at predictable resources the intragulid facilitatory processes would be affected and the order of arrivals to carcasses would differ from randomness. Specifically, the small scavengers would not arrive before the griffon vultures and the probability that these subordinate species take advantage from the food would decrease.

METHODS

FIELD PROCEDURES AND DATA COLLECTION

Between spring (April-May) and summer (June, July and August) 2004-2006 we monitored the consume by scavengers of 58 carcasses of sheep (*Ovis aries*) and pig (*Sus scrofa*). These are the domestic ungulates more frequently exploited by necrophagous birds in the study area (Donázar *et al.* 2010). Random carcasses (N=28) were placed in open field (i.e. fallows and pasturelands) all along the study area. In every place we chose adequate conditions favouring the accessibility to scavengers. Predictable carcasses (N=30) were monitored at large vulture restaurants where the availability of food is almost continuous (Cortés-Avizanda *et al.* 2010). All the carcasses used in the experiment were adult animals weighing between 50 and 90 kg which determined that the skin was hard enough to preclude that the small species were able to get food inside the carcass without the mediation of facilitatory processes i.e. by the scavenging activity of the griffon vultures.

Carcasses were placed (*c.* 2h after dawn) and were monitored until their complete consumption. Observations were made always by the same two observers from a vehicle using binoculars (10x 40) and telescopes (20-60x) fitted to car windows at a minimum distance of 300 m to avoid interfering in the bird behaviour. We systematically recorded the arrival of individuals of species at carcasses. For each one of those individuals of species other that griffon vultures, from now on: -small scavengers- we determined whether they had been seen eating actively and if this behaviour was performed before and/or after the arrival of griffon vultures.

ANALITICAL PROCEDURES

Arrival patterns description

For each studied species and carcass we defined two variables: i) order of arrival, and ii) time lasting (min) from the carcass disposal to the arrival of the first scavenger. Since arrival of individuals at carcasses were frequently clumped (e.g. territorial pairs, groups of social species) we here used as our analysis unit the group, defined as those individuals of the same species arriving within an interval <2 min one another. We also used the group to evaluate a third variable: iii) the probability that a group of griffon vultures arrive first to a carcass in relation to the proportion of vulture groups out of the total number of groups recorded in a given carcass.

Diversity, richness and facilitatory processes

We compared species diversity (Shannon index, Magurran 2003) and richness (total number of species) between random and predictable carcasses. Then, to determine the existence of facilitatory processes we performed three Generalized Linear Mixed Models (GLMM), (McCullagh & Searle 2000; SAS Institute Inc. 2009). First, we considered as response variable whether each individual belonging to a “small scavenger” species (all species less the griffon vulture) arrived to the carcass early (1) or after (0) griffon vultures. For the second analysis, and considering those individuals of small scavengers arriving before griffon vultures, we considered whether they had been observed eating (1) or not (0). The third analysis was similar to the second but considering only those small-scavenger individuals arriving after griffon vultures. In the three analyses we considered binomial error distributions and logit link functions. Two categorical explanatory variables were fitted: i) the type of food source (i.e. random or predictable) and ii) the species identity (i.e. Egyptian vulture, common raven, black and red kite). “Carcass” was fixed into the models as a random term to control for spatial and temporal heterogeneity (see Cortés-Avizanda *et al.* 2010).

Models were fitted by using a forward stepwise procedure and following well-described procedures for this kind of study system (Bolker *et al.* 2008; Cortés-Avizanda *et al.* 2010).Only significant effects ($P < 0.05$) were retained. Final models were those explaining the highest fraction of the initial deviance.

RESULTS

OCCURRENCE AND FEEDING ACTIVITY OF SCAVENGERS

Scavengers did not show a general tendency on the number of individuals arriving in random *vs.* predictable carcasses (Wilcoxon Test Z=-0.535; *P*=0.593, Table 1). In fact, striking differences were detected between species: griffon and Egyptian vultures arrived at higher proportion of carcasses and in larger numbers at predictable carcasses (see details in Table 1). The small sample size for the other species did not allowed finding statistically significant results. However, black kites and common ravens showed a clear preference for random carcasses both in total number of individuals (both species) and median group size (black kites; Table 1). Marsh harriers (*Circus aeruginosus*) and golden eagles (*Aquila chrysaetos*) visited carcasses anecdotally; despite also showed a preference for carcasses disposed randomly.

Differences on the profit that species gained from random and predictable carcasses were significant (Table 1). Egyptian vultures obtained larger profit in random carcasses, both considering the proportion of carcasses where they were recorded feeding and the frequency of successful individuals. For the other species we did not find statically differences (again possibly because of sample size) but all species and especially the black kites tended to show higher feeding efficiency in random carcasses (Table 1).

EFFECT OF CARCASS DISPOSITION UPON GUILD RICHNESS AND DIVERSITY

Richness of arriving and feeding birds were alike in both kinds of carcasses. However, the diversity was higher in random carcasses, dropping until zero for median diversity of feeding birds in predictable carcasses (Table 1).

Table 1. Carcasses exploited by each of the species and abundances of the species arriving and feeding both at random and predictable carcasses. Because the activity of griffons at carcasses was very dynamic, with continuous changes (Cortés-Avizanda 2010; authors' unpubl. data) we consider that all the griffon vultures that arrived had accessed to food resource and fed. Chi-square Tests were performed to contrast the percentages of carcasses exploited by each species. Moreover, Mann Whitney U-Test to compare the mean and the median of the Richness and Diversity as well as max, min and mean of occurrence **(a)** and feeding **(b)** species at both type of carcasses (*** P<.0001, * P <0.05).

Occurrence

(a)

	Random (n=28)					Predictable (n=30)				
Species	N	% carcasses	min^{a}	max	median	N	% carcasses	min^{a}	max	median
Gyps fulvus	2540	89.3	32	209	87	9522	100.0	67	804	287***
Neophron percnopterus	101	75.0	1	24	3	197	90.0	1	30	7*
Milvus milvus	14	25.0	1	5	2	26	33.3	1	7	2
Milvus migrans	63	14.3	1	51	6	4	13.3	1	1	1
Corvus corax	72	42.9	2	38	2	28	36.7	2	4	2
Circus aeruginosus	3	10.7	-	1	-	0	0.0	-	-	-
Aquila chrysaetos	1	3.6	-	1	-	1	3.3	-	1	-
Richness			1	5	3			1	4	3
H'			0.043	1.041	0.222			0.042	0.551	0.111*

Feeding

(b)

	Random (n=28)						Predictable (n=30)					
Species	N	% carcasses	min^{a}	max	median	% ind. success	N	% carcasses	min^{a}	max	median	% ind. success
Gyps fulvus		100.0						100.0				
Neophron percnopterus	53	90.0	1	11	3	52.5	25	33.3***	1	6	3*	12.7
Milvus milvus	6	57.1	1	3	1	42.9	11	50.0	1	7	1	42.3
Milvus migrans	15	50.0	4	11	8	23.8	0	0.0	-	-	-	0.0
Corvus corax	27	66.7	1	7	2	37.5	9	45.5	1	3	2	32.1
Circus aeruginosus	2	-	-	1	-	66.7	0		-	-	-	0.0
Aquila chrysaetos	0	-	-	-	-		1	100.0	-	1		100.0
Richness			1	4	2				1	2	1	
H'			0.078	0.86	0.171				0.022	0.032	0.000***	

ORDER OF ARRIVALS

Avian scavengers took longer to locate random [median (range) = 173min (0-841); n=28] than predictable carcasses [median (range) = 29min (0-318), n=30, Mann–Whitney *U*-test: *P* = 0.001, Fig.1]. Random carcasses were more time-consuming to encounter for griffon and Egyptian vultures (Mann–Whitney *U*-test: *P* = .000 and *P* =0.016 respectively). The other species i.e. common raven and red and black kite showed similar values (Mann–Whitney *U*-test: *P* > 0.005). No difference was found in relation to time needed to completely deplete carcasses after first arrival [(random: 288min (14-1493), n=28); predictable: 242 min (12-723 Mann–Whitney *U*-test: *P* > 0.05)].

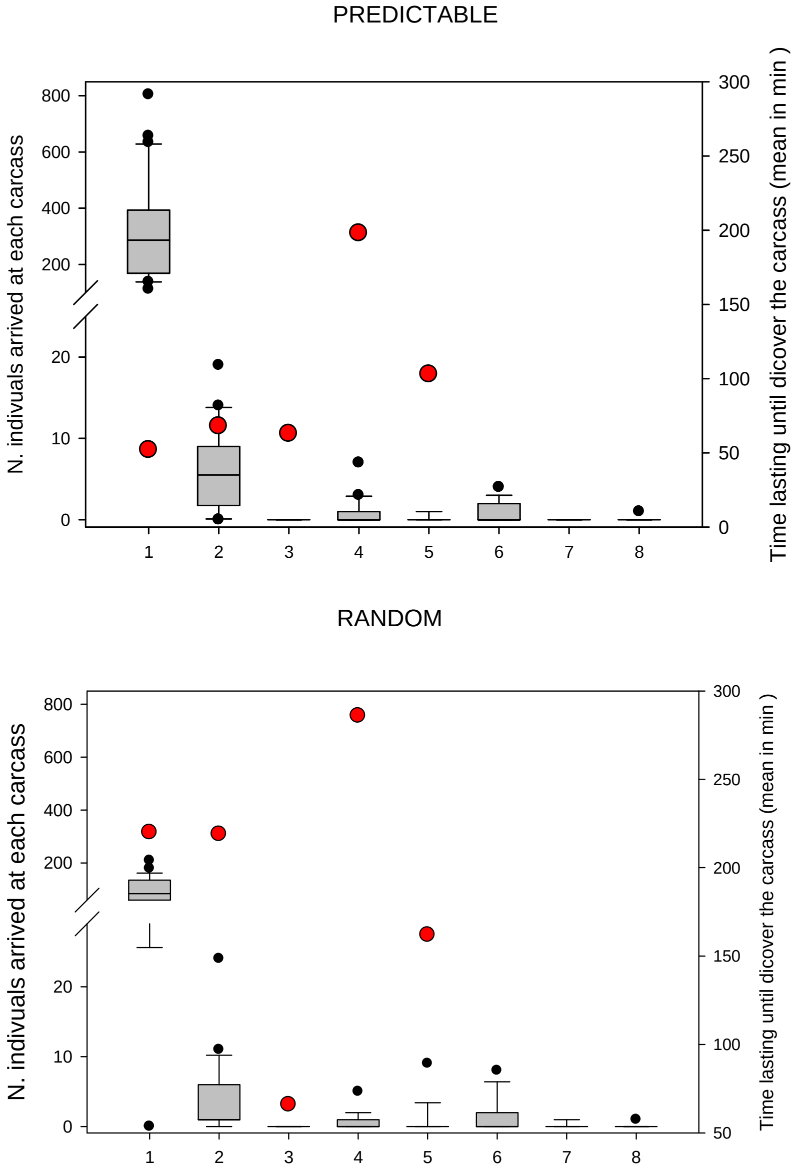

Figure 1. Box plot of birds recorded of each species in carcasses both random and predictable (n=140) and the mean of time until each species discover the carcasses.

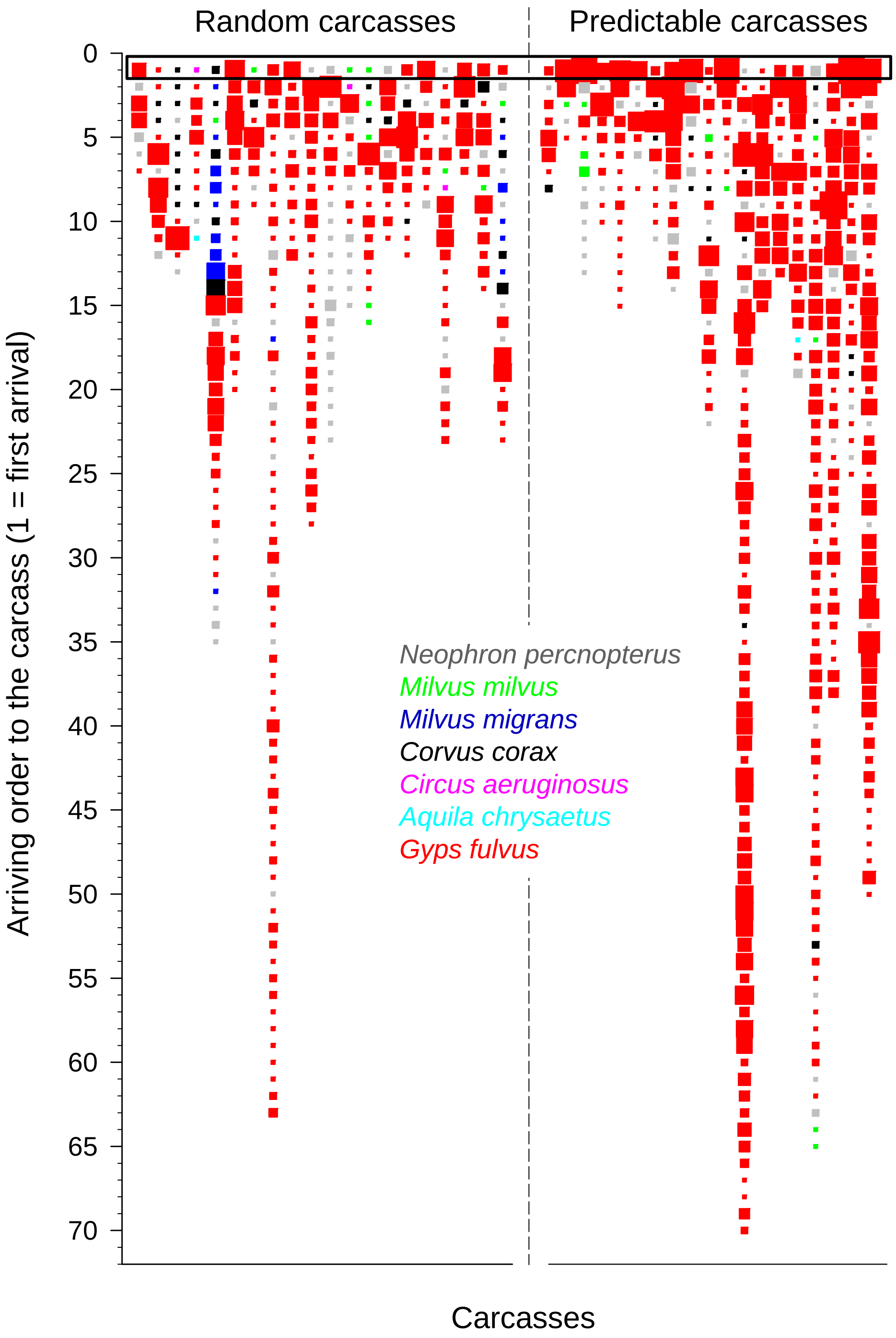

Figure 2. Representation of the arrival order of species at focal carcasses. The size of the squares show the size of the groups. The upper rectangle highlight first arrivals to each carcass.

Small scavengers arrived first at 42.9% of the random carcasses than at those disposed in predictable sites (13.3%; X^2=4.928, *P*=0.026, Fig. 1, 2). Griffons often arrived at predictable carcasses very soon [mean (min-max)=34min (0-318)]. Accordingly, in predictable carcasses, the probability that a group of griffons arrived first to the carcass was always close to 1 (100%) regardless of the relative frequency of scavenger species in each carcass (y=1.112-0.293x, R^2=0.03, $F_{1,17}$=0.547, *P*=0.469). In other words, griffons were already there “waiting for” the new carcasses (pers. obs.). By contrast, in random carcasses, the probability of griffons to arrive first increased proportional to the proportion of griffon groups recorded in the carcass (y=-0.153+1.006x, R^2=0.20, $F_{1,18}$=4.462, *P* = 0.049); that is, the probability that a group of griffons was the first to arrive to one carcass was similar to the one expected by chance alone (Fig. 3). Moreover, although griffons arrived first at predictable carcasses we did not find differences in the size of first groups to arrive at carcasses [Mann–Whitney *U*-test: *P* = 0.182 being predictable: mean (range) = 77.1 (313-1) and random: mean (range) = 12.1 (40-1)]. However, considering all the groups recorded, both griffon and Egyptian vultures showed larger group sizes at predictable resources [median (range): griffon vulture= 5 (1-313); Egyptian vulture = 1 (1-5): Mann–Whitney *U*-test: *P* < .0001 and *P* = 0.042 respectively].

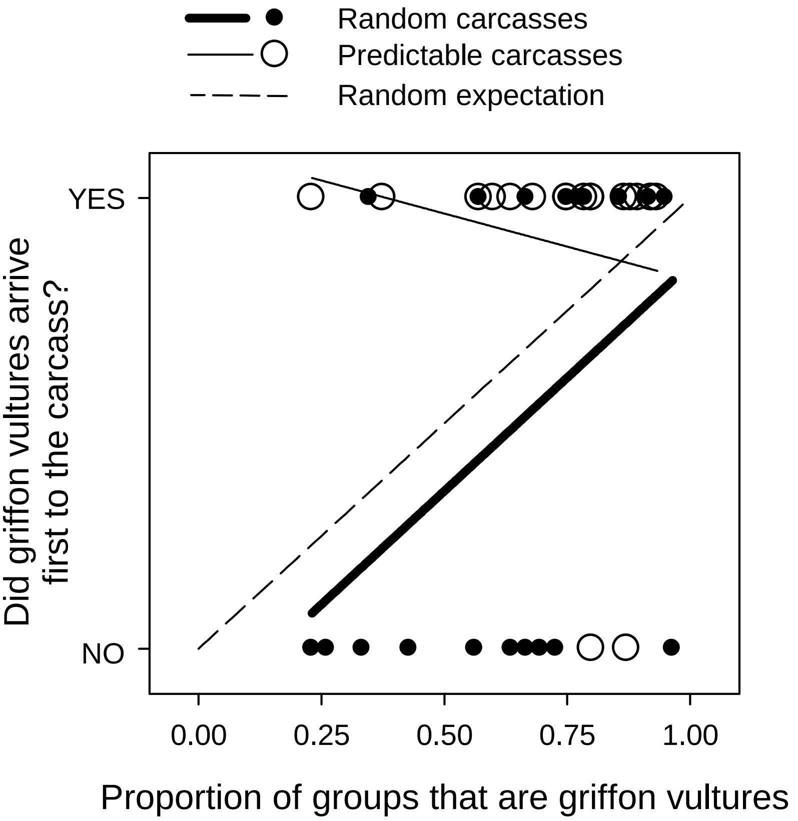

Figure 3. Graphic representations for each type of carcasses (random or predictable) of whether the griffon vultures arrive first or not in relation to the percentage of groups of vultures in relation to the total of groups recorded at each carcass. The thick line shows the expected trend if it were a random process. Note that random carcasses shown a similar trend to that expected by chance whereas, the trend for predictable carcasses were almost opposite.

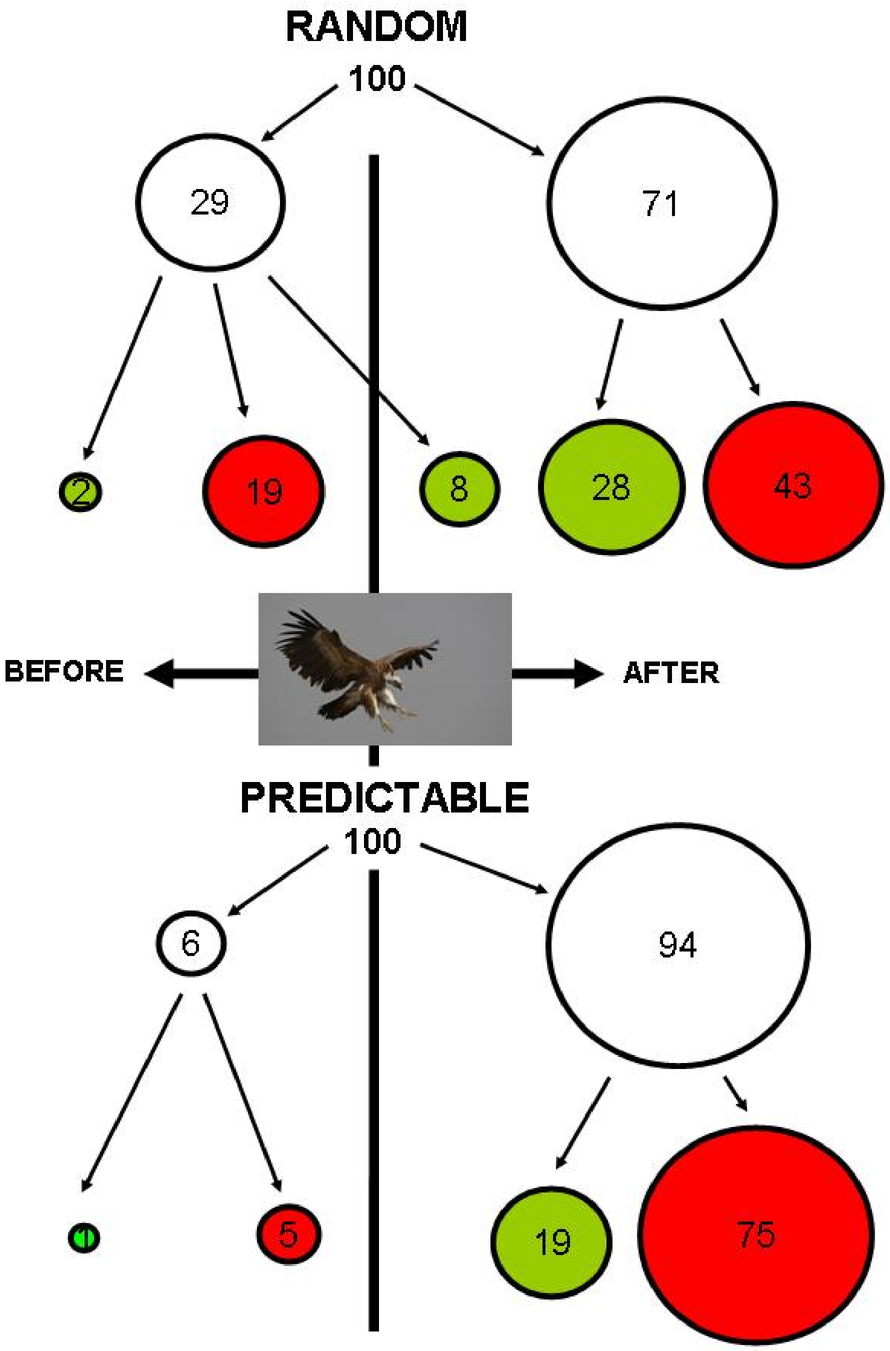

Figure 4. Conceptual model explaining the observed changes in the arriving and feeding activity of small scavengers at carcasses both predictable and random. Bold vertical black arrow represents the arriving of griffon vulture at carcasses. On a total of 100 small scavengers, blue circles represent the number of birds that arrive at carcasses; green circles represent the number of birds that take advantage whereas red circles show those unsuccessful feeding birds. More small scavengers arrived earlier that the griffons at random carcasses in comparison with predictable carcasses. Only at random carcasses facilitatory processes occur i.e. small scavengers that arrive earlier than griffons fed after they open the carcasses.

INTRAGUILD PROCESSES

In random carcasses there was a pattern consistent with a facilitatory process of small scavengers helping griffons to find the carcass because 29% of the small scavengers arriving at random carcasses did so before griffons. Interestingly, 8% of these individuals fed after the arrival of griffons (Fig. 4). However, this process was virtually absent in predictable carcasses where almost all scavengers arrived after griffons and were much less successful on feeding. Modelling procedures (Table 2) confirmed that the probability of “small scavengers” to arrive earlier than the griffon vultures was higher in the random; being particularly elevated for the two species of kites followed by the common raven and the Egyptian vulture. All “small scavengers” arriving before griffons had a low probability of feeding both at predictable and random carcasses. However, “small scavengers” arriving after the griffons had a higher probability of feeding at random carcasses; Egyptian vultures and red kites were the most successful on it, followed by common ravens and black kites.

Table 2. Effects of the type of food (1 stands for random carcasses) and the species on the exploitation patterns of small scavengers most successful on it, followed by common ravens and black kites.

	d.f.	F-value	*P*	
Arriving to carcasses before Gyps fulvus				
Food type (1)	1, 379	6.25	0.0129	
Species	3, 379	18.21	<.0001	*
Probability of feed when arrive before Gyps fulvus				
Food type (1)			n.s.	
Species			n.s.	
Probability of feed when arrive after Gyps fulvus				
Food type (1)	1, 285	14.81	0.0001	
Species	3, 285	3.20	0.0237	**

* Probability rank: Black kite>Red kite>Raven>Egyptian vulture

** Probability rank: Red kite>Egyptian vulture>Raven>Black kite

DISCUSSION

Our findings support that randomness in the distribution of food resources can be a key mechanism maintaining the diversity within guilds and governing complex ecological processes permitting the coexistence of species. Despite different research lines (Hubell 2001; Chesson 2000; Tilman 1994; Harrison *et al.* 2010) have evidenced the importance of the effects of stochastic events on community structure, the precise role of randomness has been rarely documented (Siepielski *et al.* 2010) in relation with how heterogeneity in spatial and temporal patterns of food occurrence may be key for the maintenance of communities (Begon *et al.* 2006; Fuhlendorf *et al.* 2006; Bissonette & Storck 2007).

We demonstrate that food resource randomly distributed favour positive interspecific interactions running in two opposite directions: on the one hand the early arrival of small scavengers will increase the probability of arrival of larger specialists (Buckley 1996; Jackson *et al.* 2008); on the other hand, smaller species benefit from the opening up of carcasses by large vultures (Kruuk 1967; König 1974, 1983, see introduction for more details). The spatio-temporal random nature of carcasses allowed these processes: they lasted for longer time available in the field than those disposed at predictable sites giving time to small scavenger to discover the carcasses earlier than griffons who arrived later and in lower numbers. Then, only at random carcasses small scavengers may obtain food after the arrival of griffons. In consequence, randomly disposed carcasses of domestic ungulates would evoke the conditions in which this assemblage of species co-evolved when scavengers, both specialist and facultative, needs to search for food and develop their own skills to take advantage from a pulsed carrion resource (see Houston 1988). Conversely, when the resource becomes predictable, specialist scavengers (griffons) have the opportunity of arriving early and in large numbers. In these circumstances, griffon vultures can quickly reach a ‘numeric threshold’ at which smaller species are systematically excluded from the food resources (around 200 individuals; see Cortés-Avizanda *et al.* 2010).

Species richness was similar at predictable and random sites but the diversity was clearly lower in the former dropping frequently to zero when the number of feeding birds in the carcass was considered. Henceforth, randomness promotes the increase and/or maintenance of the diversity of the assemblage. Our experimental approach complements previous observations based on punctual observations during short visits to supplementary feeding stations (Cortés-Avizanda *et al.* 2010). The loss of whole diversity at predictable resources was not caused by the arrival of lesser number of species but by the increase in numbers of a single specialist (i.e. the griffon vulture) whose numbers triplicated those found in random locations, and almost completely cancelled the diversity of species that profited from the carcass.

CONSERVATION IMPLICATIONS

The study of the consequences of biodiversity loss upon ecosystem functioning is a hot topic in ecological research (Schulze & Mooney 1993; Kinzig *et al.* 2002; Loreau *et al.* 2002; Naeem *et al*. 2003). It seems intuitive that providing an easier to find (more predictable) and abundant food resource to wildlife should be positive for those species feeding on these resources. In fact, this is the reason behind many conservation measures aimed to increase wild animal populations. However, research has shown that predictable clumped-resources may enhance interespecific competition (Petren & Case, 1996; Kiesecker *et al.* 2001 and references therein). Here we found for the first time that predictability of otherwise random food resources lowered the diversity of a scavenger assemblage because of a monopolization of the resource by the most abundant and dominant species (see also Cortés-Avizanda *et al.* 2010).

It is interesting to note that despite we did an experimental approach, vulture restaurants have produced an increase of griffon vultures throughout the study area in the last decades. Thus, griffons are expected to be also more abundant in random carcasses than would be without the vulture restaurants. Therefore, we suggest that our results of higher diversity at random carcasses would be even more striking without the historical effect of supplementary feeding stations, thus reinforcing the message of our study. More generally, we suggest that for those guilds evolved exploiting unpredictable resources, altering the random nature of the appearance of the resource (e.g. because of supplementary feeding stations) main compromise the viability of these guilds in nature, and ultimately to alter the functioning of ecosystems. Our results clearly point in this direction because of the reduced diversity of scavengers in the vulture restaurants. However, more subtle processes were involved: at predictable carcasses, Egyptian vultures were more abundant but, at the same time, obtained less food (see Table 1). For the other small scavenger species random disposition of carcasses was neutral in terms of individual feeding probability but numbers of birds were always lower at predictable carcasses, which probably preclude that the general positive trends found in favour of randomly placed carcasses did not reach statistical significant levels. However, raw data showed that in general small scavenger species were more abundant and obtained larger food rewards from random carcasses. All these findings indicate that predictable carcasses would act as "ecological traps" (Gilroy & Sutherland 2007) to which these species are attracted despite being very unprofitable. Paradoxically thus, a commonly conservationist practice (i.e. the implementation of vulture restaurants) to recover decimated populations of scavenger may be causing an ecological trap.

It has been stressed the importance of conserving not only single populations and species but also interespecific relationships and processes (Tylianakis *et al.* 2010 and references therein). According to Blondel (2003) resource partitioning often allow species coexistence and the functioning of ecosystems. Therefore, conservation of randomness of resources and the processes associated to its exploitation should be a major goal in conservation practice. From that perspective, in our study case this effect could be more striking due to it has been widely described how the free availability of carcasses in the field is declining, not only by the change in the traditional agro-grazing practices and the new restrictive European sanitary legislation but also because the decline of extensive grazing (Donázar *et al.* 2009a,b; Cortés-Avizanda *et al*. 2010). Studies on the conservation value of communities affected by human activities more commonly invoke processes such as the land use intensification as one of the most important concern of loss biodiversity (Mayfield *et al.* 2010 and references therein). Here, we drawn up on another new consequence of human activities until now unexplored and that may be exerting an important pressure on species distribution, abundance and ultimately guilds composition.

The implications of loss of randomness for wildlife population dynamics and conservation remain elusive. In this sense our results show that although large numbers of birds are recorded when resource is predictable, the proportion of birds that feed successfully is low, demonstrating ultimately that birds are choosing poor-quality places that ultimately could affect the individual fitness. Overall, this fact may outcome in mal-adaptive behaviors that may trigger negative implications for wildlife population dynamics and conservation (Kokko & Sutherland 2001; Schlaepfer *et al.* 2002; Kristan 2003; Battin 2004; Robertson & Hutto 2006). On the other hand, the loss of random resources appearance in the nature may act as an important force breaking the functioning of ecosystems. These findings open new insights on ecological and conservationist studies based on understanding either the distribution or the coexistence of species and encourage considering resource predictability as an important factor driving the viability of populations and their effects upon communities and ecosystems.

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CHAPTER II

Spatial and trophic responses of two transaharian migrant species to changes in resource distribution: a transcontinental approach

ABSTRACT

Migrant populations must cope not only with environmental changes at different biomes, but also with the continuous constraints imposed by human-induced changes through landscape transformation and resource patchiness. Theoretical studies suggest that changes in food distribution can promote changes in the social arrangement of individuals without apparent adaptive value. Empirical researches on this subject have only been performed at reduced geographical scales and/or for single species. However, the relative contribution of food patchiness and predictability both in space and time to the abundance and sociality can vary among species, depending on their degree of flexibility. By means of constrained zero-inflated Generalized Additive Models we analysed the spatial distribution of two trans-Saharan avian scavengers that breed (Europe) and winter (Africa) simpatrically, in relation to availability of feeding sources. In the summering grounds, the probability of finding large numbers of both species increase close to predictable feeding sources, whereas in the wintering grounds, where food resources are widespread, we did not find any pattern of abundances, except for the black kite which aggregates at dessert locust outbreaks. The comparison of diets in both species through stable isotopes revealed that species overlap their diets during summering, but not during wintering. These results suggest that social behaviours observed during feeding activities were linked to the clumped distribution of food resources, which have been ultimately induced by human activities. Our study thus suggests that migrant species can show an adaptive response in their foraging strategies to face the constraints imposed by food availability distribution in both wintering and summering grounds. Understanding these effects is important for predicting the fitness costs and population consequences of human activities on the viability of many endangered migratory species.

INTRODUCTION

The distribution of key resources affects the spatial structure and the social organization of animal populations (Macdonald 1981, 1983; MacArthur & Pianka 1996; Johnson *et al*. 2002). Large aggregations of food may relax intraespecific competition, thus inducing the recruitment of individuals without any apparent adaptive value (Tokeshi 1999; Maher & Lott 2000; Johnson *et al*. 2002; Revilla & Palomares 2002 and references therein). Nevertheless, most studies showing this link between animal distributions and resource availability are theoretical (see von Schantz 1984; Carr & Macdonald 1986; Tokeshi 1999 and references therein). When done, empirical studies were performed at reduced geographical scale (usually local) and/or from a monospecific approach (see Eide *et al*. 2004) so generalizations beyond the population level (guilds and communities) are unsupported.

Migratory species, from invertebrates to vertebrates, develop their vitals cycles in distant biomes, occupying wintering grounds far from their breeding areas (Bowlin *et al*. 2010 and references therein). Explanations proposed to understand migration include variation among species in dependence on temporally and spatially variable food resources (Levey & Stiles 1992; Newton 1995; Chesser & Levey 1998), competitive ability (Cox 1985; Pérez-Tris & Tellería 2002) and life history traits (Greenberg 1982). Recently, some authors have suggested that behavioural flexibility -i.e., the ability of individuals to express distinct behaviours in different contexts through innovation and learning processes (Klopfer 1962; Piersma & Drent 2003; Lefebvre *et al.* 2004) - might also influence the balance between migratory and resident strategies in environments with sharp seasonal changes (Sol *et al.* 2005). Obligate migratory species are logically enforced to respond to changeable conditions when moving from summering to wintering grounds. Within this scenario, however, it is remarkable the lack of studies tracking the response of migrant organisms to large-scale changes in the degree of heterogeneity in the spatial distribution of food resources and its relationship to spatial patterns of distribution and abundance. Recent researches suggest that animals, in particular birds, may develop specific behavioural strategies to compensate for the negative effects of environmental variability (Grimm *et al*. 2005; Wichmann *et al*. 2005). Thus, it seems important to discern whether migrant birds have flexible responses to variations in environmental conditions between summering and wintering grounds, such as changes in the availability of food resources. In addition, this information may be useful to understand large-scale variability in the role of limiting factors on the viability of populations of migrant species of conservation concern (Newton 2004; Sanderson *et al*. 2006).

Here, we examined the spatial response of individuals to changes in the distribution and availability of feeding resources between wintering and summering grounds using as study system two long-lived migratory and facultative-scavenger birds, the black kite (*Milvus migrans*) and the Egyptian vulture (*Neophron percnopterus*). These species have relatively similar foraging strategies and diets (relying on invertebrates and small-medium-sized vertebrates) and, although being territorial during breeding, they can feed together thus potentially competing for similar resources (Donázar 1992; Blanco 1994; authors' unpublished data). Previous studies of our monitored and other western European populations of Egyptian vultures and black kites indicates that individuals winter in the Sahelian region, between Senegal and Mali, as do the rest of the western Palearctic populations (Meyburg *et al*. 2004; García-Ripolles *et al*. 2010; F. Sergio unpubl. data; authors unpubl. data), also overlapping their wintering areas. Throughout their annual cycles, these species exploit food resources that are strongly affected by human economies (Anadón *et al*. 2010 and references therein). Specifically, in the European summering grounds, birds rely on rubbish dumps and supplementary feeding stations (so-called vulture restaurants) created after the prohibition of abandonment in the field of carcasses derived from the extensive livestock (Carrete *et al*. 2006; Cortés-Avizanda *et al.* 2010; Donázar *et al.* 2009, 2010). By contrast, food availability in the African wintering areas is mostly unpredictable, since livestock is under extensive regime and widespread in the field (Anadón *et al.* 2010), with predictable carcasses only available at very few disperse slaughterhouses in the neighbourhood of cities. In sub-Saharan biomes, moreover, there are particular emerging phenomena such as the outbreaks of dessert locusts (S*chistocerca gregaria).* This superabundant pulsed resource plays a key role in this arid ecosystem by providing food for some predators which aggregate in their surroundings (see for details Sánchez-Zapata *et al*. 2007 and references therein). Under this framework, we specifically test whether the variability in the ecological scenarios that these trans-Saharan migrants find may determine parallel or asymmetric responses in their distribution, abundance and trophic strategies in the two visited biomes. We hypothesize that the spatial distribution of our focal species will closely follow that of clumped resources in Europe, whereas in the sub-Saharan Africa the species will be widespread, only showing aggregated distributions linked to pulsed resources (i.e. the dessert locust outbreaks). As a corollary, we predict that trophic overlap between both species will be higher in their summering areas compared to wintering ones.

METHODS

STUDY AREAS

Our study was performed in the Ebro valley (northern Spain) and in the western Sahel region (southern third of Mauritania and the adjacent areas of Senegal and Mali), covering the summering and the wintering grounds of the Egyptian vulture and the black kite populations (Fig. 1). The first region extends over 10,000 km^2 lying between the Pyrenees, the Iberian mountains and the Ebro valley. The area has great orographic and climatic variation, with altitudes ranging between 300 to 2,400 m a.s.l. (Fig. 1). Human population concentrates in valleys with large towns and villages (Cortés-Avizanda *et al*. 2010). This region holds one of the most important European populations of both avian scavengers (Birdlife 2004; Cortés-Avizanda *et al*. 2009; Grande *et al*. 2009). There are 380 breeding territories of Egyptian vultures (ca. 30% of the Iberian population, Donázar 2004) with several communal roosts where hundreds of birds regularly concentrate (Donázar *et al.* 1996, 2010; Birdlife 2007; Cortés-Avizanda *et al.* 2010; authors unpublished data). Although no precise information is available for black kites, the species is abundant with more than 500 breeding pairs (Blanco & Viñuela 2004; Campion 2004; Birdlife 2007; author's unpublished data).

In the western Sahel region, the relief is mostly barren with sparse rocky outcrops. Human population density is low (3 inhabitants/km^2; United Nations World Population Prospects; http://esa.un.org/unpp/). Large concentrations of people inhabits in a few cities such as Nouackchott, Kiffa, Aioun and Nema (Sánchez-Zapata *et al.* 2007). Nomadic shepherds used to inhabit in temporal sparse settlements (Figure 1). In this area there are not breeding populations of the two study species but large concentrations of Western Palaearctic migrants can be found (Anadón *et al*. 2010). Indeed, radiotracking studies carried out in Spain shown that individuals summering in this area are wintering in the Sahel region, so we are confident that we are compiling information about factors affecting the same populations during summering and wintering. For further details on the study areas see Sánchez-Zapata *et al*. (2007) and Anadón *et al*. (2010).

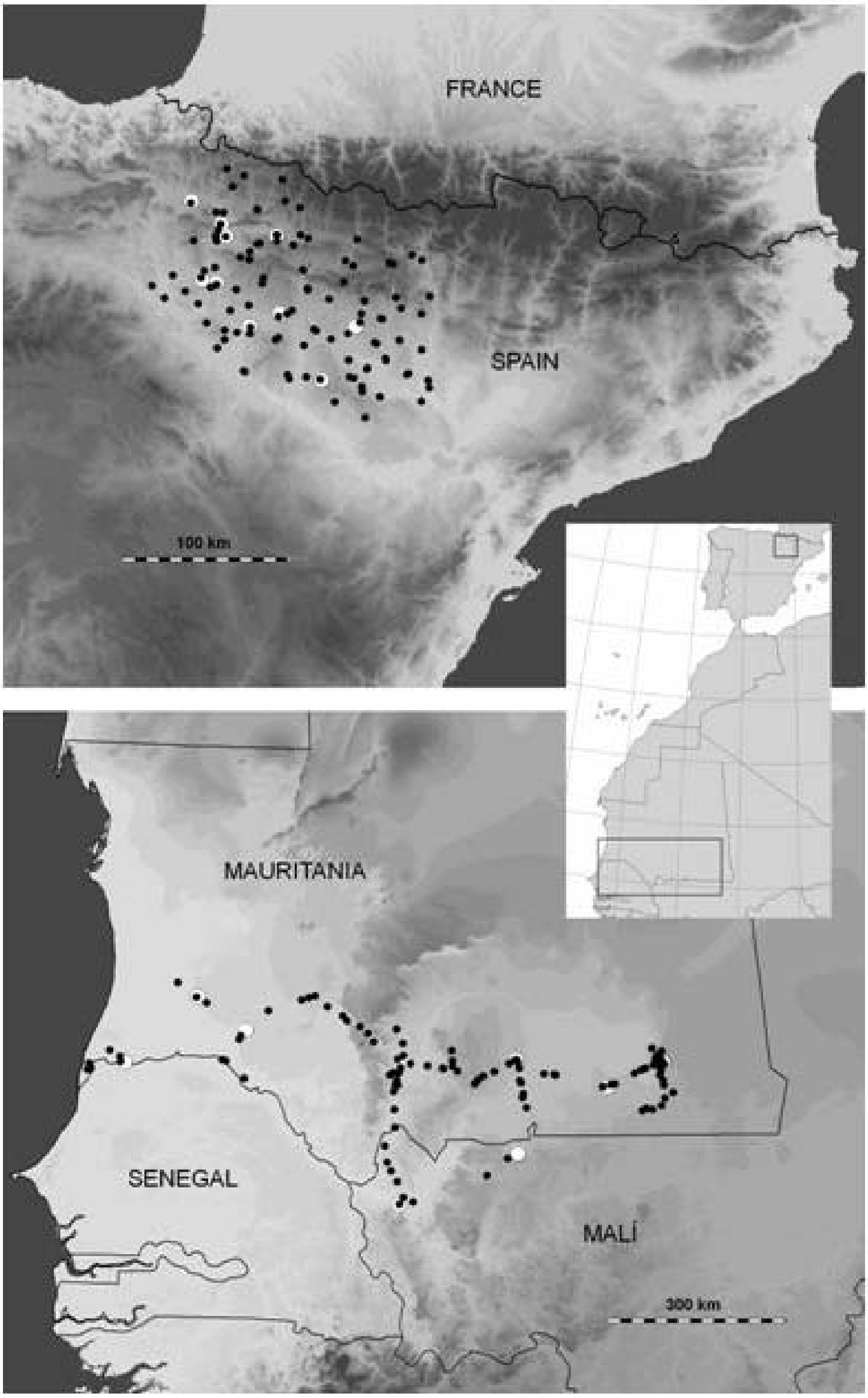

Figure 1. Maps of the studied areas with observation points and predictable feeding sources.

BIRD ABUNDANCE AND FOOD RESOURCE AVAILABILITY

Following established methodologies by Sánchez-Zapata *et al.* (2007), we surveyed the abundance of black kites and Egyptian vultures by means of 30-minutes point counts (Africa: n=42 in January 2004, and n=43 in November–December 2004; Europe: n=64 in May 2005, and n=77 in July-August 2005; Fig.1). Points were randomly distributed along both study areas, and were at least 10 km apart to avoid recounting birds. For each point, we conducted additional 5-km car transects to determine the number of livestock: cattle (*Bos primigenius*), sheep (*Ovis aries*), goat (*Capra hircus*), donkey (*Equus asinus*) and dromedary (*Camelus dromedarius*) in Africa and sheep, goat, cattle, horse (*Equus ferus*) and donkey in Europe.

We also carried out censuses of scavenger birds at predictable feeding sources (three slaughterhouses in Africa, and four 'vulture restaurants' and five rubbish dumps in Europe during 2004-2005). Visits lasted 30 min and in each occasion we recorded the maximum number of individuals observed.

EFFECT OF FOOD DISTRIBUTION AND HUMAN PRESENCE ON THE SPATIAL ABUNDANCE OF SPECIES

Field procedures

To determine whether predictable food source influenced the spatial distribution of birds in both continents, we considered as sample unit the abundance of Egyptian vultures and black kites at each observation point. As explanatory variable, we considered the distance to the nearest predictable feeding source, i.e. nearest town with associated slaughterhouses in Africa, and vulture restaurants and/or rubbish dumps in Europe, calculated by the extension of arcview "Nearest feature" (Jenness 2004). To control for the potential effects of humanization, we included the slope of the terrain at each count point performed in Europe (large towns are situated in flatter areas; see Campión (2004); Cortés-Avizanda *et al.* (2010)) and in Africa, the number of livestock because in rural areas the size of the livestock population is linked directly with number of inhabitants (Anadón *et al.* 2010, authors unpublished data see above). We also took into account the availability of additional trophic resources in Africa such as locust outbreaks. During November-December 2004 there was an important outbreak covering broad regions of Mauritania, Mali, Senegal and Morocco. Before this event the number of locust was very low in the region (see Sánchez-Zapata *et al.* 2007 for details). In consequence, we distinguished counts performed during the dessert locust outbreak (November-December 2004) from those obtained in former seasons (January 2004).

Spatial modelling of count data

Due to the nature of the survey a large portion of sampling points contained a zero count in both continents, which yielded zero-inflated distributions with a larger proportion of zeros than expected from a standard Poisson count process (Barry & Welsh 2002). Zero-inflated distributions are a *mixture* distribution in which a strong probability mass is located around 0 (the so-called 0-atom) and the remaining data behaves as a standard Poisson process, which gives rise to a regular distribution. During recent years several statistical approaches have been proposed for analyzing this particular distribution (e.g., Agarwal *et al.* 2002; Barry & Welsh 2002; Martin *et al.* 2005; Wenger & Freeman 2008). Irrespective of the method, the standard procedure has been to analyze the mixture distribution in a two-stage approach. First, the response is dichotomized into zero and non-zero counts and analyzed using a presence/absence analysis. Then, a second analysis is conducted using only the non-zero data. It is well known, however, that the two-stage approach can very easily lead to conflicting results (Liu & Chan 2010). Thus, we use here a recent and new method for ecological field data dealing with the excess 0's while allowing us to test, in a robust manner, whether the differing spatial resource distribution among continents promotes different spatial patterns on bird distribution. The base model, proposed by Liu & Chan (2010), uses a Generalized Additive Model (GAM), where no functional relationship is *a-priori* assumed in the effects of the covariates on the response (see also Chiogna & Gaetan 2007). However, in our setting the response is assumed to follow a given distribution from the zero-inflated exponential family where the probability of zero-inflation is simultaneously supposed to be some monotone function of the expected response. Therefore, the mixture distribution is analyzed with a flexible, non-parametric model for the effects of some covariates on the response variable with the further, on-line constrain that the probability of zero-inflation in the response is a lineal function of the expectation. The resulting model is the so-called constrained zero-inflated Generalized Additive Model (COZIGAM; Liu & Chan 2010). The constrained nature of the COZIGAM is useful when modelling spatio-temporal animal abundance data because the processes generating the 0 and non-0 inflation are linked through the same behavioural mechanisms (Liu & Chan 2010).

To build up the model, we consider that y_i is a count recorded in a random sampling point of the survey, and x_i is a value of the measured covariate. The mixture distribution, denoted by $h(y_i)$ is then defined as

$$y_i = Y_i \mid x_i : \; h(y_i) = \begin{cases} 0 & \text{with probability } 1 - p_i \\ f(y_i \mid \theta_i) & \text{with probability } p_i \end{cases}$$

where the 0-atom models the zero inflation and the regular distribution (the non-zero portion) comes from an exponential family with probability density $f(y_i \mid \theta_i)$, in our case a Poisson distribution. A constrain is imposed so that the probability of zero-inflation, denoted by p_i, is a monotone function of the expected values of the response variable, denoted by μ_i. Using a logit link function, this restriction is written as

$$\text{logit}(p_i) = \alpha + \delta(\mu_i) \qquad \text{Eqn. 1a}$$

where α is a constant and δ is a parameter measuring the amount of homogeneity in zero inflation. Interestingly, if δ is found to be distinct from 0 this would indicate that the distribution of 0's is not homogeneous, which means that a large proportion of zero counts accumulate along some gradient of the predictor variable. The response, with expected values denoted as μ_i in Eqn. 1a, is modelled non-parametrically with a Generalized Additive Model (Wood 2006). For Europe, this model can be written in a simplified form as

$$\mu = c + \text{s(Latitude, Longitude)} + \text{s(Distance)} + \text{s(Slope)} \qquad \text{Eqn. 1b}$$

while for Africa it would be written as

$$\mu = c + \mathrm{s}(\mathrm{Latitude, Longitude}) + \mathrm{s}(\mathrm{Distance}) + \mathrm{s}(\mathrm{Cattle}) \qquad \text{Eqn. 1c}$$

where c is a parametric constant and s $(\cdot)$ are the smooth functions measuring the non-parametric effects of covariates on the response. The term s(Latitude, Longitude) measures the non-parametric spatial component of the abundance survey (see Liu & Chan 2010). Although a preliminary analysis with a non-parametric spline correlogram (Bjørnstad & Falck 2001) suggested that the abundance data for both species lack spatial autocorrelation, we included the spatial term in eqn. 1c to check whether some spatial residual variation can be detected after estimating the covariate effects.

Eqns. 1b and c were fitted to the dataset for the corresponding spatial unit (Africa or Europe), and we further constructed alternative models by sequentially dropping the spatial term or the terms for the distance to the nearest food source and for human presence. For each covariate effect in eqn. 1 we tested whether a non-parametric ("wiggly") function is preferred over a constant or parametric ("functionally linear") one by testing if the estimated degrees-of-freedom (e.d.f.) of the non-parametric function deviates significantly from a pure parametric one, where the e.d.f is 1 (see Wood 2006). We measured the statistical performance of each model by subtracting the log-likelihood of each COZIGAM. We then calculated the Bayesian Information Criterion (BIC) of each fitted model (see Burnham & Anderson 1998). This information criterion more heavily penalizes over-parameterized models with respect to alternative information criterions, such as the AIC. The model minimizing the BIC was selected as the best model. All the statistical analyses were conducted in R 2.11.1 (R Development Core Team 2010), using the COZIGAM 2.0.3 package (Liu & Chan 2010).

TROPHIC OVERLAP BETWEEN SPECIES

Feather collection

We used stable isotopes analyses to examine the diet overlap of our focal species in Africa and Europe. This methodology has been applied to studies on trophic relationships within vertebrate communities as well as to address specific questions regarding temporal and spatial variability in diets (Fry 2006; Inger & Bearhop 2008). Here, we performed stable isotopes analyses of nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) and carbon ($\delta^{13}C/^{12}C$, $\delta^{13}C$) from feathers (Rubenstein & Hobson 2004; Michener & Lajtha 2007) collected on 41 black kite and 36 Egyptian vulture skins deposited in the Museum of Natural History of Madrid and in the Estación Biológica Doñana (CSIC). Visual inspection and knowledge of moult patterns (authors' unpublished) permitted easily distinguish the feathers recently moulted in African. We only sampled those skins of individuals collected after immediate arrival from wintering areas. From each skin, we sampled two feathers, one grew in Europe and another one grew in Africa.

Laboratory procedures

Stable carbon and nitrogen isotope assays were performed on 0.5 and 1 mg subsamples of feathers that were combusted in an elemental analyzer (Carlo Erba 1500NC) on-line with a Delta Plus XL mass spectrometer (EA-IRMS). Analysis of $\delta^{13}C$ and $\delta^{15}N$ were in triplicate. The overall precision of analyses was ± 0.1 ‰ for $\delta^{13}C$ and $\delta^{15}N$. The stable isotope composition is reported as δ values per mil: $\delta = (R_{sample}/R_{standar} - 1) *1000$, where R= $^{13}C/^{12}C$ for $\delta^{13}C$ or $^{15}N/^{14}N$ for $\delta^{15}N$ values. The international reference standard for $^{13}C/^{12}C$ is PDB (Pee Dee Belemnites, a fossil marine carbonate of biogenic origin) and for $^{15}N/^{12}N$ in the AIR (average of Atmospheric Air).

Analytical procedures

For both carbon and nitrogen, differences in isotopic signatures between the two study species within each biome were tested first for the two isotopes combined (MANOVA), then for carbon and nitrogen taken separately (one-way ANOVA) (see Popa-Lisseanu *et al.* 2008). Values are expressed as means ± SE. The statistical software used was SPSS version 17.0.

RESULTS

BIRD ABUNDANCE AND FOOD RESOURCE AVAILABILITY

Egyptian vultures were detected in 20.6 % of the African (n=121) and in 35.2 % of the European (n=142) point counts, while the frequencies of detection of black kites were

34.7% and 50.7%, respectively. Large numbers of both Egyptian vultures and black kites feeding together were detected at European predictable feeding sources (i.e. rubbish dumps and vulture restaurants), reaching maximums around 73 and 143 birds, respectively. At those places, large numbers of other six different species were also found (see Table 1). At the few African predictable feeding sources (slaughterhouses), Egyptian vultures were absent and only black kites, reaching a maximum of 500 birds. Two raven species were also detected.

Table 1. Abundance of scavenger species (measured as the maximum number of individuals observed per day during all surveys) at European (N=8) and African (N=3) predictable feeding sources. Note that data summarized in this table belongs to this and other studies (Cortés-Avizanda et al. 2010, authors' unpublished data). Focal species are shown in bold.

	Europe									**Africa**		
Species	Rubbish dumps					Vulture restaurants				Slaughterhouses		
Neophron percnopterus	30	34	40	29	73	10	59	58	18			
Milvus migrans	55	41	0	143	100	26	6	1	4	500	300	50
Gyps fulvus	100	20	0	0	35	505	259	357	522			
Gypaetus barbatus	2	0	0	0	0	0	0	0	0			
Milvus milvus	11	24	0	3	15	13	1	2	5			
Aquila chrysaetos	0	0	0	0	0	0	1	0	0			
Buteo buteo	1	0	0	0	0	0	0	0	0			
Ciconia ciconia	0	160	30	0	51	0	0	0	0			
Larus cachinnans	0	130	5	0	150	0	0	0	0			
Corvus corax	60	97	2	2	109	0	5	8	4			
Corvus corone	6	50	0	0	0	0	1	9	0			
Corvus ruficollis										50	1	1
Corvus albus										100	20	100
Pica pica	0	3	0	0	1	3	1	4	0			
N survey days	**6**	**8**	**4**	**2**	**8**	**7**	**12**	**8**	**7**	**3**	**2**	**2**

Availability of food resources was different in summering and wintering grounds. In 91.9% (n=99) of the African transects we detected some kind of livestock while in Europe just only 13% (n=77) of transects had livestock presence (χ^2=107.144, $P < 0.0001$) (Fig. 2). When we considered separately each livestock species, we also detected higher frequencies of presences in transects performed in wintering grounds (Africa:

sheep and goat=78.8%; cattle=62.6%; horse=61.6%; dromedary=36.4%; Europe: sheep and goat=11.7%; cattle=1.3%; N × M exact Test, *P* = 0.0024).

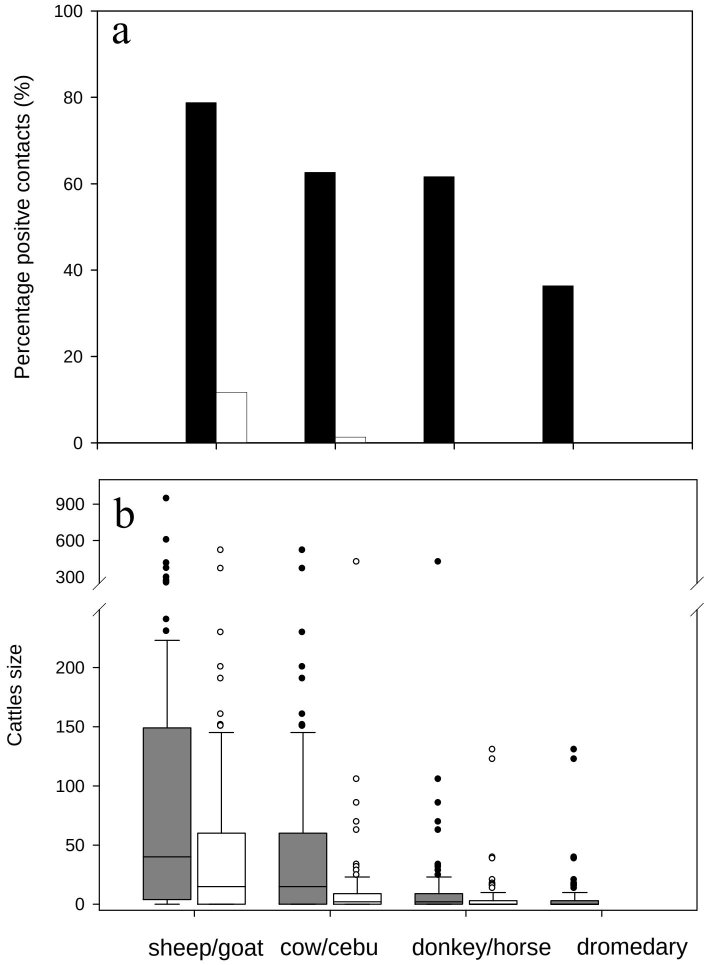

Figure 2. a) Cattle abundance (measured as percentage of positive contacts with cattle during road counts) and **b)** herd size in the summering (Europe; white) and wintering (Africa; grey) grounds of trans-Saharan migrant species. Box plots of cattle sizes represent median values (horizontal line marks), the central 50% of the data (boxes), the range (whiskers) and outliers (dots).

EFFECT OF FOOD DISTRIBUTION AND HUMAN PRESENCE ON THE SPATIAL ABUNDANCE OF SPECIES

The COZIGAMs converged well in all cases after a few iterations of the EM algorithm. A preliminary analysis suggested no differences among seasons in the way that functional forms relate covariates to bird counts. Therefore, we pooled data in a single model for each species and spatial unit. The results of the fitting of each COZIGAM are shown in Table 2. The model selection approach consistently selected models including

Table 2. Results of the fitting of a COZIGAM with Poisson link function measuring the joint effects of distance to the nearest food source and human presence on the spatial abundance of Egyptian Vultures (Neophron percnopterus) and Black Kites (Milvus migrans) in Europe and Africa. Results for each spatial unit are shown for all seasons pooled in a single model. The table shows the proportion of 0 counts (% 0) in the dataset for the dataset of each season. A linear model with a logit link function relates the probability of Zero-inflation (pi) to the covariates through the estimated spatial abundance in the GAM; in this model α is a constant and δ is a parameter measuring the homogeneity of zero-inflation. The column for the "Effect of covariates" contains the estimated degrees of freedom (e.d.f) for each non-parametric term in the GAM, unless a parametric (functionally linear) term is selected; in these cases, denoted with the symbol '*', the parametric estimate is shown instead. Statistically significant terms are shown in bold. † The BIC denotes the Bayesian Information Criterion; the model minimizing this quantity is selected as the best descriptor of the dataset within the pool of fitted models, and is shown in bold type.

Species & season		**Probability of Zero-inflation**		**Effect of covariates**				
	% 0	***α* (± SE)**	***δ* (± SE)**	**Spatial**	**Distance**	**Cattle**	**Slope**	**BIC†**
Egyptian Vulture								
Wintering	78	1.251 (0.810)	-0.979 (0.717)	**21.320**	–	–	–	35.957
Wintering		5.642 (3.251)	**-4.173 (1.979)**	–	**6.302**	**7.718**	–	***5.189***
Wintering		0.600 (0.405)	0.034 (–)	**21.895**	**1.119**	**8.839**	–	81.327
Summering	65	4.195 (2.654)	-1.703 (1.194)	**28.910**	–	–	–	-6.841
Summering		-0.727 (0.653)	**1.639 (0.680)**	–	**2.97**	–	**0.021 (0.010)***	***-143.762***
Summering		**1.389 (0.349)**	3.271 (2.533)	**28.859**	**8.793**	–	**-0.086 (0.044)***	58.645
Black Kite								
Wintering	64	0.301 (0.575)	-0.204 (0.186)	**26.310**	–	–	–	-280.850
Wintering		0.330 (0.458)	-0.273 (0.164)	–	**8.909**	**0.006 (0.001)***	–	***-446.654***
Wintering		0.459 (0.251)	-0.002 (–)	**28.063**	**8.256**	**0.005 (0.001)***	–	-22.526
Summering	49	**1.052 (0.378)**	**-0.403 (0.197)**	**27.970**	–	–	–	-232.916
Summering		0.357 (0.378)	0.215 (0.231)	–	**4.752**	–	**-0.059 (0.013)***	***-321.818***
Summering		**1.408 (0.513)**	0.014 (0.243)	**27.605**	**8.183**	–	**-0.119 (0.036)***	-97.737

distance to the nearest feeding source and human presence for both species in the two continents. Additionally, parametric (functionally linear) terms were selected for the slope in both spatial units for the two species, and the abundance of cattle for the black kite in Africa. Although the structure of the models was similar across species and continents, the profile of the non-parametric functions measuring the effects of the covariates on species abundance differed among continents, but not among species. Only for illustrative purposes, Fig. 3 and 4 depict the spatial non-parametric function fitted to the abundance of Egyptian vulture and black kite in Europe and Africa, respectively. Although these terms were not included in the final model (Table 2), they are useful for devising the spatial distribution of the focal species. After controlling for the effect of human presence in Europe (measured through the variable *slope*), the spatial abundance of Egyptian vultures and black kites decrease sharply with the distance to the nearest feeding source (Fig. 3). Note that this relationship is statistically significant (that is, the partial residual plots do not overlap 0) at distances lower than 40 km for both species. Thus, although it seems that the spatial abundance of both species increase at large distances to the feeding sources, the confidence limits widen as well (Fig 3b and e). This effect is due to a single point in both figures. Moreover, the parameter measuring the homogeneity of Zero-inflation (δ) is positive for both species and statistically significant for the Egyptian vulture (Table 2), suggesting that the 0 counts tend to accumulate at large distances from feeding sources.

In the wintering grounds, however, neither the distance to the nearest feeding source nor the human presence (measured as abundance of *cattle*) seems to have an effect on the spatial distribution of birds (Fig. 4). Additionally, the proportion of zero counts is larger in Africa (Table 2), and Fig. 4a and d suggest that the spatial distribution of birds is relatively more homogenous in Africa than in Europe, particularly for the black kite. It is worth noting that the Fig. 4a depicts the location of only 18 birds in 11 groups scattered in a large surface, so although the Egyptian vulture seems to be more aggregated in wintering grounds, we emphasize that the proportion of 0 counts is very high (78 %) and the average group size very small for this species (1.63 birds per contact). For the black kite, although the effect of the covariates is negligible for both years, the spatial distribution of birds is rather different in years with or without locust outbreaks. In Fig. 5 we plot the non-parametric terms for the spatial component

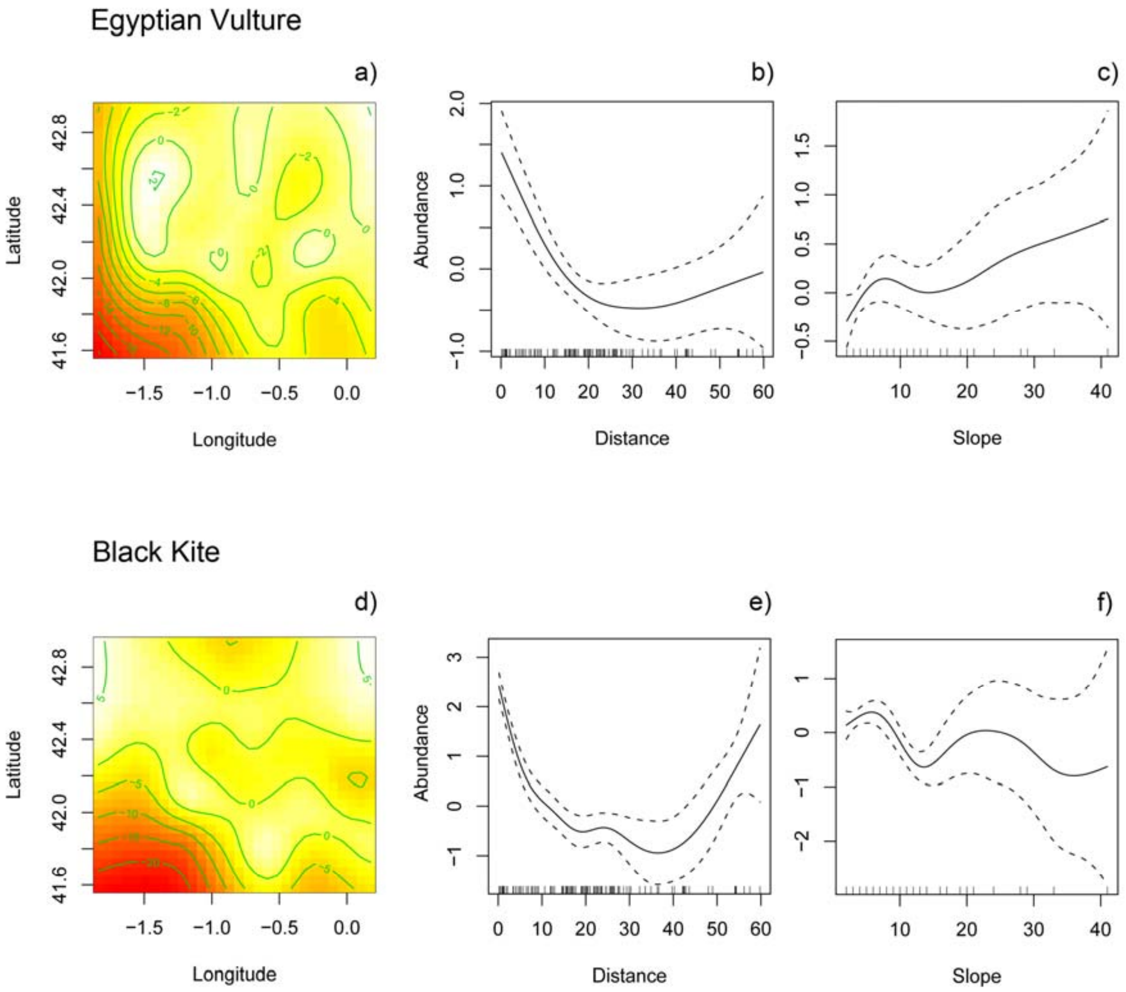

Figure 3. Plots of the additive terms (s (·) in equation 1) of the COZIGAM fitted to the Egyptian vulture **(a-c)** and black kite **(d-f)** in their summering grounds (Europe). In a) and d) the contour plot of the spatial effect in Eqn. 1, s(Latitude, Longitude), is shown. The coloured surface depicts the local probability density of the spatial distribution of counts, from low density areas (red) to high density areas (white). These colours correspond to areas with low and high bird density, respectively. The right diagrams show the partial residual plots for the effect of distance to the nearest food source (vulture restaurants and/or rubbish dumps; **b, e**) and slope of the terrain **(c, f)** on the estimated spatial abundance of each species. The additive function is depicted as a solid black line, while the dotted lines show the 95% confidence intervals. For clarity, the location of each data point is presented as a rug plot along the bottom of each plot. Note that the terms have been scaled to have a 0 mean to make the model identifiable (Wood 2006).

of the abundance of each species in the year without locust (Fig. 5a, c) and in the year with locust (Fig. 5b, d). A shift in the spatial distribution is evident in the black kite, from the first (a scattered distribution) to the second year (an aggregation around the central portion of the study area, in which the population core of the locust outbreaks was located). Average group size increases accordingly, from 6.63 (± 1.53) black kites per positive contact in the year without locusts to 32.47 (± 10.84) birds in the year with locust outbreak (t-test for samples with unequal variances, $t_{19} = 2.09$, $P = 0.029$). In the Egyptian vultures, there are no significant changes in bird abundances associated to dessert locust outbreaks (1.63 ± 0.34 in the year without locusts to 2.50 ± 0.77 in the year with locusts; $t_{18} = 2.10$, $P = 0.317$).

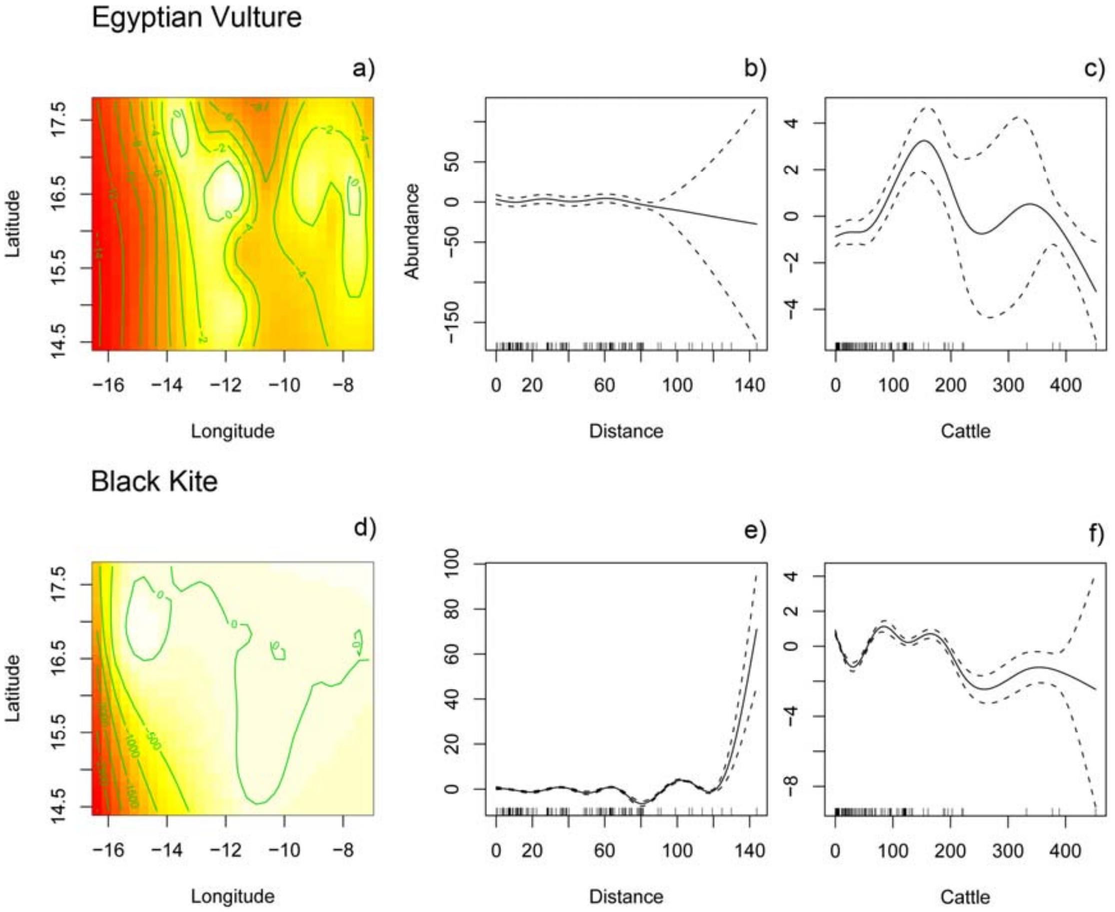

Figure 4. Plots of the additive terms of the COZIGAM fitted to the Egyptian vulture **(a-c)** and black kite **(d-f)** in their wintering quarters (Africa). In **a)** and **d)** the contour plot of the spatial effect is shown. The right diagrams show the partial residual plots for the effect of distance to the nearest food source (nearest town with slaughterhouses; **b, e**) and the degree of humanization (cattle, measured as the number of livestock; **c, f**) on the estimated spatial abundance of each species. See Fig. 3 for further details.

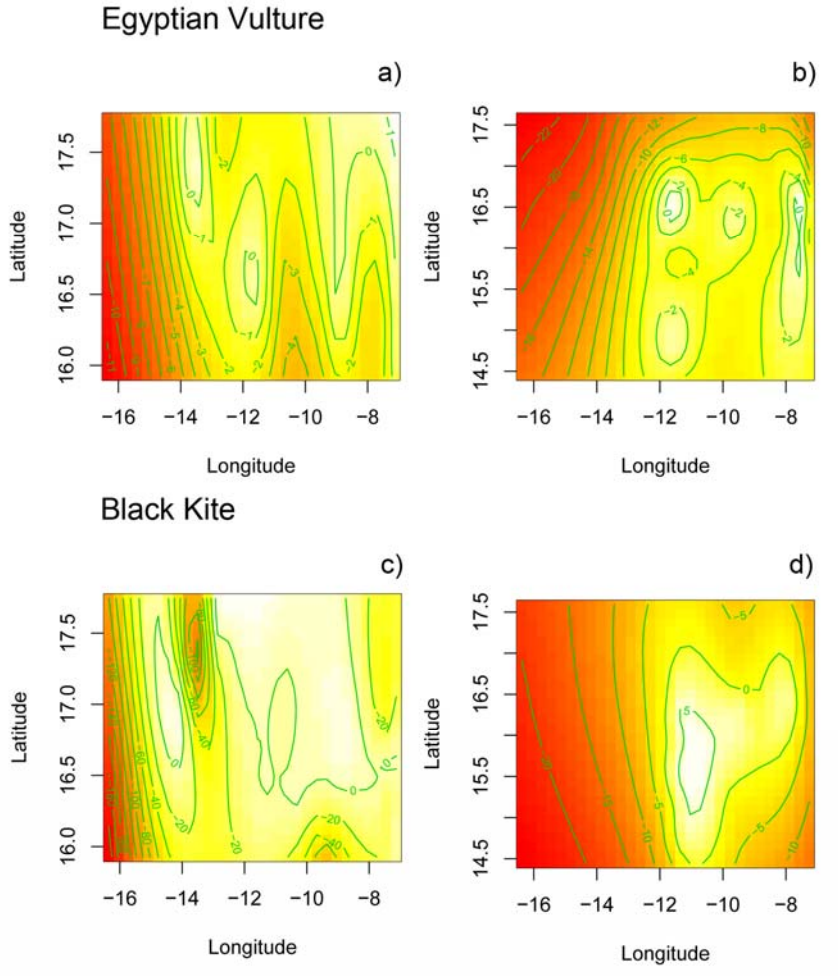

Figure 5. Contour plots of the spatial effect estimated by the COZIGAM fitted to the abundance of Egyptian vulture **(a, b)** and black kite **(c, d)** in Africa in two different years. For this plot only, the effect is shown for each species during the year without locust outbreak **(a, c)** and the year with outbreak **(b, d).**

TROPHIC OVERLAP BETWEEN SPECIES

Isotopic signatures of feathers grew in Africa were different among species (Wilks' lambda = 0.68, $F_{2,47}$= 10.81, $P < 0.001$), but no interspecific differences were detected for feathers grew in Europe (Wilks' lambda = 0.87, $F_{2,24}$= 1.73, $P = 0.2$; Fig. 6). Accordingly, when considering each isotope separately, significant interspecific differences were found among African samples, mainly regarding $\delta^{15}N$ values ($\delta^{13}C$: $F_{1,48} = 4.02$, $P = 0.051$; $\delta^{15}N$: $F_{1,48} = 18.8$, $P < 0.001$), while European samples did not shown significant differences among species in the isotopic signatures ($\delta^{13}C$: $F_{1,26} = 2.86$, $P = 0.1$; $\delta^{15}N$: $F_{1,26} = 2.2$, $P = 0.15$).

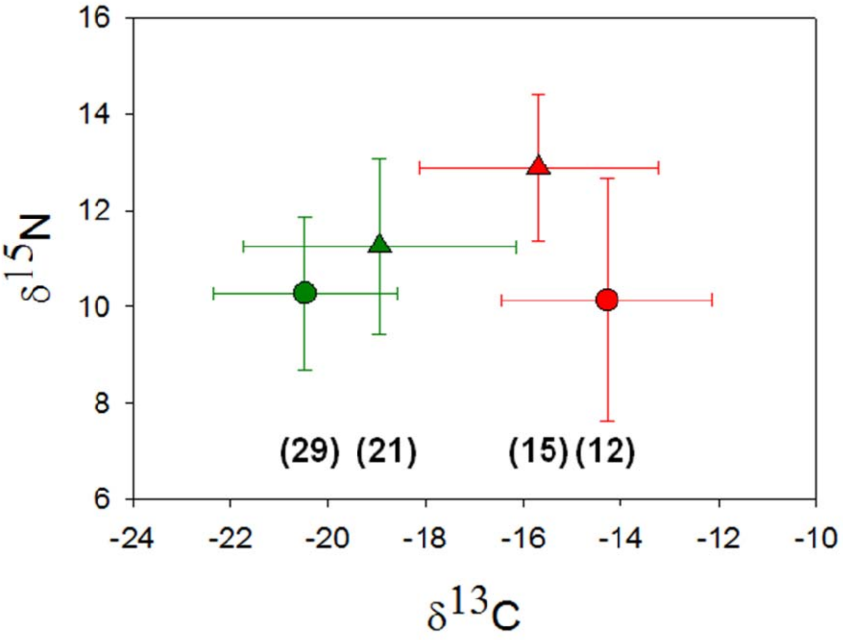

Figure 6. Stable carbon and nitrogen isotope values (mean ± SE, ‰) in feathers of Egyptian vultures (triangles) and black kites (circles) grown in their summering (Europe: green) and wintering (Africa: red) grounds. Numbers in brackets indicate sample sizes.

DISCUSSION

CHANGES IN BIRD ABUNDANCES TRACK CHANGES IN FOOD DISTRIBUTION

Animals can track changes in resource availability and, therefore, modify their foraging strategies adaptively (Stenberg & Persson 2005; Overington *et al*. 2008). In this sense, our results show how trans-Saharan migrant bird populations can exhibit different spatial arrangements depending on the food distributions found in their wintering and summering grounds. Sub-Saharan regions are considered as well-structured ecosystems (Sanchez-Zapata *et al*. 2007 and references therein) with high diversity of live prey, and numerous and diverse herds of domestic livestock widespread in the field (see results for details). European areas, however, are long-term human-modified ecosystems where food resources for vertebrate scavenger species have been subject to different pressures and management decisions that have favoured their patchiness across years. As a consequence of these differences, the same birds must aggregate during summering, when food is clumped and patchy distributed, but can remain widely and near randomly distributed during wintering, when resources are widespread. But changes in bird distribution go beyond the species level, and interspecific trophic overlap also becomes apparent in the summering scenario of resource aggregation. Conversely, when both species track resource in the less managed habitats, they have the opportunity to find and exploit pulsed resources when possible. Indeed, during the desert locust outbreaks, the black kites shift their spatial distribution in a conspicuous way, increasing group sizes markedly. This pattern has been also described for either generalist or specialist species, which shift their diet and movements in response to pulse resources (Ostfeld & Keesing 2000). The spatial distribution of the Egyptian vulture did not change after the appearance of locusts. This fact again remarks that complex and well-structured biomes allows species coexistence through resource partitioning (Schoener 1974; Tokeshi 1999; Begon *et al.* 2006), contrary to the situation found in impoverished uniform landscapes where food resource is less diverse, frequently as a consequence of human-induced transformations.

Variability in the response to environmental changes differ between species, leading to scenarios with different degrees of diet overlap and, consequently, potential interspecific competition (Bolnick *et al.* 2010). Our results show that the diets of our focus species completely overlapped in European summering areas, whereas in the African wintering grounds, they were segregated. It is well-known that stable nitrogen isotopes values show a stepwise enrichment with each trophic level (Rubenstein & Hobson 2004). In our case, there is a large between-species difference in average $\delta^{15}N$ (10.1 *vs* 12.9) during wintering, indicating separated trophic levels. The analyses of pellets of the two species in the study area revealed that black kites relied on a mixed diet of arthropods and carcasses of domestic ungulates whereas Egyptian vultures consume more wild and domestic vertebrates (authors unpublished). Although the information is partial (see e.g. Donázar & Ceballos 1988; Veiga & Hiraldo 1990) these diet differences probably took place also in Europe some decades ago within an scenario of healthier Mediterranean ecosystems, important extensive grazing and low number of predictable feeding points (Donázar *et al.* 1996). On its part, $\delta^{13}C$ values show a slight enrichment with trophic level, but can reveal micro habitat information on terrestrial ecosystems used due to the differential importance in the distribution of (C3) and (C4) plants (Rubenstein

& Hobson 2004; Carrete *et al.* 2009). In our results, the marginally significant differences in stable carbon isotopes in African samples again seems to indicate a higher consumption by black kites of arthropods dependant on C4 herbaceous vegetation (see Sánchez-Zapata *et al.* 2007 for details).

ON THE ADAPTIVE VALUE OF CHANGING GROUPING PATTERNS

The above-described scenarios, where bird populations change their local abundances following resource distribution raise questions concerning the potential adaptive value of living in groups when the resources are clumped. The main advantage of following food distribution is without doubts to guarantee the birds' vital activities. However, less evident consequences can also be important in the long term, such as the possibility of enhancing intra and inter-specific competition when resource is patchy distributed or, conversely, disrupting social interactions when resources are disperse. In particular, for the focal species, several previous evidences suggested that the first possibility is more likely, since the large concentrations of individuals of these and other facultative scavenger species commonly observed at supplementary feeding stations and rubbish dumps in southern European regions (e.g., Donázar 1992; Donázar *et al.* 2009 and references therein) lead to complex social strategies at both, the species and the guild levels. Although further research on social aspects are needed, it seems probably that bird aggregations are just the byproduct of resource dispersion that do not yield evident social benefits while increase negative interactions between individuals (Mönkkönen *et al.* 2004; Robb *et al.* 2008; Carrete *et al.* 2006; Cortés-Avizanda *et al.* 2010).

In conclusion, our results show that the spatial distribution of food might not only affect the behaviour and success of local individuals (Eide *et al.* 2004; Vahl *et al.* 2005; Overington *et al.* 2008), but can also shape the foraging strategies of entire populations, going beyond the species and potentially triggering consequences at multispecies levels. Future research should focus on the output of these strategies in the long term population dynamics of migrant birds. In particular, it would be interesting to focus on the individual response to changeable environment, as well as on its consequences at the population level. Populations composed by individuals behaving different might can have higher probabilities of success under changeable environments that those formed by more homogeneous individuals (Sol *et al.* 2010 and references therein), so under a scenario of global change, this approach can be utile in establishing probabilities of population persistence and conservation priorities.

CONSERVATION IMPLICATIONS FOR TRANS-SAHARAN MIGRANT BIRDS

More than 50% of European birds are trans-Saharan migrants, and many of them show long-term population declines (Sanderson *et al*. 2006; Thiollay 2006), so the identification of potential limiting factors operating at wintering and breeding grounds is a key point to understand their population trends (Sillet *et al.* 2000; Cotton 2003; Newton 2004). Recent studies suggest that mortality rates of migrant birds are mainly determined by factors operating at wintering grounds; in particular, survival rates of short and long-lived species have been positively associated with rainfall in the Sahelian region (Szép 1995; Sutherland 1996; Schaub *et al*. 2005; Grande *et al*. 2009; Mihoub *et al*. 2010). Regarding our results, we found that foraging avian scavengers in Africa follow a distribution pattern very similar to that on which these scavenger species have putatively co-evolved, i.e. environments where food resources are dispersed and sometimes appeared as pulsed events (Houston 1979). However, the Sahel region has degraded during recent decades as a consequence of a severe drought and human activities (see Anadón *et al.* 2010 for review). In this scenario, social and searching strategies as such described in this paper could be scarcely efficient when food resources are highly depleted in space and/or time. Recent evidences support this last point, as conditions faced by Egyptian vultures during wintering periods result in the release of more corticosterone over time than when those individuals were on their summering grounds (authors' unpublished).

In the European breeding areas, landscape transformation and habitat loss have affected the availability of food resources, being considered as major concerns for population viability of many predatory species (Villafuerte *et al.* 1998; Delibes-Mateos *et al*. 2008). In fact, in Europe the few food resources available for avian scavenges are carcasses derived from intensive livestock, which are clumped and predictable disposed at supplementary feeding points (Donázar *et al.* 2009). Interspecific competition which is enhanced at these situations can promote the extinction of a species, even when it is a slow process not likely to be observed on the time scale of most scientific studies

(Mooney & Cleland 2001). Besides ecological aspects of species and individual aggregations (Cortés-Avizanda *et al*. 2010), other constraints such as the spread of illness, veterinarian drugs and other contaminants (Blanco *et al*. 2007; Lemus & Blanco 2009) are also negatively affecting species using these feeding points. Indeed, preliminary analysis show that the detrimental effects of ingested antibiotics and the acquisition of pathogens at feeding points may decrease the health of vultures with a lethal potential, especially in nestlings and fledglings (Lemus *et al*. 2008).

The relative importance of these negative factors operating during summer should be compared to that existing in the African wintering grounds in order to properly assess conservation criteria and priorities. Meanwhile, it should be promoted an appropriate management of trophic resources focused at reducing feeding costs for birds. In this sense, future actions in Africa should focus on reducing the impoverishment of environments, avoiding landscape transformation by human overexploitation. In Europe, new management procedures should be implemented to generate a rather more heterogeneous pattern of food availability for birds (e.g. promoting traditional agro-grazing extensive practices, Donázar *et al*. 2009) thus increasing individual health condition and reducing intraguild competition.

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CHAPTER III

Carcasses increase the probability of predation of ground nesting birds: a caveat regarding the conservation value of vulture restaurants

ABSTRACT

Carcasses not only recruit carrion-eaters, but can also attract facultative scavengers which could predate on species living in the surroundings. At supplementary feeding stations (‘vulture restaurants’) carcasses are available permanently, posing a conservation dilemma: enhancing populations of endangered scavengers might introduce a predation pressure on non-target species. Here, we test if nest predation risk on ground-nesting birds increases near carcasses in Fuerteventura Island (Canary Archipelago). This is an optimal scenario for performing this study because there is a simple community of ground-nesting birds and facultative scavengers; carrion-eaters feed regularly in a unique vulture restaurant but also exploit scattered carcasses of goats. We placed artificial nests along different lines located at variable distances (200m to 34 km) from the vulture restaurant or from single carcasses. Sixty-seven per cent of lines and up to 90% of nests within lines were predated. Predation risk was higher in lines near carcasses that are single carcasses or the vulture restaurant. Thus, our study alerts that choosing the location for vulture restaurants may be the key not only for scavengers but also for the conservation of the species living nearby.

INTRODUCTION

Animal carcasses appear with a variable spatio-temporal predictability (Rose & Polis 1998; Ostfeld & Keesing 2000) and affect ecosystem diversity and functioning (Towne 2000; DeVault *et al.* 2003; Roth 2003; Melis *et al.* 2004). They provide the primary food resource for guilds of scavengers composed not only of specialist but also of facultative carnivore and avian scavengers (Kristan & Boarman 2003; Wilmers *et al.* 2003). These aggregations of facultative scavengers, which are also important predators, can increase predatory pressure in the area surrounding carcasses having profound impacts on prey species (Cortés- Avizanda *et al.* 2009).

Currently, stock-raising and big-game hunting are ensuring that the availability of vertebrate carcasses, an otherwise spatially random food resource, become predictable at certain sites (Wilmers *et al.* 2003; Gilbert *et al.* 2007). A particular case are the so-called 'vulture restaurants' (places with a constant carcass supply) which are increasingly considered key management tools in the worldwide conservation of endangered scavenger populations (Koenig 2006; Swan *et al.* 2006). However, this management action can trigger local scale processes associated with the attractiveness of vulture restaurants for facultative scavengers (Piper 2006). In temperate and warm regions where vulture restaurants are placed within the range of endangered steppe birds (Gangoso *et al.* 2005), they can lead to undesirable predation pressures and therefore to conservation conflicts.

Using as a study model a simple scavenger community in the Canary Islands, we examined whether carcasses (both single and aggregated in a vulture restaurant) increase nest predation risk for steppe birds by attracting facultative scavengers to their vicinity.

STUDY AREA AND METHODS

We conducted the study in the spring of 2006 (26 March to 1 April) on the island of Fuerteventura (Canary Archipelago), where both natural and human-provided carcasses are available (Gangoso *et al.* 2005). Goat herds roam freely on the island and their carcasses become available for scavengers. Moreover, there is a vulture restaurant in the centre of the island (Fig. 1) where goat and pig carcasses (1-4 per week) and slaughterhouse remains (c. 200 kg week^{-1}) are left to provide supplementary food for the endemic endangered Egyptian vulture *Neophron percnopterus majorensis*. Thus, our research was carried out within a scenario in which both predictable and unpredictable carcasses are found. Potential nest predators in the island are native facultative avian scavengers (Egyptian vultures, common ravens *Corvus corax* and yellow-legged gulls *Larus michaellis*); wild carnivores are absent and only a few feral cats *Felis catus* and dogs

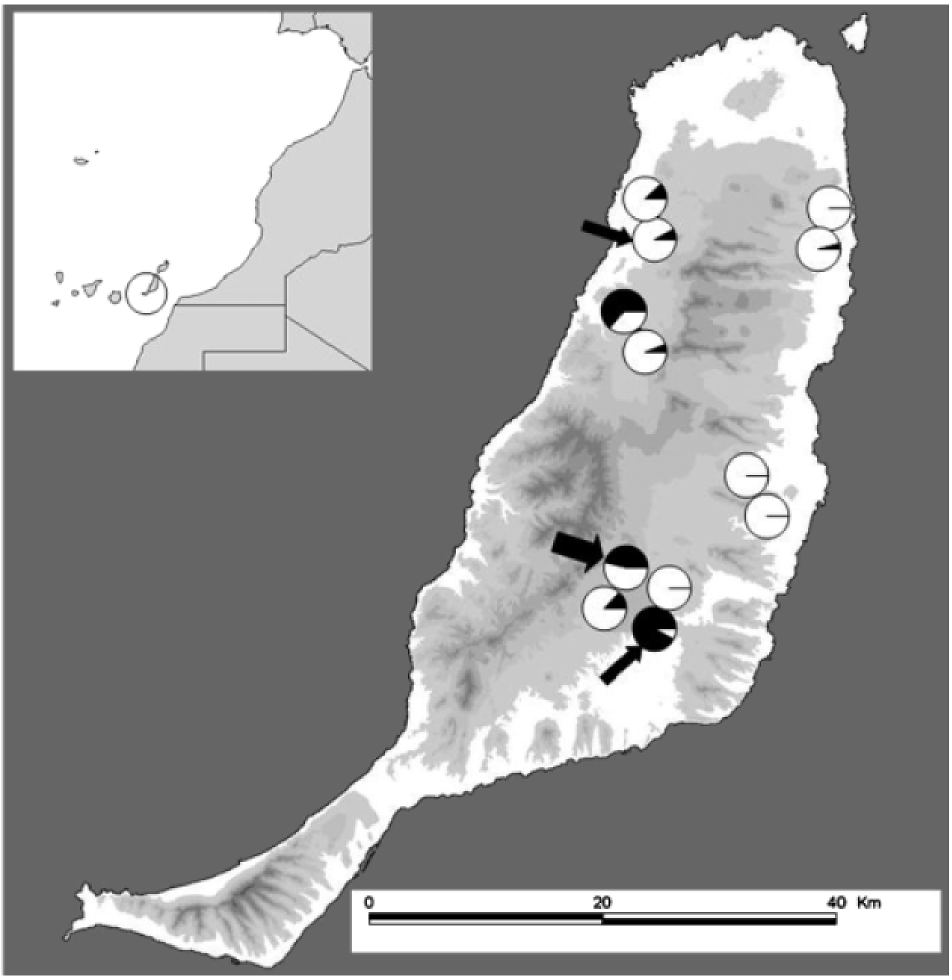


Figure 1. Study area showing the percentage of nest predated (in black) and the presence of fresh carcasses (black arrows; the thickest one shows the vulture restaurant).

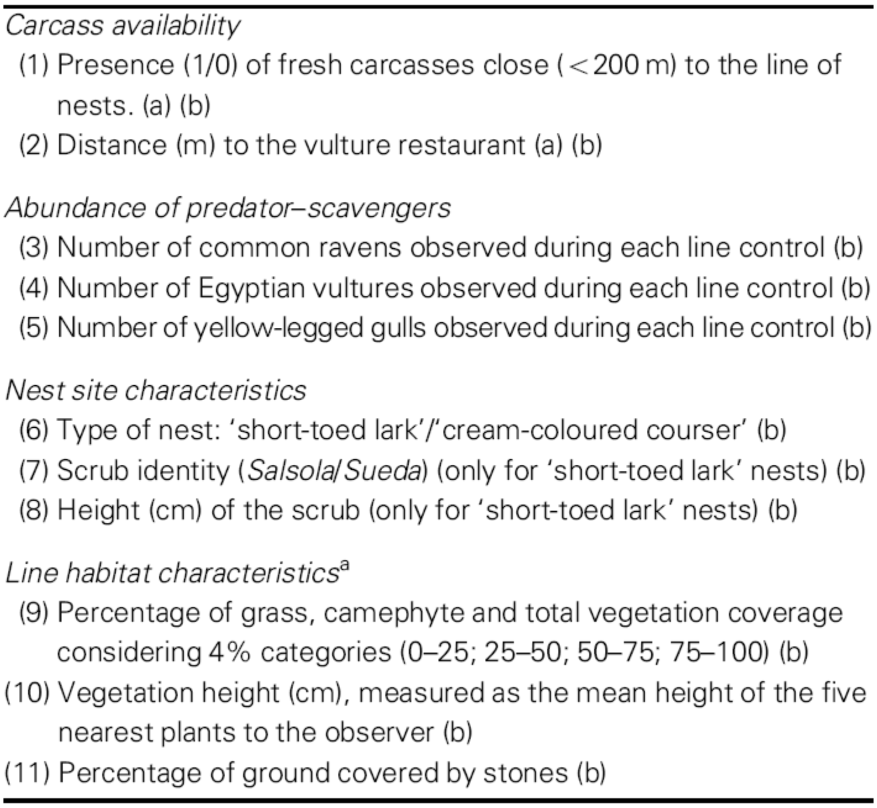
Canis familiaris are occasionally encountered in the vicinity of towns. Ground-nesting species are mainly steppe birds such as lesser short-toed larks *Calandrella* *rufescens*, Berthelot's pipits *Anthus berthelotti* and, locally, cream-coloured coursers *Cursorius cursor*, stone curlews *Burhinus oedicnemus*, black-bellied sandgrouses *Pterocles orientalis* and houbara bustards *Chlamidotys undulata*. Thus, this area constitutes an optimal scenario for testing the hypothesis that aggregations of facultative scavengers around carcasses can increase predation pressure on surrounding passerine nests.

Inferences drawn from data generated by well-designed artificial nest studies can be useful in addressing a number of ecological questions (Moore & Robinson 2004). Thus, we constructed 312 artificial nests imitating those of two steppe species with different nest-building patterns: the lesser short toed lark which builds a typical passerine nest in a shallow scrape under a small shrub, and the cream-coloured courser which lays its eggs in a shallow scrape on bare ground without any nesting material. We placed 25–30 artificial nests separated by c. 30m along 12 lines (312 nests in total) grouped in five different zones at different distances from the vulture restaurant (200–33 500m; Fig. 1) and far from any human settlement. Within each zone the distance between paired lines varied between around 700 and 1500m. Lark nests were simulated by using natural straw, while courser nests were built by just creating a shallow scrape. Within each nest, we put two fresh Japanese quail eggs to imitate natural clutches. Nest positions were recorded with a GPS to avoid visible signs to mark nests. Artificial nests were placed and examined at dawn and dusk to avoid attracting predators. Lines were checked at least once a day over 5-6 days (total exposure time ranged from 53 to 71 daylight hours; mean ± SD: 61.5 ± 6.3). A nest was considered predated when at least one egg disappeared or showed evident signs of damage. During each control we noted the presence and number of facultative scavengers observed near lines (<100m), either perched or flying, as well as carcasses in the surroundings (<200m). Besides those of the vulture restaurant, two fresh carcasses (one goat carcass and one yellow legged gull) were found near different lines (Fig. 1).

We used generalized linear mixed models (GLMM) (Little *et al.* 1996) to relate the abundance of facultative scavengers (link function: logarithmic, error distribution: Poisson, dependent variable: number of Egyptian vultures, ravens or yellow legged gulls per visit) and nest predation (link function: logit, error distribution: binomial, dependent variable: predated and non-predated nest) to the presence of fresh carcasses (single carcasses or aggregated in the vulture restaurant), and distance to the vulture restaurant, while controlling for nest and line characteristics (Table 1).Models were fitted by using

a forward stepwise procedure (Donázar *et al.* 1993), where significant effects ($P < 0.05$) were retained. To avoid non-independence of the data, all models included 'line' nested in 'zone' as a random term.

Table 1. Explanatory variables used in the GLMMs aimed at determining factors influencing **(a)** predator–scavenger abundance, **(b)** the probability of nest predation



Carcass availability

(1) Presence (1/0) of fresh carcasses close (< 200 m) to the line of nests. (a) (b)

(2) Distance (m) to the vulture restaurant (a) (b)

Abundance of predator–scavengers

(3) Number of common ravens observed during each line control (b)

(4) Number of Egyptian vultures observed during each line control (b)

(5) Number of yellow-legged gulls observed during each line control (b)

Nest site characteristics

(6) Type of nest: 'short-toed lark'/'cream-coloured courser' (b)

(7) Scrub identity (*Salsola*/*Sueda*) (only for 'short-toed lark' nests) (b)

(8) Height (cm) of the scrub (only for 'short-toed lark' nests) (b)

Line habitat characteristics[a]

(9) Percentage of grass, camephyte and total vegetation coverage considering 4% categories (0–25; 25–50; 50–75; 75–100) (b)

(10) Vegetation height (cm), measured as the mean height of the five nearest plants to the observer (b)

(11) Percentage of ground covered by stones (b)

[a] Estimated visually following Carrete *et al.* (in press).

GLMM, generalized linear mixed model.

RESULTS

Numbers of common ravens and Egyptian vultures were positively related to distance to the vulture restaurant ($F_{1,57}$=4.31, P = 0.042; and $F_{1,58}$=4.32, P = 0.042, respectively), with maximum numbers (15 common ravens and nine Egyptian vultures) in the closest line. Abundance of yellow-legged gulls was not correlated to the explanatory variables considered.

Nest predation was detected in 67% of the lines, with a maximum frequency within lines of 92% (mean ± SD: 20.0±33.8; n=12; Fig. 1). In all cases the eggs were extracted, broken and eaten in the immediate vicinity of the nest and, when available, the structure of the nests was completely destroyed. On two occasions we discovered common ravens predating on nests in this fashion. Lines with carcass presence showed higher predation rates (8-92%) than their respective paired lines where carcasses were absent (0-12%, see Fig. 1). The probability of nest predation increased with carcass availability ($F_{1,302}$=100.3, P <0.0001) and raven abundance ($F_{1,57}$=4.3, P = 0.0424) but decreased with vegetation cover ($F_{1,302}$=78.0, P < 0.0001). Once carcass presence was included in the model, no other variable significantly improved it significantly. This last result indicates that nest predation risk increases when a carcass appears.

DISCUSSION

Carcasses can play an important role in ecosystem diversity and community structure (DeVault *et al.* 2003). Indeed, we show how fresh carrion, both scattered and concentrated at predictable sites such as vulture restaurants, can increase nest predation risk in their immediate surroundings (c. 500m) due to the aggregation of scavengers which are also facultative predators (or vice versa). This result, obtained on an island with a relatively simple vertebrate community, should be taken into account when considering other regions where much more complex assemblages of carrion-eaters with broad trophic niches are present (Hiraldo *et al.*1991; Travaini *et al.* 1998; Selva & Fortuna 2007). Experiments with artificial nests may not replicate predation rates on natural populations (Weidinger 2001), thus we encourage future research designed to evaluate the effects of carcasses on non-target species breeding near vulture restaurants.

The vulture restaurant is a special case of a carcass site where facultative scavengers concentrate permanently because of a constant food supply. There, the probability of predation risk could be persistent over time, having a stronger effect on the population dynamics of prey species. Although our study was not designed to detect differences between single, scattered carcasses and vulture restaurants, previous studies support this possibility (Kristan & Boarman 2003; Cortés-Avizanda *et al.* 2009). Thus, information regarding populations of sympatric endangered prey species should be taken into account during the design of vulture restaurants to avoid conflicts between conservation strategies. In particular, species of conservation concern such as most of those living in open habitats can be seriously affected by secondary predation (Yanes & Suárez 1996), and their distribution should be considered during planning.

Vulture restaurants are a widespread tool for scavenger conservation, and current legislation often promotes their establishment as the only alternative to extensive ranching. However, they are not a panacea and different studies are showing negative consequences for target populations (e.g. Carrete *et al.* 2006; Blanco *et al.* 2007; Lemus *et al.* 2008) as well as for non-target species (Cortés-Avizanda *et al.* 2009; present results). In the latter sense, whole ecosystem management should be favoured instead of single-species approaches, which can trigger undesirable effects on species of conservation concern.

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CHAPTER IV

Effects of carrion resources on herbivore spatial distribution are mediated by facultative scavengers

ABSTRACT

Carcasses of large herbivores are pulsed resources whose impact on animal communities and ecological processes is poorly understood. In temperate forests, long-lasting ungulate carcasses are a prime resource for many species of birds and mammals during winter. Facultative carrion-eaters also consume live prey, thus potentially leading to unexpected secondary effects on populations of species not directly linked to carcass exploitation. By snow-tracking and direct observations we investigated in Białowieża Forest (E. Poland) whether large ungulate carcasses elicit spatial responses in facultative scavengers and their prey. We found that in the vicinity of carcass sites the probability of the presence of common ravens (*Corvus corax*), jays (*Garrulus glandarius*) and red foxes (*Vulpes vulpes*) increased significantly. Indeed, large groups of the two bird species were exclusively found in those places. Because of these aggregations, the probability of predator–prey encounters (red foxes and brown hares *Lepus europaeus*) was significantly higher near carcass sites. Accordingly, the abundance of hares and other live prey such as red squirrels (*Sciurus vulgaris*) decreased at their vicinities, probably as a consequence of direct killing and/or predator avoidance. This study provides the first evidence of carrion pulses permeating into apparently distant trophic levels, such as herbivores, via facultative scavengers, thus highlighting some unnoticed but relevant effects of carrion resources on community structure.

INTRODUCTION

Pulsed resources – defined as temporary food bonanzas, which then become depleted in time – play decisive roles in ecosystems; in particular, they may provoke functional and numerical responses of consumers and even elicit bottom-up and top-down regulation of populations through different trophic levels (see the review by Ostfeld & Keesing 2000). Animal carcasses can be considered as resource pulses appearing with a variable spatio-temporal predictability (Ostfeld & Keesing 2000; Rose & Polis 1998; Wilmers *et al.* 2003). Examples are available for almost every world biome, from beached whales to mass mortality of a variety of organisms such as ungulates or aquatic vertebrates (Houston 1978, 1979; Selva 2004; Valverde 1967; Wilmers *et al.* 2003). Carcasses may affect the movements and spatial distribution of species (Heinrich 1988; Kamler *et al.* 2004; White 2006) and have relevant effects on ecosystem diversity and functioning, as well as on population dynamics of consumers (Towne 2000; De Vault *et al.* 2003; Roth 2003; Melis *et al.* 2004).

Most research on carrion and scavenging ecology has been focused on guild structure descriptions (Donázar 1993; Selva & Fortuna 2007 and references therein), but little is known on more complex aspects dealing with the consequences of these pulses in the energy flow through food webs (De Vault *et al.* 2003). At high-latitude regions, large carcasses can last for long periods, sometimes the whole winter (Selva *et al.* 2003). They may represent an essential food resource for the community of predator-scavengers (Houston 1978; Wilmers *et al.* 2003; Selva 2004; Selva *et al.* 2005). Under this scenario of food bonanzas, facultative scavengers may also increase their predation pressure on populations of their main prey, a fact that could have further consequences on the population dynamics and structure of prey communities. However, the effects of carrion pulses on trophic levels other than scavengers have remained largely unexplored.

The aim of this work was to examine to what extent large, long-lasting ungulate carcasses can influence the spatial distribution of vertebrate species during winter. We hypothesized that these carrion pulses could have effects on two trophic levels – predators and herbivores – triggered by an increase in the predation risk at the vicinity of carcass sites. Specifically, we first predicted that at carcass sites a higher number of facultative scavengers would be recruited, so the probability of the presence of these species would increase locally. Second, under this scenario, the occurrence of scavenger's main prey was expected to decrease in the proximity of carcass sites. Third, as a measure of predation risk associated with this aggregation of facultative scavengers at carcass sites, we expected that the probability of the simultaneous presence of a predator and its potential prey would be higher at the vicinity of the carcasses. An individual prey will be more likely to encounter a predator at those places where predator density is higher.

We conducted this study in the Białowieża Forest (E. Poland), where large herbivore carcasses, both natural and human-provided, are available for very long periods, especially during the cold season (Selva *et al.* 2003). This region is a well-preserved woodland with a diverse guild of scanvengers comprising more than 30 species of birds and mammals (Selva 2004; Selva *et al.* 2003; 2005; Selva & Fortuna 2007). Apart from carrion, facultative scavengers consume live prey; large predators feed mainly on ungulates, whereas medium-sized predators consume a variety of prey, including lagomorphs, rodents, amphibians and small birds (Jędrzejewska & Jędrzejewski 1998). Thus, this region constitutes an optimal scenario to investigate the ecological consequences of carrion pulses on various trophic levels.

MATERIALS AND METHODS

STUDY AREA

The study was conducted in the Polish part of Białowieża Forest (ca. 600 km^2), located in the Polish–Belarusian borderland (Fig. 1). This is one of the best preserved lowland temperate forests in Europe. It includes a protected area (Białowieża National Park, 100 km^2) and a larger part, which is commercially managed for timber extraction and game hunting. The land is quite flat (135–202 m a.s.l.), with a transitional climate between continental and Atlantic types, with mean temperatures in January and July of -1.4 and 19.7 °C, respectively. Annual rainfall average is 578 mm, and in winter snow cover persists for 60–96 days on average, with maximum depths ranging from 13 to 37 cm (Selva 2004).

The forest is characterized by the simultaneous presence of deciduous and evergreen coniferous forest. The main types are the deciduous oak-lime-hornbeam forest (*Quercus robur, Tilia cordata, Carpinus betulus*); the coniferous forest (dominated by Norway spruce *Picea abie*s and Scots pine *Pinus sylvestris*); and the alderwoods (associated with wet areas, and dominated by black alder *Alnus glutinosa* and ash *Fraxinus excelsior*, see Faliński 1986 for more details). Open areas are rare (only 4% of the forest area) and include village glades, meadows and small clearings.

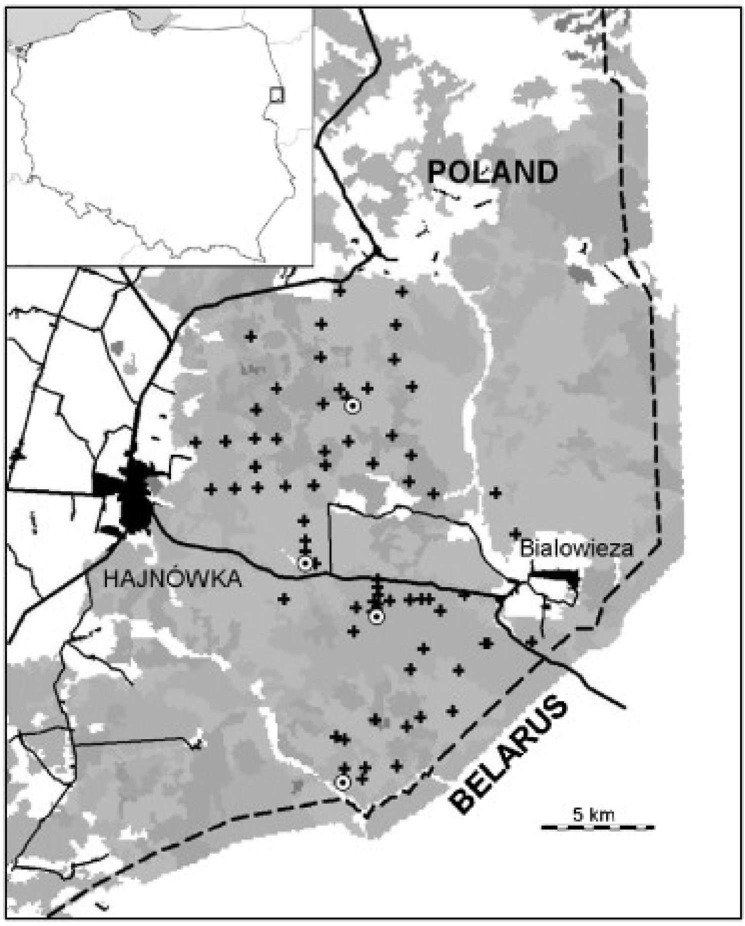

Figure 1. Map of the study area (Białowieża Forest, E. Poland) showing carcass sites (circles, N = 4) and the 1-ha plots (crosses, N = 77) sampled during winter 2006. Gray zones represent forested areas.

The vertebrate community comprises five ungulate species and 40 species of carnivores and raptors, including viable populations of grey wolf and Eurasian lynx (Jędrzejewska & Jędrzejewski 1998; see Table 1). Human density in Białowieża Forest is about 7 inhabitants per km^2, mainly concentrated in one town (Hajnówka) and two villages. Most human settlements are located at the forest edge. The forest is divided into 1×1 km compartments limited by unpaved roads. Only about 50 km of paved roads are intensively used by the public (Theuerkauf *et al.* 2003).

Table 1. Percentage of sampling plots (N = 77) with presence of facultative scavengers and their potential prey comprised at two different buffer zones: in a radius <1 km from the nearest carcass site (N = 16) and in a radius > 1 km from the nearest carcass site (N = 61).

Species	**<1 km**	**>1 km**
Predator-scavengers		
Grey wolf (*Canis lupus*)	6.3	6.6
Red fox (*Vulpes vulpes*)	93.8	45.9
Raccoon dog (*Nyctereutes procyonoides*)	25.0	24.6
Stoat (*Mustela erminea*)	0	1.6
Weasel (*Mustela nivalis*)	37.5	16.4
Polecat (*Mustela putorius*)	6.3	6.6
Pine marten (*Martes Martes*)	62.5	52.4
Badger (*Meles meles*)	0	1.6
Eurasian lynx (*Lynx lynx*)	0	4.9
White-tailed eagle (*Haliaeetus albicilla*)	6.3	0
Jay (*Garrulus glandarius*)	31.3	3.3
Common raven (*Corvus corax*)	37.5	13.1
Prey		
Brown hare (*Lepus europaeus*)	43.8	37.7
Red squirrel (*Sciurus vulgaris*)	43.8	45.9
Wild boar (*Sus scrofa*)	50.0	34.4
European bison (*Bison bonasus*)	18.8	8.2
Red deer (*Cervus elaphus*)	31.3	42.6
Moose (*Alces alces*)	6.2	0
Roe deer (*Capreolus capreolus*)	43.8	36.1

Mammals were determined by snow-tracking and birds through direct observations and/or calls. Note that these are raw data; analyses corrected by spatial autocorrelation are shown in Table 2.

FIELD PROCEDURES

The study was conducted at the end of winter 2006 (20 February – 8 March). We tried to concentrate data collection in time to standardize environmental conditions. Winter 2006 was harsh and weather conditions were typical of the season in these latitudes (Jędrzejewska & Jędrzejewski 1998). In that winter, snow cover (mean depth 27 cm) lasted for 120 days. During the study, the average mean daily temperature was −4.5 °C and ranged from 0° to −23 °C.

Our study focused on 4 carcass sites (Fig. 1) irregularly supplied with carcasses of large wild and domestic herbivores (>300 kg), such as European bison and horses. At three of these sites, carcasses of large ungulates are provided by hunters and foresters almost every winter. During our study they contained: (i) two horses almost totally consumed plus a young bison; (ii) four horses, two fresh and two half-consumed; and, (iii) three half-consumed horses. At the fourth carcass site, established arbitrarily in the midst of the forest, a freshly killed horse was exposed. All carcasses were placed since at least one month before data collection started. We are confident that no other carcasses of large ungulates were available in Białowieża Forest during the study period.

We assessed the presence of mammals and birds across the forest by snow-tracking. We identified footprints in 77 sampling plots of 1-ha size (100 m×100 m) distributed in the forest (Fig. 1), excluding the areas with restricted access. Bird presence was determined by recording sightings and/or calls of individuals in the plot and its immediate vicinity (<200 m). Plots were selected close to forest roads and not more than 8 km away from carcass sites. A higher number of sampling plots were located near the carcass sites to detect the short-distance variability produced by carrion resources. Every plot position was GPS-recorded using the Universal Transverse Mercator System (UTM). Each plot was surveyed once by three observers walking parallel along 100-m transects separated by 50 m from each other. Sampling was done 10–44 h after snowfall (mean=25.4 h, S.E.±14.1) and included at least one night. We only recorded fresh tracks reflecting mammal activity after the last snowfall. Identification was possible thanks to the large experience of one of the observers (NS) in the study area; reference track guides (Mammal Research Institute in Białowieża, unpublished) were also consulted if necessary. Each plot was considered as a sampling unit; the presence/absence of each species was obtained by merging information of the three transects comprised in one plot.

Although we recorded the presence of all mammals and birds (Table 1), further analyses were focused on the main facultative carrion consumers described in Białowieża Forest by Selva (2004), namely the red fox, the raccoon dog, the wolf, the common raven and the jay (Table 1). As to the potential prey species, whose populations could be susceptible to local depletion by the above-mentioned facultative scavengers, we focused on two main groups: ungulates and lagomorphs. Ungulate species, mainly red and roe deer are the main prey of wolf and lynx, respectively. brown hare, red squirrel and small rodents are regularly present in the winter diets of medium and small-sized predators in Białowieża Forest (Jędrzejewska & Jędrzejewski 1998; Table 1). Additionally, these prey are easily detectable by tracks in the snow and are sufficiently abundant to obtain statistical inference from data. Rodent tracks were not considered because, according to Jędrzejewski & Jędrzejewska (1993), the probability of detecting these animals decreases with snow depth.

ANALYTICAL PROCEDURES AND MODEL FITTING

To investigate the patterns of spatial distribution of facultative scavengers and their potential prey in relation to the distances to carrion sites, we performed generalized linear models (GLMs) to describe the factors related to the presence/absence (1/0) of focal species (scavengers and their live prey) using a logit link function and binomial error distribution (McCullagh & Nelder 1989). To evaluate the potential predation risk encountered by prey, we followed the same procedure to model the co-occurrence of the most frequently detected predator and prey species: the red fox and the brown hare. Because predation risk was evaluated as the probability of a hare encountering a fox, this sample included only the plots where hares were recorded. The value of the response variable was 1 if both species were present and 0 if only hare was recorded.

We chose seven explanatory variables. Three variables described characteristics inherent to carcass sites and food supply: (1) distance (m) to the nearest carcass site; (2) amount of fresh carrion available at the nearest carcass sites (<100 kg, 100–250 kg, >250 kg); (3) predictability of the carcass site (predictable: sites 1, 2, 3; unpredictable: site 4). Another four variables evaluated the environmental features: (4) time (hours) elapsed since the last snowfall; (5) dominant forest type within the plot (deciduous, coniferous or alderwoods), obtained from the Forest Inventory and Management Maps (FIMM, see Jędrzejewska & Jędrzejewski 1998); (6) dominant age of the tree stands within the plot (young or mature trees; FIMM); and (7) human disturbance. Values for this last variable followed results by Theuerkauf *et al.* (2003), who determined the limits of wolf, among the most sensitive species, tolerance to humans. We assumed that plots potentially affected by human disturbance were those located at <1 km from public roads and small villages and at <2 km from the main towns (Białowieża and Hajnówka). Otherwise, we considered that plots had a low level of human disturbance.

We accounted for the unknown effects of spatial-related factors potentially affecting the distribution of the studied species (e.g. territorial and/or social behavior) by including in every model a spatial term of the form $bx+by+bx^2+bxy+by^2+bx^3+bx^2y+bxy^2+by^3$, where x is the longitude and y the latitude of the sampling plot. This cubic trend surface ensures that not only linear gradient patterns but also more complex features, such as patches or gaps, which require quadratic and cubic terms to be correctly described, are extracted (for more details see Legendre & Legendre 1998).

Modelling procedures began by fitting the spatial term and calculating the percentage of deviance explained as $100-(100*(\text{deviance}_{\text{spatial term}}/\text{deviance}_{\text{null model}}))$. Then, we fitted the explanatory variables using a forward stepwise procedure that resulted in multivariate models, in which only significant effects ($P < 0.05$) were retained (see Donázar *et al.* 1993). The percentage of deviance explained by each variable was calculated on the basis of the remaining deviance after including the spatial term. Two-degree polynomial terms were fitted if data distribution suggested this. We only tested combinations of variables allowing plausible ecological interpretations.

RESULTS

Red foxes were the most frequently detected mammal, followed by pine martens, red squirrels, red deer and brown hares (Table 1). Common ravens and jays were the dominant bird species, being observed in 18.2% and 9.1% of plots, respectively. All the contacts with these bird species included 1 or 2 individuals, except at the carcass sites, where groups of up to 20 ravens and 10 jays were observed. White-tailed eagles were recorded only in one plot near a carcass site and eleven further species were detected in our study plots (Table 1).

Table 2. Generalized linear models for the probability of detecting predator-scavenger species and their potential prey in the sampling plots

Species	Variables	Estimate	SE	*p*	%Deviance final model	%Deviance spatial term
Scavengers						
Red fox	Distance to carcass site	$-3.0E^{-4}$	$1.0E^{-4}$	0.0355	16.43	74.55
Common raven	Distance to carcass site	$-6.0E^{-4}$	$2.0E^{-4}$	0.0026	19.66	36.85
Jay	Distance to carcass site	$-4.6E^{-3}$	$2.6E^{-3}$	0.0002	65.51	56.33
Raccoon dog	Hours snowfall	$9.82E^{-2}$	$4.4E^{-2}$	0.0071	44.36	80.78
Pine marten	Forest type[a]			<0.0001	30.04	40.67
Prey						
Brown hare	Distance to carcass site	$3.0E^{-4}$	$2.0E^{-4}$	0.0226	17.12	70.51
Red squirrel						
Model 1	Hours snowfall	$6.45E^{-2}$	$2.95E^{-2}$	0.0209	33.64	81.17
Model 2	Distance to carcass site	$3.0E^{-4}$	$2.0E^{-4}$	0.0453	31.08	87.85
Wild boar	Hours snowfall	$6.43E^{-2}$	$2.73E^{-2}$	0.0120	11.20	38.54
Red deer	Forest type[a]			0.0013	58.17	40.72
	Hours snowfall	0.25	$9.12E^{-2}$	0.0039		

[a] Alderwoods > deciduous forest=coniferous forest.

PATTERNS OF SPATIAL DISTRIBUTION OF FACULTATIVE SCAVENGERS AND THEIR POTENTIAL PREY

Model fitting revealed that the probability of presence of red foxes, common ravens and jays increased significantly in the proximities to carcass sites; conversely, brown hares and squirrels showed the opposite trend (Table 2). The time elapsed since the last snowfall positively affected the probability of detecting raccoon dogs, wild boar, red deer and red squirrels. Furthermore, for this last species an alternative model including the distance to the nearest carcass site was obtained. Finally, the type of forest affected the probability of encountering tracks of pine martens and red deer. The spatial term explained high proportions of the total variability in the data set, reaching high values in the red squirrel (>80%), the raccoon dog (80.8%), the red fox (74.5%), and the brown hare (70.5%). Once this effect was accounted for, models explained between 11.2% and 65.5% of the remaining deviance (Table 2).

Species whose models did not show significant effects are not shown. The percentage of the initial deviance explained by the final model and the spatial term are also indicated. The spatial term was included into every model, but detailed results are not shown for simplicity. Models were fitted under binomial errors and logit-link function.

EVALUATION OF THE PREDATION RISK OF LIVE PREY

Simultaneous tracks of brown hares and red foxes were found in all plots within 1 km radius from carcass sites (100%, N = 7 plots), but only in 18 plots placed >1 km away (25.8%, N = 70) (see Fig. 2). The probability of encountering a predator with predator was higher for those hares living closer to carcass sites. The model revealed that the spatial term accounted for 77.0% of the initial deviance. After accounting for spatial effects, the final model explained 59.2% of the remaining deviance and included a single explanatory variable (distance to the nearest carcass site, estimate: $-2.5*E^{-3}\pm9*E^{-3}$, $P = 0.0174$).

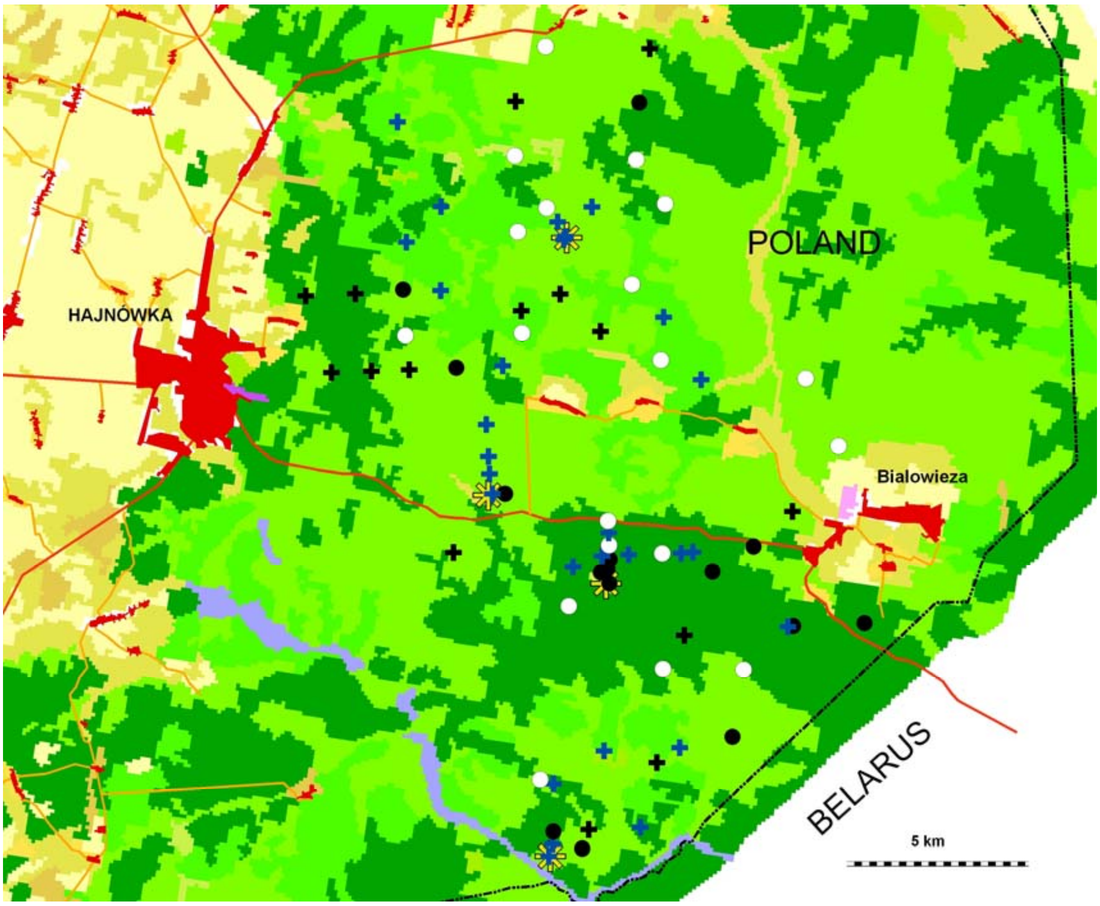

Figure 2. Study area showing the location of carcass sites (yellow asterisks) and study plots with records of hare only (black cross), fox only (blue cross), hare and fox simultaneously (black dots), and without presence of these two species (white dots). The background is based on the CORINE Land Cover Database (CEC.1991. CORINE Land Cover. Commission of the European Communities: ECSC-EEC-EAEC, Brussels, Luxembourg).

DISCUSSION

Our study stresses the role of carrion pulses in structuring local vertebrate communities. These pulses can not only induce spatial changes in the local densities of carrion consumers, but also may indirectly affect other trophic levels. Here, we demonstrate both an increase in the presence of facultative scavengers and a decrease of their potential prey in the vicinity of long-lasting carcasses. This effect was significant, even when taking into account the influence of the spatial autocorrelation term which explained up to 80% of the variability in the data set, revealing variable patterns of distribution among focal species. The main facultative avian scavengers, common ravens and jays, tended to aggregate in the vicinity of carcass sites. Their numbers decreased sharply with the distance to these places. Both species have shown excellent abilities to track and exploit these kind of resources (Houston 1979; Heinrich 1988; Wilmers *et al.* 2003). Especially non-breeding ravens, which congregate in communal roosts and actively recruit other ravens at food bonanzas, exploit carrion resources over the whole study area (Rösner & Selva 2005). Among mammals, the red fox was the only species whose presence increased near carcass sites. Red foxes have a flexible spatial organization and it is known that food outbreaks can cause changes in the territorial organization and space use of different carnivores (Baker *et al.* 2000; Revilla 2003; Kamler *et al.* 2004).

Carrion pulses indirectly affected another trophic level, the herbivores. As predicted, the presence of some prey species, especially the brown hare, was less likely near carcass sites, where they suffered from higher probability of encountering predators. After rodents, hares are the most important prey for red foxes in Białowieża Forest (Jędrzejewska & Jędrzejewski 1998). Fox and hare tracks coincided significantly more often close to carcass sites, suggesting a higher risk of predation there. These effects were evident even when accounting for the spatial autocorrelation, type and age of the forest, and time elapsed after the last snowfall. The observed pattern of spatial distribution in brown hares may be explained not only by a differential predation pressure but also by hare displacement to safer areas. In spite of their high degree of residence, lagomorphs may also abandon their territories when they are highly disturbed by predators (Pielowski 1972). In this respect, a total of 19 species of potential predators, including those modelled in this study, have been detected at ungulate carcasses in Białowieża Forest (Selva 2004). Many of these predator-scavengers include hares and red squirrels in their diets (Jędrzejewska & Jędrzejewski 1998; Laudet & Selva 2005). Thus, the pressure exerted by the whole predator community may also contribute to the effects observed on prey species.

Contrary to our expectations, we did not find a clear effect of carrion subsidies on wolf, a top-predator which includes carrion in its diet (e.g. Jędrzejewski *et al.* 2002). This could be explained by the fact that Białowieża Forest is a well-preserved ecosystem, where wolves exploit a diverse and abundant ungulate community and do not have to rely on winter carrion. Probably as a consequence of this, the distance to carcass sites did not influence the presence of roe deer, red deer and wild boar, all of them potential prey of wolves in the study area (Jędrzejewski *et al.* 2002). Additionally, the fact that top predators were not attracted to carcass sites may release other carnivores, particularly foxes, from interference competition with wolves, also contributing to the higher presence of this meso-predator near carcasses (Linnell & Strand 2000; Terborgh *et al.* 2001).

Forest type did not influence much the presence of the study species, only affecting red deer and pine martens, which were more frequently detected in alderwoods. As one would expect (see Alexander *et al.* 2006), the time elapsed since the last snowfall influenced the probability of presence of mammal species (see Table 2). The raccoon dog, although a frequent scavenger, was rarely detected during our study, probably due to its long periods of inactivity in winter, which reduces significantly its presence at carcasses during severe weather conditions (Selva *et al.* 2005).

To sum up, the long duration of large herbivore carcasses observed in our study area determines spatial changes in the distribution of vertebrates belonging to two trophic levels. This phenomenon may be more pronounced at high latitudes, where cold temperatures during long winters are retarding the activity of bacteria, fungi and invertebrates (De Vault *et al.* 2003). Additionally, these effects might be more evident in cold biomes, where there is a lack of specialist carrion-feeders, which quickly locate and deplete food resources and which, being unable to kill, cannot exert any predation pressure on other vertebrate populations (Houston 1979; Donázar 1993). Finally, from our results it could be hypothesized that carrion resources may trigger top-down (from predator-scavengers to their prey) and bottom-up (from carrion resources to facultative scavengers) regulation processes, at least at local scales. As it happens with other pulsed resources, carrion may also permeate through food webs and affect other trophic levels. In this sense, it would be necessary to investigate whether the effects of carrion pulses could extend over further trophic levels (e.g. producers) and elicit trophic cascades (Polis *et al.* 2000). More research on the effects of carrion resources on the functioning of ecosystems is necessary.

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CHAPTER V

Dietary shifts in two vultures after the demise of supplementary feeding stations: consequences of the EU sanitary legislation

ABSTRACT

Among vertebrates, specialization in scavenging has appeared only in “true” Gyps vultures, which usually base their diet almost exclusively on carcasses of medium and large-sized mammals, whereas all other scavengers rely on broader ranges of prey. The availability of food for scavengers in Western Europe has not been limited during recent decades permitting the existence and growth of huge vulture populations. From 2000 onwards, however, EU sanitary legislation has progressively limited the abandonment of dead animals in the field resulting in a sudden reduction of food availability with unknown ecological and conservation consequences. Here, we examine the dietary response of a tandem of carrion eaters, the griffon vulture (*Gyps fulvus*) and the Egyptian vulture (*Neophron percnopterus*), showing different degrees of dietary specialization. Our results showed that after the reduction in numbers of supplementary feeding stations (vulture restaurants) the niche breadth of the griffon vulture has broadened and now includes significant amounts of wild rabbits (*Oryctolagus cuniculus*) and garbage. The diet of the Egyptian vulture, on the contrary, did not vary substantially. The diet overlap showed patterns probably conditioned by interspecific competition and the progressive exploitation of unpredictable carcasses. On a short-term scale, consequences for smaller scavengers could be negative due to the monopolization of resources by the dominant and much more abundant griffon vulture, however in the long-term all guild species would benefit from the exploitation of unpredictable carcasses, which could enhance the possibilities of coexistence.

INTRODUCTION

Coexistence of species exploiting the same resource is facilitated by heterogeneous environments, which allow differential use of patches with variable environmental features and resource availability (Brown *et al.* 1994; Wauters *et al.* 2002; Carrete *et al.* 2005; Stephens *et al.* 2007). Within those guilds embracing species having carnivore food habits, the diversity of the diet may be also based mainly on the variability in size of the prey (Begon *et al.* 2006). In the case of carrion-eater guilds, the degree of sharing of common resources (carcasses) depends on morphological and behavioral traits (Mundy *et al.* 1992; Hertel 1994; Hertel & Lehman 1998). Thus, in each geographical region, there is one or two species of “true” scavengers (“Gyps” vultures and some Cathartidae in the Old and New World, respectively); their morphological adaptations and their social behavior allow these vultures to specialize in the consumption of large carcasses (Houston 1983; König 1983; Wallace & Temple 1987). On the contrary, other scavengers are more polyphagous and, although they also exploit large carcasses, they invariably consume a number of small and medium-sized prey (Hiraldo *et al.* 1991a; Mundy *et al.* 1992; Travaini *et al.* 1998). When several species concur at the same carcass, coexistence is made possible on the basis of resource partitioning, involving facilitatory and competitive processes still not well understood and apparently dependent on constraints linked to the species' life-history strategies and local conditions inherent to each carcass (Kruuk 1967; Wallace & Temple 1987; Mundy *et al.* 1992; Margalida *et al.* 2009). Facing scarce resources, competitive displacement may appear to permit the monopolization of the food source by the most aggressive (and eventually abundant) species (Hiraldo *et al.* 1991b).

Given the scenario of a global vulture crisis (Koenig 2006), it is remarkable that the Iberian Peninsula and in particular, Spain, still holds the largest populations of avian scavengers in Europe and probably in the Old World (BirdLife International 2008; Margalida *et al.* 2009). This is the result of both legal protection and high food availability. During the second half of the 20th century, food availability was well above that required to maintain the scavenger populations leading to a spectacular increase in population size, especially that of the griffon vulture (around 500% between 1979 and 1999; Donázar & Fernández 1990; Parra & Tellería 2004; Del Moral & Martí 2001). This situation was exacerbated by a failure to comply with sanitation laws enforced since the 1950s which forbade the abandonment of carcasses in the field

(Donázar *et al.* 2009a). In 1999, bovine spongiform encephalopathies (BSEs) brought about strict EU legislation aimed at the elimination of animal by-products (Tella 2001). As a consequence, state and regional administrations reinforced measures requiring farmers to remove or destroy the remains of dead livestock (Donázar *et al.* 2009a). Such laws were implemented from 2000 onwards but they have been much more strongly enforced since 2005. Consequently, after decades of high food availability for scavengers, there was a sudden decrease in the number of carcasses abandoned by farmers both in the field and in supplementary feeding stations "vulture restaurants" (see Camiña & Montelío 2006; Donázar *et al.* 2009a). Further EU regulations have allowed the possibility of maintaining some feeding stations aimed to conserve vulture populations, but the number of these places and the amount of food supplied are still very low in relation to population size.

In our study, we examined the impact of recent shortterm changes in the abundance and distribution of resources in a system with two scavenger species: the griffon vulture (*Gyps fulvus*) and the Egyptian vulture (*Neophron percnopterus*). Both are members of the same scavenger guild but present a clear trophic segregation (König 1983). The griffon vulture is a large (ca. 10,000 g) specialist whose diets based on medium and large-sized ungulate carcasses whereas the Egyptian vulture (ca. 2,000 g), although also exploiting large carcasses, consumes high frequencies of small and medium-sized vertebrates, and garbage (see Donázar 1993; BirdLife International 2008). We hypothesized that the progressive disappearance of food resources linked to large ungulate carcasses (swine, sheep) has provoked asymmetric changes in the diet of the two scavengers. Specifically, we predicted that the trophic specialization of the griffon vulture would lead to few changes in its diet following the decrease in food availability; on the contrary, the Egyptian vulture would respond according to these variations, increasing the consumption of alternative prey.

MATERIALS AND METHODS

STUDY AREA

Our study was carried out between 2005 and 2008 in Navarre and Aragón, Northern Spain (Fig. 1). This region is characterized by a relatively abrupt relief (300–1,500 m in altitude) and variable climate (300–800 mm of annual precipitation). The landscape is mostly dominated by agriculture (cereals, irrigated fields) and pasturelands with some forests occupying slopes and mountains (see Donázar *et al.* 1996a for more details). The breeding populations of griffon and Egyptian vultures were estimated in 2004 at around 2,400 and 380 pairs, respectively. In 2005, there were around 250 feeding stations or "vulture restaurants" established at which dead animals were regularly disposed for consumption by avian scavengers. Most of these feeding stations were associated with intensive swine farms and, to a lesser extent, sheep raising. Although the closing of the feeding stations began in the study area prior to 2005(Camiña & Montelío 2006), the main quantitative change took place after this date. Thus, during the spring and summer of 2007, following EU legislation, most of the feeding stations in Aragón (western study area) were closed. During the autumn and winter of 2007, similar measures were taken in Navarra (eastern study area). Currently, large carcasses are only available in some feeding places (less than 25 in the entire study area). Apart from this, some owners of either extensive operations in remote areas (mountains) or small intensive farms continue to abandon carcasses in the field though these are minimal in comparison to those that existed before the EU legislation. Overall, it has been estimated that more than 80% of the formerly existing supplementary feeding stations were closed in the study area between 2007 and 2008; thus, only a third of the requirements of the vulture populations would be covered by the remnant vulture restaurants (Donázar *et al.* 2009a; Regional Governments, unpublished data).

FIELD PROCEDURES

Pellet collection was carried out in communal roosts existing in an area of around 5,000 km2 located around Ejea de los Caballeros (420750N, 10820W, Ebro valley; Fig. 1). During the summers (July–August) of 2005, 2007, and 2008 we collected pellets of griffon vultures in four communal roosts. They were located in cliffs and trees on abrupt slopes. During the same period, we also collected pellets of Egyptian vultures in three communal roosts placed in woody areas. Two of these roosts (A and B) were associated with predictable food resources (intensive farm areas and garbage dumps) and the third (C) was in an area with high densities of wild rabbit (*Oryctolagus cuniculus*) and extensive sheep farming; immature and adult birds were observed regularly in all these roosts (see Donázar *et al.* 1996a for more details). Three of the roosts (A, B, and C) were shared by the two studied species, however, within roosts, well-separated places were used for perching which permitted us to identify the species that had cast the pellet. Because all the samples were collected at the end of the breeding season, our data samples can be considered as representative of the food habits of these scavengers during the summer (last part of the reproductive period, when the main roost are formed, Donázar *et al.* 1996a). It should be noted that the population of griffon vultures is sedentary whereas the Egyptian vulture has migratory habits, arriving in March and leaving the region in September (Donázar 1993). The pellets were collected on a single day in each location and all were fresh and/or not dismembered. Hence, it can be inferred that pellets were deposited in the weeks prior to the collection. All the vulture roosts were monospecific, known from observations done during longterm monitoring of these populations (see e.g., Donázar *et al.* 1996a; Grande 2006; Cortés-Avizanda *et al.* 2009). Hair, bone, feathers, and scales were used to identify prey remains by comparison to a reference collection. For the griffon vulture and with the purposes of diet quantification, we considered the following prey categories: wild rabbits, sheep (*Ovis aries*), swine (*Sus scrofa*), undetermined ungulate (Bovidae, Equidae, and Cervidae), carnivores (Carnivora), poultry (*Gallus gallus*), and garbage (indicated by the presence of plastic, glass, etc.). For the Egyptian vulture, we considered the same categories and, in addition: rodents (Rodentia); undetermined birds (Aves), insects (Coleoptera), and maggots (Diptera; corresponding to carrion-eater species and not related to pellet decomposition). As is habitual in scavenger diet studies and because bones rarely appeared in pellets, we did not calculate minimum numbers. Alternatively, we estimated the frequency of occurrence of each prey species (percentage of the total number of pellets in which the prey was detected) (see e.g., Hiraldo *et al.* 1991b; Lambertucci *et al.* 2009). Although pellet analyses may present some biases (in particular due to the underestimation of items with soft tissues) it is a valid procedure to compare diets of species having parallel food habits as is the case of scavengers (see Hiraldo *et al.* 1991b; Kelly *et al.* 2007, and references therein).

ANALYTICAL PROCEDURES

We examined the changes in diet composition of griffon and Egyptian vultures during three periods:

1. Year 2005, when the availability of feeding stations was high.
2. Year 2007, after the closing of the feeding stations located in the eastern study area (Aragón).

3. Year 2008, after the closing of the last remaining feeding stations, located in the western study area (Navarra).

We used Generalized Linear Models (GLM; McCullagh & Nelder 1989; link function, logit; error distribution, binomial) to detect interannual changes in the probability of occurrence of each prey category in the diet of griffon vultures. We considered each pellet as a simple unit and the presence/absence (1/0) of each prey as a response variable (link function, logit; error distribution, binomial). The year was considered an explanatory continuous variable reflecting the continuous decrease in the availability of food resources during the study period. Because the range of movements of griffon vultures (up to 75 km; Donázar 1993) clearly exceeds the distance between the studied roosts (maximum 60 km) we did not consider them as independent sampling zones. For the Egyptian vulture, we used Generalized Linear Mixed Models (GLMM; McCullagh & Searle 2000). It is well-known that Egyptian vulture roosts are associated with food sources and that the same individuals frequently remain attached to the same

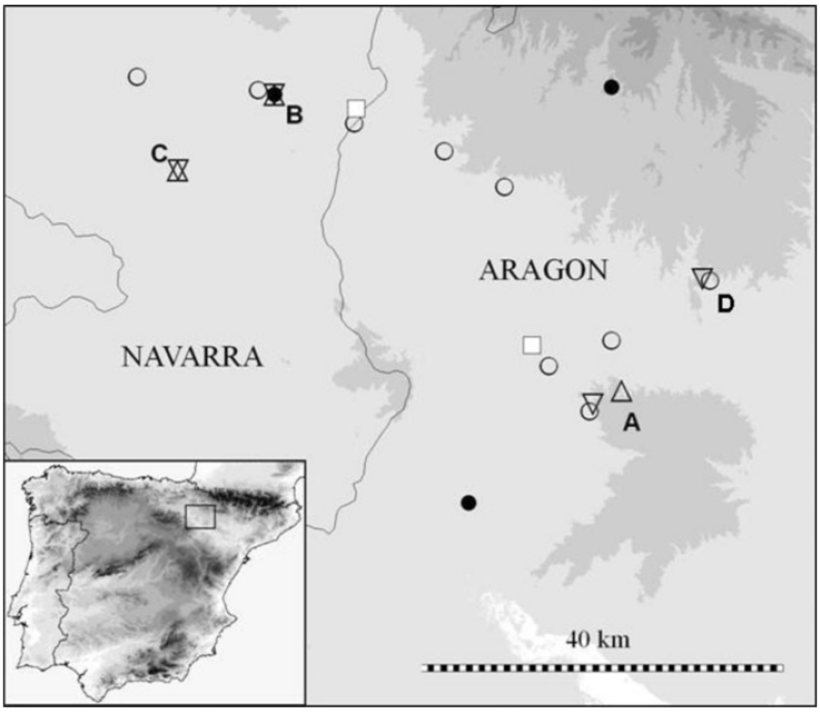


Figure 1. Study area (Ebro Valley, N. Spain) showing the four studied roosting areas (**A–D** griffon vulture: inverted triangle; Egyptian vulture: triangle). Main predictable sources of food in the surroundings: rubbish dumps: squares, supplementary feeding stations: circles; open circles represent feeding stations closed during the study period.

roosts for periods of days or weeks (Donázar *et al.* 1996a; authors personal observation). In addition, the range of movements of individuals is usually below 15 km (Donázar 1993; authors unpublished). For these reasons, to control for potential variability among roosts as well as to avoid non-independence of the data, we fixed in models the roost as a random term. Response and explanatory variables were similar to those considered in the analyses for griffon vultures. Following Mysterud (2000), niche breadth (B) was calculated on the basis of the Shannon–Wiener information measure (Hanski 1978): $B_j = -\ \Sigma_j\ p_{ij}\ \ln(p_{ij})$. The overlap in diet ($O_{ge}$) between griffon (*g*) and Egyptian vultures (*e*), was calculated with the Schoener's index (Schoener 1968): $O_{ge} = 1-1/2\ \Sigma|\ p_{ig} - p_{ie}|$, where p_{ig} and p_{ie} were the proportions of the prey category *i* in the diet of the griffon and the Egyptian vulture, respectively. Overlap varies between 0 (absent) to 1 (complete).

RESULTS

We analyzed 844 pellets (griffon vulture, 403; Egyptian vulture, 441) throughout the study area. The number of pellets collected in each roost and year varied from 20 to 70 (mean = 44) for the griffon vulture and from 9 to 81 (mean = 48) for the Egyptian vulture. The frequencies of occurrence of wild rabbit, poultry, and garbage showed a significant increase in the diet of the griffon vulture during the study period (respectively, $\chi^2=8.51$, $P = 0.003$; $\chi^2=8.24$, $P = 0.004$; $\chi^2=7.89$, $P = 0.005$; Fig. 2). In 2008, wild rabbits occurred in almost 10% of the pellets (Fig. 2, Appendix 1). The frequency of swine showed the opposite trend ($\chi^2=9.77$, $P = 0.002$; Fig. 2) in parallel with the closing of the main feeding stations (Fig. 2). Only poultry varied significantly within the Egyptian vulture's diet, decreasing during the study period ($F_{1,428}=33.45$, $P < 0.0001$; Fig. 2). Wild rabbits did not show significant variations with frequencies close to 20% (Fig. 2).

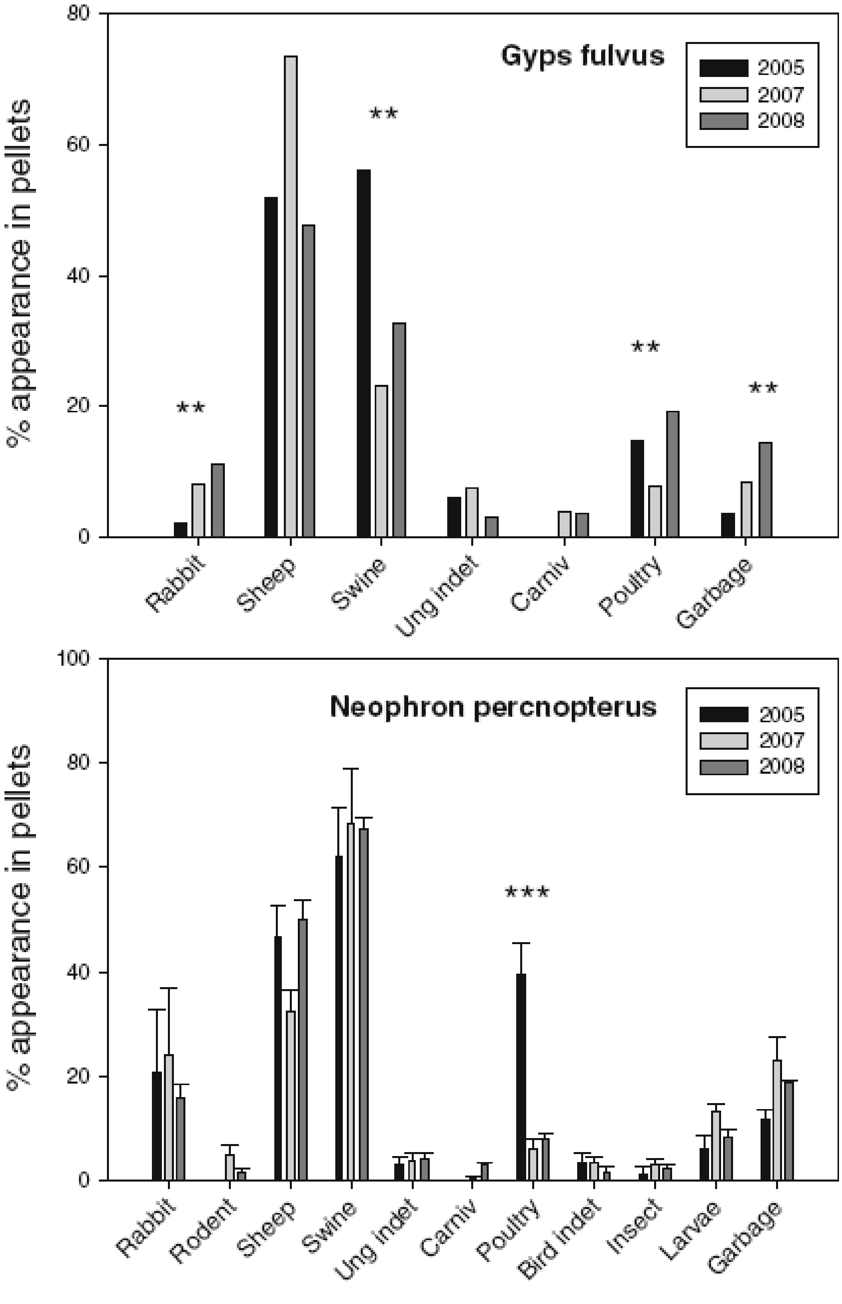
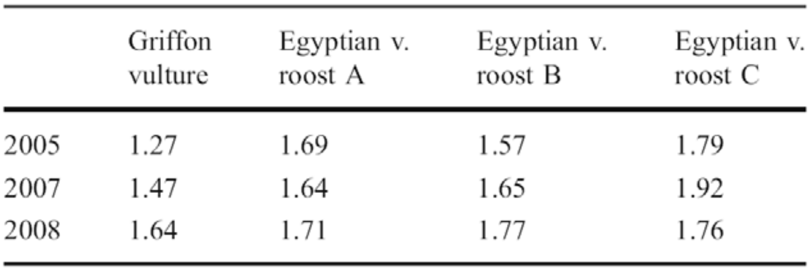


Figure 2. Variations in the food habits of the griffon and Egyptian vultures along the study period: <2007: prior to the closure of feeding stations; 2007: During the closure; 2008: after the closure. For the griffon vulture and because pellets collected in the same year were considered as a single sample total values are shown (without error bars). For the Egyptian vulture we considered separately the samples collected in each communal roost; annual mean values and standard errors are shown. Differences between periods were estimated on the basis of modelling procedures (see "Materials and methods"): $^{**}P<0.01$; $^{***}P<0.001$.

Niche breadth of both species increased progressively during the study period (Table 1) although the differences between periods, considering each roost independently, did not reach significance in the case of the Egyptian vulture (Kruskal–Wallis test, $P = 0.281$). Diet overlap between the two species revealed divergent results in relation to each Egyptian vulture roost (Table 2). During the study period, griffon vultures showed a growing overlap with those Egyptian vultures roosting in areas where resources were unpredictable (roost C). Overlap with Egyptian vultures depending on predictable resources (vulture restaurants and rubbish dumps; roosts A and B) was similar during the first and last part of the study period and showed minimum values during 2007, when some of the feeding stations had been closed (Fig. 3).

Table 1. Changes in the niche breadth (Shannon–Wiener index) of the griffon and Egyptian vultures in the three considered study periods: 2005: prior to the closure of feeding stations; 2007: during the closure; 2008: after the closure.



	Griffon vulture	Egyptian v. roost A	Egyptian v. roost B	Egyptian v. roost C
2005	1.27	1.69	1.57	1.79
2007	1.47	1.64	1.65	1.92
2008	1.64	1.71	1.77	1.76

In the roosts A and B, the diet of the Egyptian vultures relied mainly on large ungulate carcasses and garbage; in the roost C, wild rabbit was the main prey.

Table 2. Change in the overlap (Schoener Index) between the diet of the griffon vulture and the diet of the Egyptian vulture in three communal roosts.

	Egyptian v. roost A	Egyptian v. roost B	Egyptian v. roost C
2005	0.77	0.81	0.51
2007	0.43	0.53	0.53
2008	0.73	0.78	0.63

Three periods have been distinguished: 2005: prior to the closure of feeding stations; 2007: during the closure; 2008: after the closure. In the roosts A and B, the diet of the Egyptian vultures relied mainly on large ungulate carcasses and garbage; in the roost C, wild rabbit was the main prey.

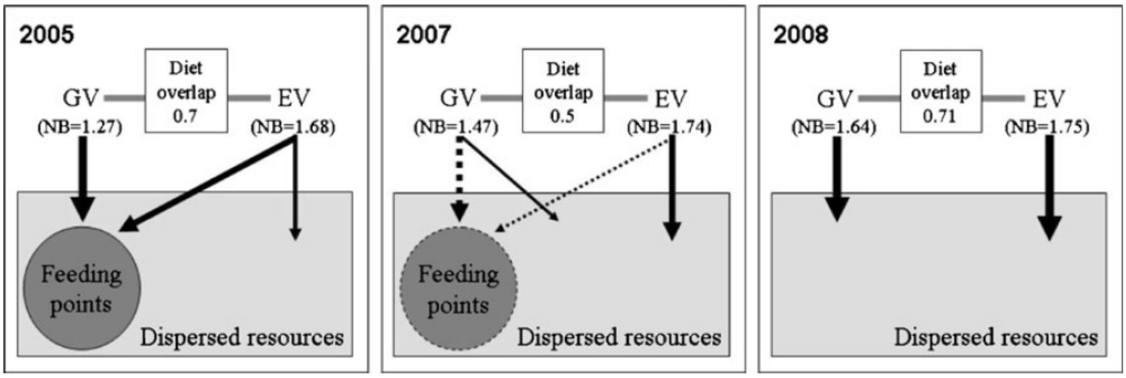


Figure 3. Conceptual model explaining the observed changes in the diet overlap between griffon (GV) and Egyptian vultures (EV) according to results obtained in this study. In 2005, supplementary feeding stations and unpredictable sources of food were available; both vultures fed mainly at feeding stations (high overlap). In 2007, the number of feeding stations decreased, and could have been monopolized by griffon vultures which also would begin to exploit unpredictable resources which were also heavily exploited by Egyptian vultures (low overlap). In 2008, most of the feeding stations disappeared and the two vultures relied mainly on unpredictable sources of food (high overlap).

Appendix 1

Table 3 Percent of occurrence in fresh summer pellets of the two studied vulture species at four roosting areas in northern Spain

	Griffon vulture									Egyptian vulture								
	2005		2007			2008				2005			2007			2008		
	A	B	A	B	D	A	B	C	D	A	B	C	A	B	C	A	B	C
Rabbit	2.6	1.9	6.2	17.8	0.0	15.2	8.6	9.8	10.7	1.9	7.7	66.7	0.0	12.2	60.0	18.5	9.3	20.0
Rodent	0.0	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9	10.0	2.5	2.3	0.0
Sheep	43.6	60.4	63.1	62.2	95.0	33.3	52.9	29.3	75.0	50.9	61.5	55.6	21.3	41.5	34.3	60.5	44.2	45.0
Swine	66.7	45.3	43.1	11.1	15.0	60.6	24.3	24.4	21.4	67.9	84.6	22.2	83.6	82.9	38.6	71.6	69.8	60.0
Other Ung	2.6	9.4	9.2	13.3	0.0	0.0	5.7	2.4	3.6	5.7	0.0	0.0	8.2	2.4	1.4	3.7	7.0	1.7
Carnivore	0.0	0.0	0.0	6.7	5.0	6.1	4.3	0.0	3.6	0.0	0.0	0.0	1.6	0.0	0.0	3.7	2.3	3.3
Poultry	5.1	24.5	1.5	22.2	0.0	9.1	31.4	22.0	14.3	47.2	46.2	44.4	4.9	2.4	11.4	4.9	9.3	10.0
Other Bird	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.1	4.9	0.0	5.7	3.7	0.0	1.7
Insect	0.0	0.0	0.0	4.4	0.0	0.0	0.0	0.0	0.0	0.0	7.7	0.0	4.9	0.0	4.3	3.7	2.3	1.7
Larvae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.7	15.4	11.1	11.5	17.1	11.4	12.3	4.7	8.3
Garbage	5.1	1.9	15.4	4.4	5.0	12.1	5.7	22.0	17.9	9.4	15.4	11.1	31.1	26.8	11.4	19.8	18.6	18.3
N pellets	39	53	65	45	20	33	70	41	28	53	13	9	61	41	70	81	43	60

We considered three study periods: 2005: prior to the closure of feeding stations; 2007: during the closure; 2008: after the closure

DISCUSSION

Our results, contrary to those predicted, showed that the decline in food availability due to EU regulations prohibiting the disposal of carcasses in the field has triggered significant changes in the diet composition of the griffon vulture. After the closing of most feeding stations it has begun to consume significant numbers of small vertebrates increasing its niche breadth. Carnivores show a preference for items rewarding higher benefits (Begon *et al.* 2006). When the diet is extremely specialized, however, these changes are not expected and the preferred prey would be consumed independent of the abundance of alternative items (see Pyke *et al.* 1977; Stephens *et al.* 2007). Gyps vultures are specialists exploiting large carcasses having evolved in fluctuating environments where carcass availability was dependent on the displacement of large migratory ungulates. Large body size and soaring flight strategies permit these species to search for food in extremely large regions thus buffering the effects of weather and herd displacements (Houston 1983). Concordantly, all studies carried out on the diet of the griffon vulture in western Europe and other Old World regions show higher and almost exclusive consumption of medium and large-body size vertebrate (mainly ungulate) carcasses such as cow, horses, deer, swine, sheep and goats (Fernández 1975; Elosegi 1989; Mundy *et al.* 1992; but see Margalida 1997). Consequently, our results show an unusual and unexpected phenomenon probably linked to extreme food conditions with very low availability of food in relation to the size of the griffon vulture population.

Other carnivores with opportunistic diets can reduce the consumption of key prey items when they become less profitable than alternative prey (Glasser 1982). However, the Egyptian vulture in northern Spain has not shown such trends in parallel to the closing of the main feeding stations. In fact, it appears to currently exploit the same prey and in similar proportions to that reported two decades ago in the same study area (wild rabbit, 4–42%; swine, 8–47%; sheep, 20–73%; poultry, 10–95%; garbage, 2–51%; Ceballos & Donázar 1990). Most likely, other environmental factors determine a very high variability in the diet of this opportunistic feeder, thus masking the effects of the closing of the feeding stations. In fact, we found important differences in the diet between roosts probably because the primary food source is variable (wild rabbits in one case, and ungulate carcasses and garbage in the other two studied cases). Moreover, the large population decline in wild rabbits in the study area during the last decade was caused by rabbit haemorrhagic disease (Villafuerte *et al.* 1995) may also have contributed to the observed variability since rabbit populations have recovered only partially, showing important spatial variations in density (Calvete et al. 2006).

Trends in food habits of the two species are considered on a broader scale, our results strongly suggest close interdependence and reflect a scenario of interspecific exploitation competition (Tokeshi 1999), in this case determined by different body size (Cody & Diamond 1975; Wilson 1975). In accordance with this scenario, we observed an increasing overlap in the diet of the two species when the Egyptian vulture depended on unpredictable resources. In the other two zones, however, overlap was minimal during 2007 when some of the feeding stations had been closed. This could reflect different degrees of spatial concurrence in patches with changing food availability as is schematically represented in Fig. 3. Thus, the patches of food would be the feeding stations (predictable sources) and the carcasses found at unpredictable locations (small farms, extensive exploitations, and wild animals). The concurrence between griffon and Egyptian vultures would be maximal in either condition of high food availability, when the scavengers would preferably exploit feeding stations (2005) or, on the other hand, when after the closing of these stations (2008) the two vultures must share primarily unpredictable resources. Even after the closing of most of the feeding stations the diet of the two species is still based on ungulate carcasses. The birds should intensively exploit the few predictable locations remaining but many carcasses should also be provided by extensive grazing practices, which are still common in abrupt mountain areas (Donázar *et al.* 1996b) and still provide many dead animals whose carcasses remain in zones difficult to access. In addition, many carcasses, mainly swine, should be found in the vicinity of small farms where the regulation of carcass elimination is not strongly enforced. Because of the illegal nature of this activity it is very difficult to quantify the availability of these resources but it is clear that they are important to the vulture population.

After decades of legal protection and high availability of food, the population of griffon vultures has seen a sudden reduction in the amount of available carcasses. This may lead to a new scenario of population regulation, marked not only by a lower trophic carrying capacity but also by the more unpredictable spatial distribution of resources. In the short-term, changes are expected in the spatial structure of the population not attached to breeding places. There is also evidence that immature vultures are not longer concentrating in those regions in which abundant and predictable food resources are becoming scarce (Camiña & Montelío 2006). From a long-term perspective, the demographic regulation of the griffon vulture population can be expected on the basis of the new environmental carrying capacity. During recent years (2006–2008) the number of individuals found dead or starving has increased dramatically in the Iberian Peninsula. Moreover, in 2007 and 2008 the breeding success of griffon vultures dropped consistently in populations of northern Spain depending heavily on carcasses from intensive farming (see reviews in Donázar *et al.* 2009a). Consequently, it can be predicted that the growth of Iberian griffon vulture populations could end in the short-term and even begin to decline in the long-term. Breeding counts carried out in northern Spain during 2007 and 2008 indicate this trend (Margalida *et al.* 2009).

Interspecific relationships could also be strongly affected by this new scenario. The scarcity of the main food resources exploited by the griffon vultures (predictable large carcasses) would lead to an increase in indirect competition with subordinate species for small and medium-sized carcasses, in a process similar to the hyperpredation observed in predator–prey systems (Courchamp *et al.* 2000). In the Iberian Peninsula the carcasses of wild rabbits are heavily exploited by facultative predators and carrion-eaters (Delibes-Mateos *et al.* 2008) and for some threatened species like the Egyptian vulture, the cinereous vulture (*Aegypius monachus*) and the bearded vulture (*Gypaetus barbatus*) constitute an essential part of the diet during the breeding period (Hiraldo 1976; Donázar & Ceballos 1988; Margalida *et al.* 2009). In a field experiment carried out during 2005 and 2006, when the availability of large carcasses was still high, we observed that 30% of the wild rabbit carcasses were consumed by griffon vultures, which displaced other species like Egyptian vultures, red kites (*Milvus milvus*), black kites (*Milvus migrans*), marh harriers (*Circus aeruginosus*), common European buzzards (*Buteo buteo*), and common ravens (*Corvus corax*). In addition, food sources like garbage dumps that until now have been exploited exclusively by opportunistic scavengers (Donázar 1992) can now be monopolized, at least partially, by griffon vultures. Apart of this, the growing consumption of garbage may have serious consequences for the populations of these species because it increases the probability of ingestion of toxic substances (Houston *et al.* 2007).

In conclusion, the implementation of recent EU legislation is directly affecting the availability of food for the specialist avian scavengers but could also be modifying the trophic relationships within the guild. From a long-term perspective, the structure and functioning of the guild could be highly dependent on the regulation of the griffon vulture population given the new availability and spatial distribution of resources. Even if, in the short-term, negative consequences for populations of more threatened scavengers such as the Egyptian vulture are expected, in the long-term the situation could improve the conservation outlook because all the species would depend on more unpredictable resources. In the end, this scenario would be more similar to those in which the foraging strategies of avian scavengers evolved. Moreover, there would be fewer incidences of other negative factors threatening the populations of carrion eaters depending on intensive livestock such as the ingestion of veterinary drugs and pathogen transmission (Blanco *et al.* 2007; Lemus *et al.* 2008). Also, a higher availability of carcasses would reduce the probability of ingestion of poisoned preys (Margalida et al. 2008). It is necessary for EU legislation and the regulation of the states and regions to have enough flexibility to authorize owners of extensive operations to abandon the carcasses of their livestock in order to sustain populations of avian scavengers (Donázar *et al.* 2009b).

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CHAPTER VI

Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria

ABSTRACT

Current European sanitary laws are promoting the concentration of domestic livestock carcasses in limited locations called ‘vulture restaurants’ or supplementary feeding stations in order to safeguard human health. However, this type of food concentration could lead to monopolization by a few, large dominant species. Management guidelines are urgently needed to ensure that potentially less competitive and more endangered scavengers can also benefit from this resource, considering that once abundant carcasses are now absent from the field. Here, we assess factors affecting the abundance of six avian scavenger species at 17 feeding stations in northern Spain, considering aspects such as carrion availability, physiographic features, humanization, presence of heterospecifics and densities of scavengers during both winter and summer seasons. Results indicate that conditions for interspecific facilitatory processes are possible at low numbers (<100 individuals) of griffon vultures (*Gyps fulvus*). Otherwise, the other avian scavengers are excluded. In a few cases, spatio-temporal patterns of segregation become apparent. Differences in the size of carcasses supplied to feeding stations as well as the local characteristics influence the balance of species at these points and, therefore, how species of conservation concern use feeding stations. Future legislation should encourage the opening of numerous feeding stations supplied with low quantities of food to mimic the original condition of temporal and spatial unpredictability of carcasses and to maintain ecological relationships within the scavenger guild.

INTRODUCTION

Public health issues and subsequent sanitary laws are increasingly interacting with environmental policies mainly because of the possibility of disease transmission between wildlife and domestic species and humans (Daszak *et al.* 2000; Cleaveland *et al.* 2001). One example is the European sanitary laws approved after the outbreak of the Bovine Spongiform Encephalopathy (BSE) in late 1990s that made obligatory the removal and cremation of all livestock carcasses. Traditional practices, especially in remote areas, have included the abandonment of carcasses in the field, which have maintained complex ecological processes affecting the soil, vegetation and consumers, from invertebrate to large vertebrates (DeVault *et al.* 2003; Selva and Cortés-Avizanda, 2009). Avian scavengers of southern Europe and other warm and temperate Old World regions have positively responded to these practices, and have been historically dependent on livestock carcasses associated with human activities such as traditional agro-grazing practices and transhumance (Mundy *et al.* 1992; Donázar *et al.* 1996a; Olea and Mateo-Tomás, 2009).

The onset of generalized collection of carcasses is expected to have consequences for avian scavenger populations (Tella, 2001) and this has led to new regulations (EU1774/2002; EU322/2003; EU830/2005; CE 1069/2009) permitting carcasses to be left in the field to feed scavengers. In any case, legal constraints are still very important and the abandonment of dead animals is only possible in specific locations (Deygout *et al.* 2009; Donázar *et al.* 2009a,b). Thus, state and regional governments in Mediterranean countries are following a common strategy, whereby a few sites – commonly termed supplementary feeding stations or ‘‘vulture restaurants” – are supplied with carcass remains to feed vultures (Piper, 2006). While waiting for future legislations that will allow scavengers to feed again on extensive livestock carcasses, vulture restaurants currently are an urgency measure. However, in some cases the use of supplementary feeding stations may become permanent in some Mediterranean regions because the current decline of the extensive grazing practices (Donázar *et al.* 2009b). Because of the strong restrictions imposed by sanitary regulations, the number of these sites is estimated to be less than 20% of the formerly existing feeding places that were traditionally associated with small farms and villages (Donázar *et al.* 2009a). This new scenario of food concentration is promoting large aggregations of the largest and most common species, the griffon vulture *Gyps fulvus* (see below), and could be affecting carcass consumption by other less abundant, smaller species of great conservation concern belonging to the same guild or functional group (sensu Blondel, 2003).

The dynamics of scavenging processes, and their role in the function of food webs and ecosystems, are strongly dependent on the concurrence of specialist and facultative scavengers, and on the competitive processes in which they are involved (DeVault *et al.* 2003). Old World scavengers share a common food resource (i.e., carrion; Hertel, 1994; Hertel and Lehman, 1998) and have evolved particular morphological and/or behavioural skills that allow their coexistence through an ordered resource-partitioning process (König, 1983; Houston, 1988). Facilitatory and/or competitive processes seem to take place according to the species and the number of individuals present at a carcass. In particular, smaller species would benefit from the presence of larger ones (mainly vultures of the Gyps genus) that open tough skins and increase the overall availability of resources (facilitatory processes; Kruuk, 1967; König, 1974). However, when larger and dominant species greatly outnumber the others, a monopolization of resources may occur (Mönkkönen *et al.* 2004). Consequently, guidelines aimed at avoiding these imbalances in the use of supplementary feeding stations are urgently needed to sustain healthy populations of scavengers as well as to maintain ecological and evolutionary processes.

The aim of this paper is to explore some potential ecological consequences of the implementation of the new European sanitary legislation of carcass removal and concentration on the avian scavenger guild. Specifically, we evaluate the use made by six scavenger species (the griffon vulture *Gyps fulvus*, the Egyptian vulture *Neophron percnopterus*, the bearded vulture *Gypaetus barbatus*, the red kite *Milvus milvus*, the black kite Milvus migrans, and the common raven *Corvus corax*) of 17 supplementary feeding stations that differ in their local characteristics and management (mainly in terms of time, quantity, and type of food provided). Taking into account the information available on the guild structure, the population size of scavengers in the study area (see below), and the foraging behaviour of each species, we hypothesize that: (1) large aggregations of griffon vultures, the largest and most abundant scavenger, would inhibit suitable conditions for facilitatory processes, reducing the abundance of other, smaller scavengers at these sites, and (2) features such as geographic location, and availability and type of food supplied to feeding stations would favor their use by some species at the expense of others. Under the first hypothesis, we predict that abundances of griffon vultures should be negatively related to the abundance of the other scavengers consequently reducing the diversity of the guild. Under the second hypothesis, we predict that griffon vultures, a large sized species with well-developed social foraging behaviour (Houston, 1983), would use feeding stations with abundant large carcasses, whereas medium and small sized carrion eaters would use feeding stations supplied with smaller-sized carrion.

MATERIALS AND METHODS

SCAVENGER SPECIES AND POPULATIONS IN THE STUDY AREA

The study was performed in a 10,000 km2 area located in Northern Spain (Fig. 1), where large local densities of scavengers have been reported. The breeding population of griffon vultures (ca. 10,500 g, resident) is around 2400 pairs (ca. 11% of the Iberian population) and, mainly during summer, co-exists with hundreds of immature birds that aggregate at communal roosts (Del Moral and Martí, 2001; authors' unpublished data). Egyptian vultures (ca. 2000 g; migratory) occupy 380 breeding territories (ca. 30% of the Iberian population) and there are six large communal roosts that may attract, during the summer, up to 200 birds from a wide geographic area (Donázar *et al.* 1996b; author's unpublished data). Bearded vultures (ca. 6000 g; resident) occupy eight breeding territories (ca. 10% of the Iberian population) in the western part of the Pyrenees (Margalida and Heredia, 2005). Finally, there are around 300 breeding pairs (10% of the Iberian population) of red kites (ca. 1000 g; resident), as well as over 3000 wintering individuals (Viñuela *et al.* 1999; Gorosti, 2007). No reliable information is available for black kites (ca. 800 g, migratory) and common ravens (ca. 1100 g, resident), although they seem to be abundant in the study area and there are probably hundreds of breeding pairs, as well as important winter and summer communal roosts (Campión, 2004; authors' unpublished data).

FIELD PROCEDURES

We monitored 17 supplementary feeding stations during the summer of 2005 (n = 16) and winter of 2005–2006 (n = 15). Observations were concentrated during the central months of each season (June–August and December–February) to maximize the presence and abundance of species with marked seasonal changes in abundance (mainly

Egyptian vultures and black and red kites, see above). Monitoring length varied between 10–17 days (winter) and 5–24 days (summer). The visits were not simultaneous and were performed from 9 a.m. to 4 p.m. and from 8 a.m. to 8 p.m. during winter and summer, respectively. All the surveys were conducted under good weather conditions permitting foraging activities of the studied species. During each visit, we recorded every 20 min (our sampling unit) individual presence and abundance for each species at the feeding stations and in the immediate surroundings (ca. 200 m). The total numbers of censuses undertaken were 427 in winter and 407 in summer. Although the proximity in time between censuses (20 min) could suggest that the observations were not independent, the activity at feeding stations is very dynamic, with continuous changes in the number of individuals because of the incessant arrivals and departures of birds (authors'unpublished data). To reduce some potential spatial autocorrelation in the data set and to control for this non-independence, we fitted ''Date" as a random factor in the analytic procedures (see below).

Data were recorded from a vehicle using binoculars (10x 40) and telescopes (20-60x) fitted to car windows at a minimum distance of 300 m to avoid interfering in the activity of birds.

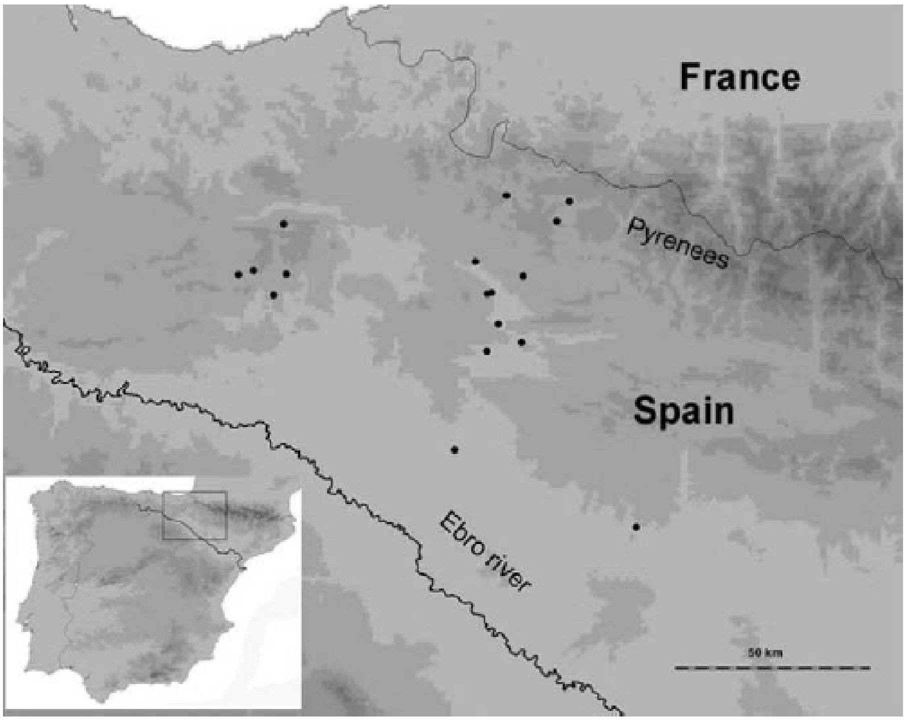


Figure 1. Study area showing the location of the monitored feeding stations.

ANALYTICAL PROCEDURES

Prediction 1: ***abundances of griffon vultures should be negatively related to abundances of the other scavengers and guild diversity***

We used Principal Component Analyses (PCA, Digby and Kempton, 1987) to detect association patterns between griffon vultures and the other studied species. Data were previously log (+1) transformed to obtain normality. A Varimax rotation was applied. Additionally, we used Generalized Linear Mixed Models (GLMM, McCullagh and Searle, 2000; SAS Institute Inc., 2009) to assess the effects of the number of griffon vultures on the diversity of species using feeding stations (link function: identity, error distribution: normal). Diversity was calculated using the Shannon index (Magurran, 2003). Subsequently, we explored the relationship between the abundance of griffon vultures and that of the other smaller species (link function: logarithmic, error distribution: Poisson) to detect interspecific differences. We included the time of day at which censuses were performed (morning: <12 a.m.; afternoon: >12 a.m.) to detect temporal segregation between species. ‘‘Feeding station” and ‘‘Date” were fixed into models as random terms to control for spatial and temporal heterogeneity as well as to reduce non-independence of the data.

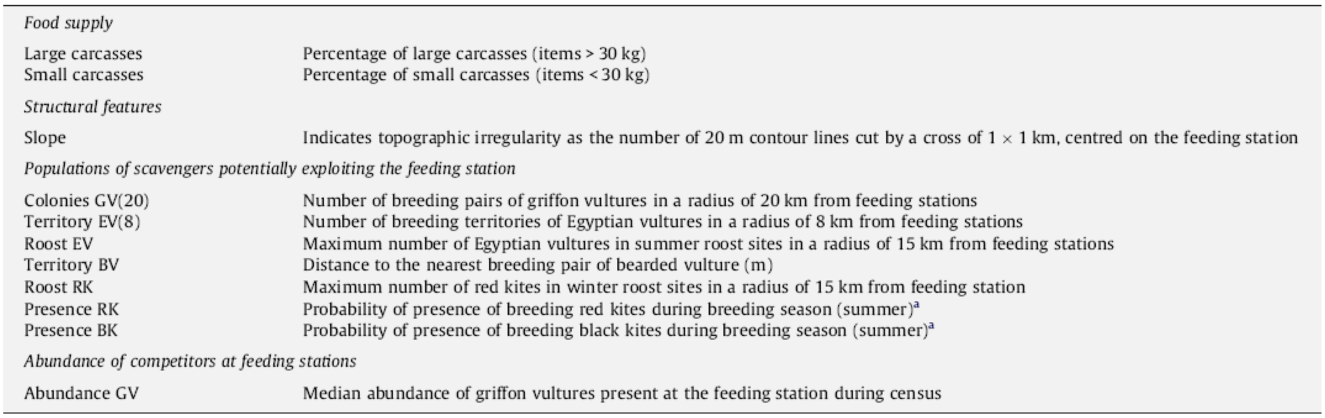
Prediction 2***: feeding station features may favor their differential use by some species.***

We used Generalized Linear Models (GLM, McCullagh and Nelder, 1989; SAS Institute Inc., 2009) to identify those characteristics of feeding stations affecting their differential use by scavengers (see below and Table 1). We only considered feeding stations with more than 5 positive surveys (i.e., at least one bird of the study species present; winter n = 15; summer n = 12). As response variables we considered: (i) the relative presence of each focal species, which was assessed as the proportion of positive surveys out of the total number of surveys performed (link function: logit, error distribution: binomial) (ii) the diversity of small and medium sized scavengers, excluding griffon vultures (link function: identity, error distribution: normal).

EXPLANATORY VARIABLES

Table 1 summarizes all explanatory variables used to model species relationships. The availability of large or small carcasses at each feeding station was estimated by averaging the weight (in kg) of fresh carcasses observed during each census. The mean

Table 1. Variables used to explain the abundance of avian scavengers in feeding stations in Northern Spain.



Food supply	
Large carcasses	Percentage of large carcasses (items > 30 kg)
Small carcasses	Percentage of small carcasses (items < 30 kg)
Structural features	
Slope	Indicates topographic irregularity as the number of 20 m contour lines cut by a cross of 1 × 1 km, centred on the feeding station
Populations of scavengers potentially exploiting the feeding station	
Colonies GV(20)	Number of breeding pairs of griffon vultures in a radius of 20 km from feeding stations
Territory EV(8)	Number of breeding territories of Egyptian vultures in a radius of 8 km from feeding stations
Roost EV	Maximum number of Egyptian vultures in summer roost sites in a radius of 15 km from feeding stations
Territory BV	Distance to the nearest breeding pair of bearded vulture (m)
Roost RK	Maximum number of red kites in winter roost sites in a radius of 15 km from feeding station
Presence RK	Probability of presence of breeding red kites during breeding season (summer)[a]
Presence BK	Probability of presence of breeding black kites during breeding season (summer)[a]
Abundance of competitors at feeding stations	
Abundance GV	Median abundance of griffon vultures present at the feeding station during census

[a] On the basis of predictive models of the probability of presence of foraging birds based on landscape features (surface of open areas, proximity to rivers and altitude) determined by the results of previous studies modelling habitat selection by these species in the same study area (Campión, 2004).

weight of each species of livestock was determined on the basis of values obtained from local farmers: horse: 300 kg, cow: 350 kg, donkey: 150 kg, calf: 150 kg, sheep and goat: 35 kg, lamb: 10 kg, wild boar: 60 kg, pig: from 10 to 150 kg, according to the size of the animal; dog: 25 kg, chicken and rabbit: 1–2 kg, slaughterhouse remains: from 2 to 20 kg.

Physiographic characteristics (slope) were derived from a digital elevation model (DEM) with a spatial resolution of 100 m. In the study area slope reflects confidently the degree of humanization (villages and infrastructures are concentrated in flat areas; see Campión (2004)). The abundance of scavengers in the area was estimated using information on their population sizes and distributions. We estimated the number of breeding pairs of every studied species within a radius around each feeding station representing the area of average movements of birds during foraging activity (Ceballos and Donázar, 1988; Donázar, 1993; authors' unpublished data). For Egyptian vultures and red kites, we also considered their numbers at communal roosts within a radius of 15 km and 8 km of the feeding stations, respectively. These figures correspond to the movements of radio-tracked individuals of both species (De Pablo, 2004; Gorosti, 2007; authors' unpublished data). Because there is no information on the location of breeding territories of red and black kites we used predictive models of the probability of presence of foraging birds based on landscape features (surface of open areas, proximity to rivers and altitude) determined by the results of previous studies modelling habitat selection by these species in the same study area (Campión, 2004). No information is available on the spatial distribution of breeding pairs or roost sites of common ravens in the study area.

MODEL FITTING

Models were fitted by using a forward stepwise procedure (Donázar *et al.* 1993) that resulted in multivariate models in which only significant effects ($p < 0.05$) were retained. Final models were those explaining the highest percentages of the initial deviance.

RESULTS

CARCASS AVAILABILITY AND SEASONAL USE OF FEEDING STATIONS BY SCAVENGERS

Feeding stations were supplied with more carcasses in winter than in summer (Fig. 2). Large carcasses (>30 kg) dominated (86%) and the relative contribution of large and small items did not change between seasons. Resident scavengers visited a larger proportion of feeding stations during winter (griffon vulture and red kite: 100% vs. 56%; bearded vulture: 26% vs. 12%, and common raven: 87% vs. 62%). Despite these trends, seasonal differences in the frequency of surveys with positive contacts and the median number of individuals were only significant for red kites and common ravens (Fig. 2). Egyptian vultures and black kites, both summer visitors, used a similar proportion of feeding stations (56%).

Hypothesis 1: large aggregations of the largest and most abundant scavenger would reduce the abundance of the other, smaller scavengers and guild diversity.

Field data suggested that at huge concentrations of griffon vultures (e.g. more than 200 individuals), small body size scavengers were almost absent from feeding stations (Fig. 3). This pattern seemed to be the same in the two sampled seasons. Multivariate analyses (PCAs) partially supported this idea. In winter, when the largest abundances of griffon vultures were recorded, we found no association between this species and the other scavengers (Table 2).

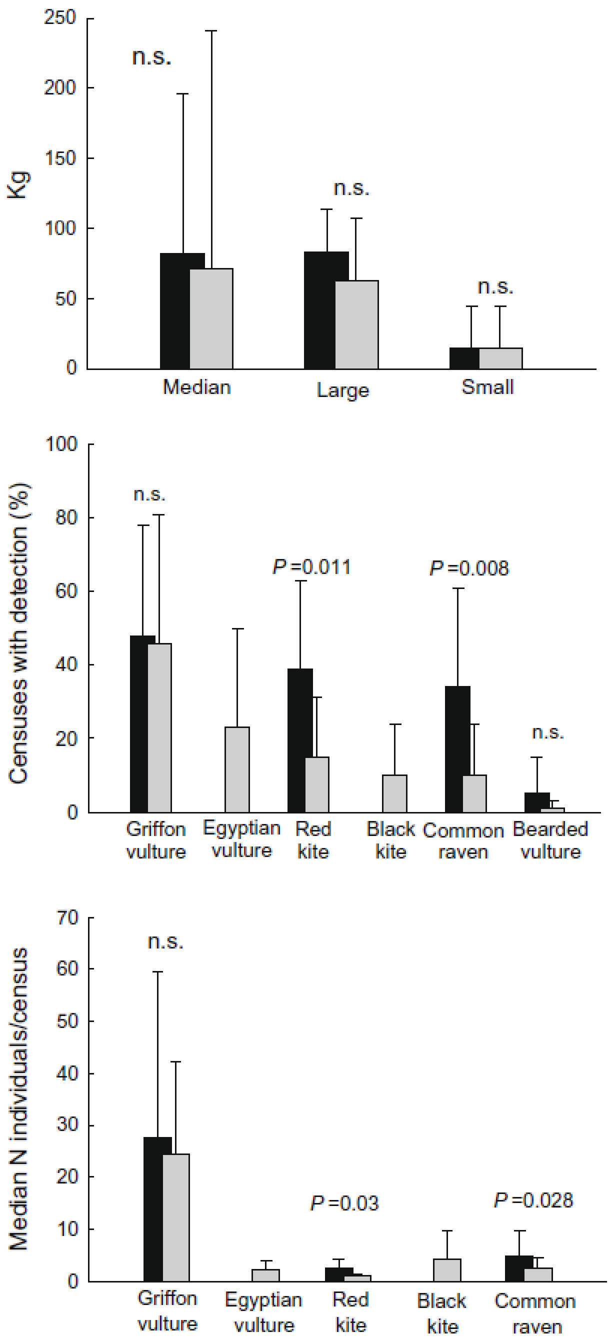


Figure 2. Seasonal variability in resource availability and scavenger presence in the studied feeding stations (winter: **black**, n = 15 stations; summer: **grey**, n = 16 s.). The means and standard errors shown were calculated on the basis of median values for each station. Significant differences between winter and summer are shown; n.s. = not significant.

During this season, Factor I of the PCA (37.7% of variance) reflected that red kites and common ravens were largely associated, while griffon vultures (Factor II, 24.3% of variance) and bearded vultures (Factor III, 23.0% of variance) did not show association with any other species. In summer, however, there was a positive association between griffon and Egyptian vultures (Factor II, 22.8% of variance). Small scavengers such as red and black kites and common ravens were also associated (Factor I, 23.7% of variance) while the bearded vulture remained as a solitary feeder (Factor III, 16.0% of variance).

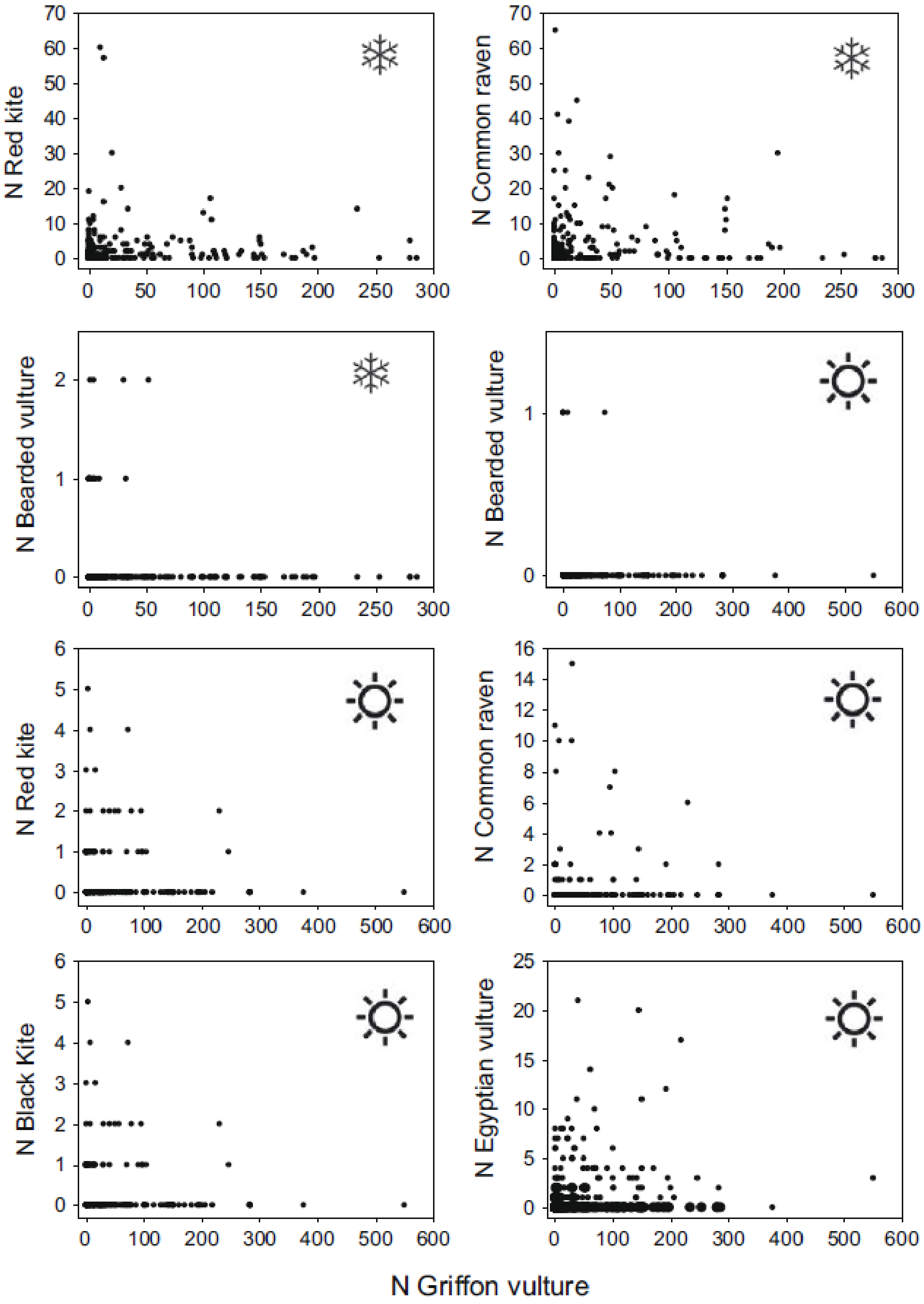
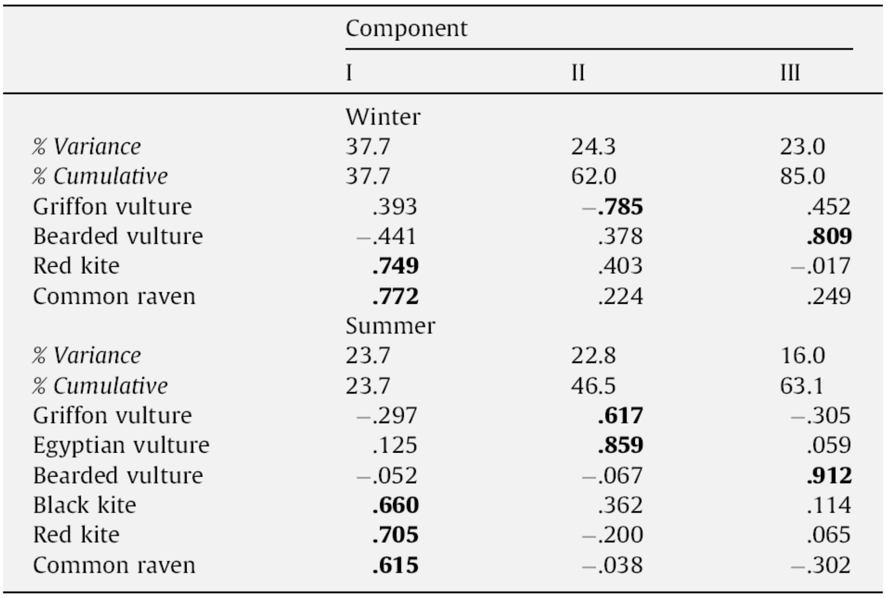


Figure 3. Abundance of small and medium-sized scavengers in relation to the total number of griffon vultures present at feeding stations in winter and summer.

After controlling for feeding station and date as random terms, wintering abundances of red kites at feeding stations were significantly higher during the afternoon ($F_{1,184} = 12.29$, $p = 0.0006$), whereas griffon vultures visited feeding stations mainly during the morning ($F_{1,206} = 12.16$, $p = 0.0006$). This result supports a negative relationship between both species which is maintained through a temporal segregation pattern. The abundances of medium to small-sized scavengers were not related to the abundance of griffon vultures. However, the overall diversity of the guild at feeding stations was lower when the number of griffon vultures increased (winter: $F_{1,122} = 22{,}26$, $p < .0001$; summer: $F_{1,88} = 43.99$, $p < .0001$, Fig. 4).

Table 2. Loadings of the numbers of individuals of each scavenger species on the first three principal components extracted from a correlation matrix. Bold numbers indicate loadings above (below) 0.5 (-0.5).



	Component		
	I	II	III
	Winter		
% Variance	37.7	24.3	23.0
% Cumulative	37.7	62.0	85.0
Griffon vulture	.393	**−.785**	.452
Bearded vulture	−.441	.378	**.809**
Red kite	**.749**	.403	−.017
Common raven	**.772**	.224	.249
	Summer		
% Variance	23.7	22.8	16.0
% Cumulative	23.7	46.5	63.1
Griffon vulture	−.297	**.617**	−.305
Egyptian vulture	.125	**.859**	.059
Bearded vulture	−.052	−.067	**.912**
Black kite	**.660**	.362	.114
Red kite	**.705**	−.200	.065
Common raven	**.615**	−.038	−.302

Hypothesis 2*: feeding station features may favour their differential use by some species.*

No significant models were obtained to explain changes in the global diversity of small to medium-sized scavengers at feeding stations. However, the relative presence (frequency of censuses with presence) of each species was largely explained by physiographic characteristics (slope) (Table 3). Feeding stations placed in rugged areas received more visits of bearded vultures whereas common ravens, black kites, griffon and Egyptian vultures used places located in flat areas. The distribution and abundance of these scavenger populations also affect the use of feeding stations. Egyptian and bearded vultures preferentially used feeding stations placed near their breeding territories and communal roosts, while griffon vultures more intensively used feeding stations far from their breeding colonies. During summer (breeding season), red kites used those sites placed in areas with habitat characteristics showing high probabilities of being used in foraging activities significantly more than other sites (Table 3).

Availability of food resources was also related to the use of feeding stations by scavengers. Larger numbers of small scavengers such as red kites and common ravens were observed in feeding stations supplied with small carcasses. Conversely, Egyptian vultures showed a positive association with the availability of large carcasses (Table 3). Finally, the relative presence of red kites was negatively related to the average abundance of griffon vultures at feeding stations.

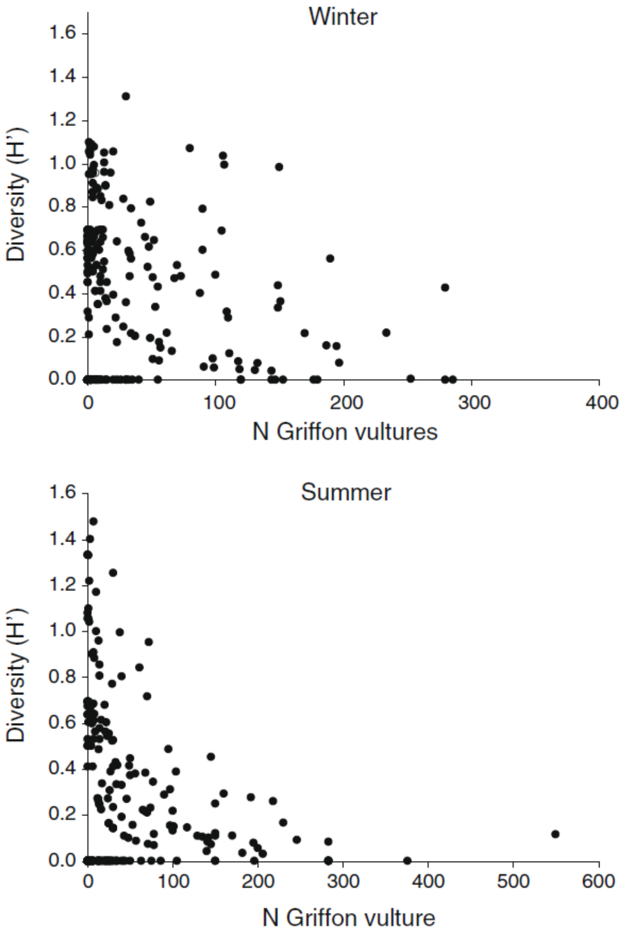
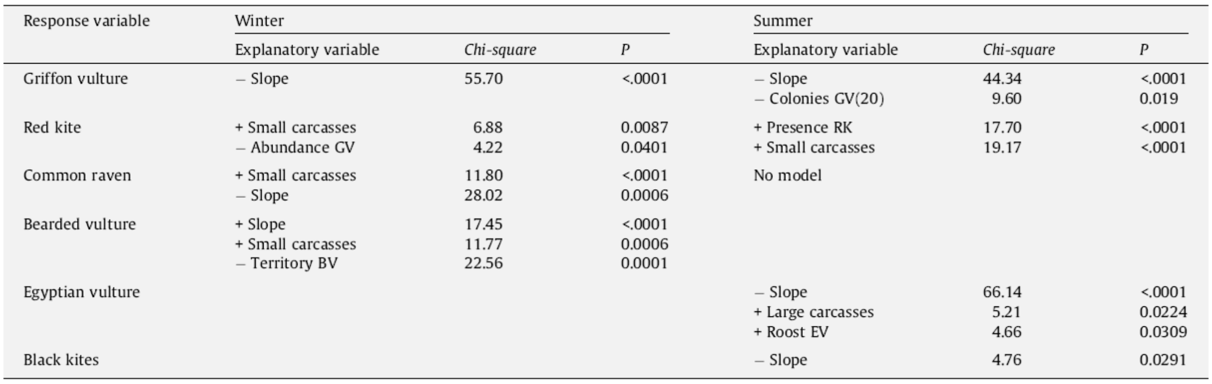


Figure 4. Diversity of species at feeding stations in relation to the abundance of griffon vultures present both in winter and summer.

Table 3. Effects of characteristics of feeding stations on the frequency of positive counts of focal scavengers.



Response variable	Winter			Summer		
	Explanatory variable	*Chi-square*	*P*	Explanatory variable	*Chi-square*	*P*
Griffon vulture	– Slope	55.70	<.0001	– Slope	44.34	<.0001
				– Colonies GV(20)	9.60	0.019
Red kite	+ Small carcasses	6.88	0.0087	+ Presence RK	17.70	<.0001
	– Abundance GV	4.22	0.0401	+ Small carcasses	19.17	<.0001
Common raven	+ Small carcasses	11.80	<.0001	No model		
	– Slope	28.02	0.0006			
Bearded vulture	+ Slope	17.45	<.0001			
	+ Small carcasses	11.77	0.0006			
	– Territory BV	22.56	0.0001			
Egyptian vulture				– Slope	66.14	<.0001
				+ Large carcasses	5.21	0.0224
				+ Roost EV	4.66	0.0309
Black kites				– Slope	4.76	0.0291

Only significant models (P < 0.05) are shown. Symbols indicate the type of response (+: linear and positive; –: linear and negative).

DISCUSSION

Avian scavengers are charismatic birds that have always held a prominent place in public consciousness as a result of their close, long-standing relationship with human activities (Houston, 2001) and the interest they engender in developed societies (Becker *et al.* 2004). Nevertheless, despite the time and money invested by conservation managers and governments, most of the world's avian scavengers are undergoing a serious decline (BirdLife, 2004). The creation of the so-called 'vulture restaurants' is a common feature of many conservation programmes and in Europe now more than ever supplementary feeding may be the only way of providing these birds with sufficient food (Donázar *et al.* 2009b). Within this context it is important to make sense of the overall situation and here we present a number of guidelines as to how these supplementary feeding stations could be re-designed and managed in order to guarantee the efficiency of the conservation measures that target avian scavengers. These birds interact closely and as such should be treated as a single group and not on a species-by-species basis (Mills *et al.* 1993; Soulé *et al.* 2005; Oro *et al.* 2009).

FEATURES OF SUPPLEMENTARY FEEDING STATIONS AND THEIR USE BY SCAVENGERS

Our results show that birds react in a great variety of ways to supplementary feeding stations due to their scattered locations and the complex effects of factors operating on local scales. We tried to capture this variation in our analyses by characterizing the features and other variables associated with management and the species that use feeding stations (see Section 2 for details). As a first step, and because it is well-known that prey-size segregation favours coexistence within carnivorous (Begon *et al.* 2006) and scavenger guilds (Houston, 1983; König, 1983; but see Margalida, 1997), we aimed to use carcass size as an easily controllable tool that would allow us to focus on the species of greatest conservation concern. However, we found that griffon vultures did not prefer feeding stations supplied with large carcasses, probably because of the sheer size of the griffon vulture population in the study area (see Section 2) that causes these birds to consume food items that would otherwise be the exclusive resource of smaller species (Donázar *et al.* 2010). The remaining scavenger species are much scarcer and are not constrained by population size and show clear preferences for carcasses of different dimensions: Egyptian vultures preferred feeding stations supplied with large carcasses (see alsoMeretsky and Mannan, 1999), whereas red kites and common ravens relied on much smaller items. Consequently, carcass-size manipulation may be a valuable tool for directing supplementary feeding towards species of interest. The extremely dissimilar sizes of the scavenger populations in the study area, largely dominated by griffon vultures, would preclude the effective use of this type of measure there, although this scenario may be more appropriate in other regions with more balanced scavenger populations.

The spatial position of the feeding station must also be taken into account in any attempt to increase the probabilities of use by breeding threatened species. This is particularly true for bearded vultures and red kites. In our study we found that both species were more commonly detected at feeding stations in areas with favourable characteristics for their foraging activities: in the former this means rugged areas near breeding territories and in the latter mid-altitude areas with landscape mosaics. The consistency of our results regarding the large-scale patterns of habitat selection in these species (Donázar *et al.* 1993; Campión, 2004) suggests that these preferences are not merely the product of a population response to a new trophic resource, as has been found on other occasions (Carrete *et al.* 2007; Benítez *et al.* 2009).

Finally, we found a preference of some scavengers (i.e., griffon and Egyptian vultures, black kites, common ravens) for those feeding stations placed in flat intensively humanized areas that may reflect the indifference of scavengers towards humans derived from the increasing respect for these birds enshrined in the legal protection established in the 1970s (Morillo and Gómez-Campo, 2000). Nonetheless, different results have been found in other region of Europe (Gavashelishvili and McGrady, 2006), which suggests that the response of scavengers to the humanization of the surroundings of feeding stations is probably dependent on historical local factors. Therefore, we encourage the carefully studied of the humanization tolerance of local populations of focal species before conservation programmes are enacted.

INTERSPECIFIC RELATIONSHIPS DETERMINE THE USE OF FEEDING STATIONS

In their original conception, supplementary feeding stations (‘vulture restaurants’) were devised as a general tool for the conservation of scavenger populations, being applicable to a number of species with differing feeding and life-history strategies (Wilbur and Jackson, 1983; Houston, 1987; Brown, 1990; Mundy *et al.* 1992; Piper, 2006; Carrete *et al.* 2006; Gilbert *et al.* 2007; Oro *et al.* 2008). Vultures and associated facultative scavengers, however, are members of guilds composed of strongly interacting species (Hertel, 1994). In particular, the larger species’ ability to locate carcasses is improved by the behaviour of smaller scavengers (Buckley, 1996; Jackson *et al.* 2008), while smaller species benefit from the opening up of carcasses by large vultures (König, 1983). Our results show a negative relationship derived from griffon vulture abundances, demonstrating that the occurrence of the number of species – and thus guild diversity – is only high when there are fewer than 100 griffon vultures present, a similar maximum figure to that found around ungulate carcasses placed experimentally and unpredictably in the wild (authors’ unpublished). Consequently, and as has been observed in other interspecific competition scenarios (Petren and Case, 1996; Kieseecker *et al.* 2001), large aggregations of feeding individuals (up to 600 birds) of the dominant griffon vulture do not provide a framework that will satisfy the requisites of complex interspecific patterns like facilitation processes. When numbers are lower, however, some associations suggesting the maintenance of facilitation appear similar to that observed between griffon and Egyptian vultures (although large groups of Egyptian vultures only occur when there are fewer than 200 griffons present).

When using these feeding stations small and medium-sized avian scavengers may avoid direct interspecific interaction with griffon vultures by temporal segregation, as has been seen in other pairs of species with similar ecological requirements (Cody, 1974; Carothers and Jaksíc, 1984; Moril and Boydl, 2004; Begon *et al.* 2006; Blázquez *et al.* 2009). Thus, during winter, when the availability of alternative prey is low, red kites avoid co-occurring temporally with griffon vultures by using feeding stations in the afternoon. During this period soaring conditions are unfavourable for vultures and they return earlier to their breeding or roosting sites. This finding may provide a basis for a guideline: small scavengers may benefit from food supplied when griffon vultures are less active. Thus, we propose that, given the possible disappearance of facilitatory processes, diversifying the time at which carrion is left at feeding sites may be an efficient way of avoiding direct competition.

FUTURE PROSPECTS FOR MANAGEMENT DECISIONS IN CONSERVATION

In the long term it is desirable that legal dispositions be passed in order to ensure that carcasses generated by extensive livestock production (i.e., those that fulfill all mandatory sanitary requisites) remain in the field. This scenario would recreate the type of carrion availability that occurred up to quite recently in Mediterranean landscapes with traditional agricultural/livestock production (Donázar *et al.* 1996a; Margalida *et al.* 2007; Olea and Mateo-Tomás, 2009). The reality, however, is that despite the fact that the restrictive European sanitary legislation that obliges all livestock carcasses to be removed from the wild (EU999/2001) has been complemented by a series of regulations that allow supplementary feeding to be used as a strategy for the conservation of avian scavengers in southern Europe (EU1774/2002; EU322/ 2003; EU830/2005; CE 1069/2009), the implementation of these policies at the local level is promoting the concentration of carcasses at just a few sites or ‘vulture restaurants’. It is logical to assume that this situation is not going to change in the short or midterm and that feeding stations will remain as a key management tool for endangered scavengers. Therefore, the management of supplementary feeding stations must improve, as much from a sanitary point-of-view (Blanco *et al.* 2006; Lemus *et al.* 2008) as from the technical standpoint of how to effectively resolve in situ questions that range from the actual site of the feeding station to the management of the carrion provided.

Our study provides for the first time clear guidelines that will help managers favour species that do not act independently but work as part of a guild that exploits similar resources. Modern conservation premises encourage not only the conservation of single species and populations but also of ecological and evolutionary processes involving complex species interactions (Soulé *et al.* 2005). Thus, our findings will help to avoid undesirable consequences deriving from strong interspecific hierarchies that can lead to the monopolization of resources by dominant species as a result of its size and degree of sociability and aggressiveness. Management actions should be directed towards the creation of a chain of feeding stations supplied sporadically with food, which would thus avoid the concentration of resources in just a few places (see also Deygout *et al.* 2009). Other important aspects to take into account include: (a) the need to provide small carcasses, which will benefit the smaller facultative scavengers; (b) the importance of providing food at times at which the dominant species, the griffon vulture, is absent; and (c) that the location of feeding stations be studied carefully in order to maximise the possibility of use by certain species with clear patterns of habitat selection. These kinds of recommendations have begun to be used in the 'vulture restaurants' in Spain that have been specifically created to aid the region's endangered vulture populations (Benítez *et al.* 2009; Margalida *et al.* 2009; Moreno-Opo *et al.* 2010). It is worth noting that our approach may also be applicable to other regions of the world and, in particular, to large areas of Africa, the Middle East and Asia (Green *et al.* 2004; Shultz *et al.* 2004; Thiollay, 2006; Koenig, 2006) where scavenger species are in sharp decline and where scavenger guilds have similar species composition and/or structures [gregarious specialists of the genus Gyps and a broad range of more facultative species, König (1983), Hertel (1994), Hertel and Lehman (1998)].

The management of 'vulture restaurants' must be regarded as part of a dynamic system whose creation and management must be constantly monitored in order to detect any indications that will give rise to new strategies and techniques that will be of use in the future. Through exhaustive field monitoring managers can learn about the processes occurring at vulture restaurants and thus be in a position to design new conservation measures in accordance with any new conditions and constraints that may arise. It is to be expected that, due to their life strategies, the various species involved will not respond in the same way to management measures, and also that responses will vary over space and time. In our study system, the dominant species, the griffon vulture, has enjoyed populational growth rates of almost 500% in recent decades (Del Moral and Martí, 2001) – way above those of other species – that have not occurred in other areas of Europe (see reviews in Donázar et al. (2009a). Managers must regard the supplementary feeding of scavengers in 'vulture restaurants' as a valuable conservation tool in cases in which the maintenance of populations purely on the basis of natural resources and carcasses derived from extensive grazing is in jeopardy, and as a management tool that can be aimed at satisfying specific objectives. In this context and in a dynamic environmental and legislative scenario, the active adaptive management of supplementary feeding is essential if we are to learn about the effectiveness of these conservation decisions (McCarthy and Possingham, 2007; Possingham *et al.* 2001).

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SYNTHESIS

During decades theoretical studies on habitat selection through to studies on optimal foraging, have acknowledged the role of food resource availability in animal distribution and abundance, (Mac Arthur & Pianka 1996; Verner *et al.* 1986; Rosenzweig 1991; Giraldeau & Caraco 2000; Jones 2001; Begon *et al.* 2006; Hancock & Milner-Gulland 2006 and references therein). Most of them rely on theoretical modelling to try to describe the ways in which foragers track food in order to maximize their fitness (Fretwell & Lucas 1970; Pettifor *et al.* 2000; Nonaka & Holme 2007; Stephens *et al.* 2007; Overington *et al.* 2008). Empirical studies, on the other hand, tend to deal with the consequences of factors such as predation, social interactions, and future changing environmental conditions coupled to climate change (Marra 2000; Mönkkönen *et al.* 2004; Wilmers & Getz 2005; Groom *et al.* 2006; Coulson & Malo 2008). However, as we already mentioned in the introduction of this thesis, experimental studies based on the ecological effects of food resource distribution and its predictability are almost inexistent. Within this scenario, our main aims were to examine in depth the potential consequences of food resource predictability, often induced by human activities, on the spatial distribution on organisms, on interspecific relationships and ultimately how they might permeate to distant trophic levels. Finally, focusing on avian scavengers and the currently implemented conservation tool devoted to recover their decimated populations, i.e. the supplementary feeding stations (or so-called vulture restaurants); we have provided several guidelines to improve their effectiveness through adaptive management.

MAIN CONTRIBUTIONS

Randomness and coexistence

The first result that emerges from our research is that, the positive relationships within the avian scavenger guild are maintained only when food availability is unpredictable i.e. the presence of some species enable the access to food for others (Chapter I). On the contrary, when resources become clumped and predictable they can be monopolized by a single dominant species (Chapter I & VI). Up to date, this fact remains unexplored and those studies which try to face these issues take the opposite perspective, evaluating the potential role played by food predictability on territorial behaviour and as a profitable vector for invasive species (Petren & Case, 1996; Eide *et* *al.* 2004). We propose that the preservation of randomness in nature may be a key determinant to maintain complex interespecific relationships within guilds and communities. Our findings support the message given by current studies, which highlight the implications of alterating interespecific interaction networks by global environmental change drivers, since they may exert important ecosystem-level consequences. In this sense, it is necessary to deepen in the conservation value of networks themselves in the currently described scenario (Tylianakis *et al.* 2010) but also to establish an ecosystem-oriented conservation research instead of focusing on single-species approaches (Mace *et al.* 2007; Lindermayer *et al.* 2007). This is particularly true for our study system, i.e. the avian scavengers; up to date, the scant ecological studies are focused on the demographic and population effects of supplementary feeding stations on those species target of conservation efforts (Carrete *et al.* 2006; Bosé & Sarrazin 2007; Oro *et al.* 2008; and see for more examples Donázar *et al.* 2009). In this thesis we departed from a wider perspective, focusing on the community level, and found that clumped food favours dominant specialists, promoting a despotic use and/or a monopolization of the resource (Chapters I & VI). In other words, we found an accentuation of hierarchies (Petren & Case 1996; Pusey & Packer 1997) which can determine the exclusion of subordinate species from resources and consequently plummet the intra-guild diversity. In this context, these species are forced to develop strategies such as temporary segregation to gain access to resources (Chapter VI and see other examples in Cody 1974; Carothers & Jaksíc 1984; Moril & Boydl 2004; Begon *et al.* 2006; Blázquez *et al.* 2009).

Distribution of abundances of feeding birds according to food sources

Variations in the spatial distribution of food may well be the basis underlying both the interactions between individuals (Vahl *et al.* 2007; Bissonette & Storch 2007) and the adaptive foraging strategies (Stenberg & Persson 2005; Overington *et al.* 2008). In this thesis we have found that facultative scavenger species may track changes in the spatial distribution of food resources, showing differential aggregation patterns between biomes according to variations in the availability (Chapter II). Recent studies suggest that organism, and birds in particular, may develop specific behavioural strategies which enable them to compensate for the environmentally limiting factors and increase their chances of survival (Grimm *et al.* 2005; Wichmann *et al.* 2005), a trait that is especially relevant for migrant birds. This scenario has received preferential attention in this thesis. We found that whereas African grounds are well-structured ecosystems with a high availability of food resources (i.e. from predictable slaughterhouse to dessert locust outbreaks) in Europe food availability for scavengers is more limiting (Villafuerte *et al.* 1998; Delibes-Mateos *et al.* 2008 and references therein) and available mainly at predictable places (i.e. rubbish dumps and supplementary feeding stations) where birds are forced to aggregate (Chapter II).

Our results deal with suggestions given by Mooney & Cleland (2001) on how strong interspecific competition can play a role in extinction processes even if this cannot be detected on the time scale of most scientific studies. The variability in the response to changing environments differs substantially between species, resulting in different degrees of interspecific competition and diet overlap (Tokeshi 1999; Bolnick *et al.* 2010 Chapter II, IV). Meanwhile, the diet overlap detected by us in European breeding areas might be suggesting that the induced co-existence group-living, shown here by large groups of birds feeding together, may be not profitable in the long term, at least for some individuals (Maher & Lott 2000; Johnson *et al.* 2002; Eide *et al.* 2004, Chapter I, II, VI). Although we are aware that focal species may show different degrees of social behaviour, e.g. in Africa birds may sporadically conform small roosts (unpublished data), the pattern of huge arrangements found in Europe lead us to suspect that they would be far from profitable for birds (see above). We take as an example the population of Egyptian vultures at our study area (Ebro valley, northern Spain) which has been subjected to continuous monitoring over the last 20 years. The large aggregations that form both at roosts (over 60 birds), and at predictable feeding sites (more than 20 at the same time, unpublished data) are likely to play an important role in mate finding (Blanco & Tella 1999) and in increasing the probability of persistence of neighbouring territories (Grande *et al.* 2009). Yet what, this thesis highlights is that they may become ecological traps based on conspecific attraction (Chapter I).

To sum up, the identification of potential limiting factors operating both at wintering and breeding grounds is a key step for the understanding of population trends (Sillet *et al.* 2000; Cotton 2003; Newton 2004; Sanderson *et al.* 2006), especially if we consider that over 50% of European birds are trans-Saharan migrants, and many of them show long-term population declines (Sanderson *et al.* 2006; Thiollay 2006). In this thesis, we focused exclusively on the spatial patterns of feeders and their activities at food resources of different degrees of predictability, and found that when food resources are clumped, competition is exacerbated and diets overlap, determining lower probabilities of coexistence.

Predation risk on external communities

Our findings suggest that places where food resources are clumped, facultative predators aggregate triggering negative consequences on communities of prey living in the vicinity. Up to date, the literature has only described how the large availability of food can cause a sharp increase in certain population of predators which, subsequently, might affect the viability of endemic species (Kristan & Boarman 2003). Here, we empirically demonstrate for the first time that aggregations of facultative predators at carcasses may have population consequences on organisms not directly related to the processes of consumption of food resources (Chapter III-IV), thus stressing the importance of the role of carrion resources in structuring local vertebrate communities. This phenomenon may be more accurate in areas lacking specialist carrion-feeders like, for instance, cold biomes and/or insular systems with relatively simple vertebrate communities composed of scarce and diverse species (Siepielski *et al.* 2010 and references therein) adding extra selection pressure. From a conservation perspective, our findings highlight that the probability of predation on non-scavenger organisms should be taken into account at the time of planning and designing the location of supplementary feeding stations with predictable food resources.

JUSTIFICATION AND SELF-CRITICISM

In this thesis we have missed certain effects which, we believe, are difficult to control when carrying out field work in natural environments. For example, it is reasonable to expect that there will be non-controlled carcasses in the study area and, besides, that some of the studied species may exploit those alternative food resources (randomly-distributed carcasses impossible to locate, such as small vertebrates). In the particular case of griffon vultures, the effect of non-independence among food sites could be particularly important given their large foraging radius (frequently reaching more than 100 km, see Pennycuick 1972; Mundy *et al.* 1992; Donázar 1993; C. Fernández: unpublished data of birds from our study area marked with satellite radiotransmitters). In any case, the nature of our studies made it impossible to control for this effect - a common constraint in field research on scavenging processes which does not invalidate the work (see among others Hernández *et al.* 1987; Wallace & Temple 1987; Hiraldo *et al.* 1991; Travaini *et al.* 1998; Meretsky & Mannan 1999; Gavashelishvili & McGrady 2006; Deygout *et al.* 2009; Blázquez *et al.* 2009; Carrete *et al.* 2010; Moreno-Opo *et al.* 2010).

This kind of environmental noise may have also affected the results of the study conducted at supplementary feeding stations (Chapter VI) because it was not an experimental work. We performed the study in a natural and largely unpredictable system covering a broad region. Consequently, we were not able to control, for example, the amount of food available simultaneously in the supplementary feeding stations and in the wild (see above). Moreover, in natural systems such as our study area it is virtually impossible to individually monitor all birds that are foraging or feeding. These constraints are typical and common to all studies conducted on large populations of scavengers under natural conditions (Deygout *et al.* 2009). It could be argued that this fact can be solved with individual marking but it is obvious that this is unviable when research is done on large populations. It should be noted that the study area holds very large scavenger populations with thousands birds. For example, after decades of intensive monitoring of Egyptian vultures in the study region (more than 600 marked individuals, see Grande *et al.* 2009), only a small fraction were observed regularly at the feeding stations, and most observations were of unmarked birds. Thus, as in the bulk of ecological studies, we have improved the scale but only at the cost of losing detailed individual information.

PERSPECTIVES

Ecological organization levels can be compared to a stair with increasing levels of complexity: individuals, populations and communities. Ecological studies dealing with the effects of resource predictability have focused almost exclusively on the population level (Eide *et al.* 2004 and references therein). In this thesis we have tried to move our research up one step: guilds and communities. However, the relationship between food resource distribution and the base level i.e. the individual organism remains scarcely explored. We are gaining knowledge on several traits such us age, sex, body condition, stress level, genetic and/or personalities which may decisively impact on individual fitness. We hypothesized that patterns of exploitation of random/clumped food resources would also be dependent of these individual traits. Moreover, individual differences in the use of random/predictable resources may have important consequences from a conservation point of view. Abundant and predictable food resources may produce extreme bias derived from the sharp increase in the survival of individuals who would have otherwise disappeared as a result of natural selection processes (Blanco 2006; and see review in Donázar *et al.* 2009).

Recently, Jackson *et al.* (2008) put forward an attractive idea based on a modelling approach: vultures form a cloud of individuals in the sky, flying at high altitudes. With this in mind we began to investigate the ways in which information spreads in these groups. This fact, and how individuals use this information are key issues for understanding the fitness benefits of living in groups (Krause & Ruxton 2002). Group movement is an active area in spatial ecology (Nathan 2008). This is because it is viewed as an interesting system for studying the power of self-organization to create global patterns from interactions between group members (e.g. Pratt & Sumpter 2006; Halloy *et al.* 2007; Ballerini *et al.* 2008). Often, these studies are conducted under laboratory conditions (e.g. using fish, cockroaches or grasshoppers), but studies under natural conditions are still scarce. In this sense, vultures are a paradigmatic study model for investigation on group foraging and information transfer, even when predictable and random carrion resources are available.

Moreover, avian scavengers, and vultures in particular, may play an interesting role rendering a scavenging service (Deygout *et al.* 2009) which, from an economic perspective and/or as an ecosystem service *per se,* until now remains unevaluated. The ecosystem service is a current hot topic (Gretchen &Matson 2008) which has even been studied as an avian ecological function (Sekercioglu 2006). In this sense, scavengers represent a new relevant topic which needs to start to be studied in depth and, which conservationist managers should take into account (Daily & Matson 2008).

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CONCLUSIONES

1. La distribución azarosa en la naturaleza de recursos tróficos (Ej. las carroñas) permite el establecimiento de interacciones positivas entre las especies que los explotan, dando lugar al desarrollo de procesos ecológicos intra-gremiales como la facilitación trófica. Por el contrario, la predecibilidad de estos recursos en el espacio y en el tiempo provoca la desestructuración del gremio favoreciendo únicamente al taxón más especialista y dominante en detrimento del resto de especies, provocando el desplome de la diversidad intra-gremial y desapareciendo los procesos facilitatorios.

2. Las poblaciones de aves carroñeras migrantes transaharianas adaptan sus estrategias de forrajeo en respuesta a la distribución y disponibilidad de las fuentes de alimento a lo largo de los distantes biomas que visitan. Así, en sus áreas de nidificación europeas alimoches y milanos negros mostraron un patrón de agregación en torno a puntos de alimento predecible como basureros y muladares y un alto grado de solapamiento de sus dietas. Por el contrario en las áreas de invernada africanas donde la disponibilidad de alimento es mas dispersa, con rebaños pastoreando bajo régimen extensivo, ambas especies mostraron distribuciones no agregadas en el espacio y no solaparon sus dietas. El milano negro además mostró incluso una mayor flexibilidad trófica que le permitió aprovechar los recursos pulsados como son las explosiones de langosta que aparecen esporádicamente en el Sahel.

3. La atracción que pueden llegar a ejercer los recursos predecibles, en nuestro caso de estudio las carroñas predecibles, sobre muchas especies que usan estas fuentes de alimento de modo facultativo provoca efectos indirectos sobre otras especies que no presenta vinculación alguna con la explotación directa del recurso. Esto se demostró a través de estudios diseñados en biomas con diferentes comunidades de carroñeros. En bosques templados, donde las carroñas perduran hasta varios meses durante el invierno sus efectos permean a través de muy distantes niveles tróficos, afectando la distribución espacial de especies herbívoras que ven incrementado su riesgo de predación por carroñeros facultativos. En otro experimento de campo llevado a cabo en un sistema insular más simple se demostró que el riesgo de depredación sobre las puestas simuladas de aves esteparias que nidifican en el suelo fue mayor en el entorno de carroñas y muladares.

4. La reducción en la disponibilidad de recursos alimenticios unido a la concertación del escaso alimento disponible puede llevar a un incremento de las jerarquías y un uso despótico del recurso. Así en nuestro caso de estudio, el actual declive de la ganadería extensiva unido a una cada vez más restrictiva legislación sanitaria ha limitado la disponibilidad de alimento para las aves carroñeras y puede provocar un incremento de la competencia interespecífica. Hemos detectado que cuando se redujo la disponibilidad de alimento por el cierre de la mayor parte de los muladares, el buitre leonado amplió su nicho trófico pasando a alimentarse de presas subóptimas como conejo silvestre y basura. De esta manera solapa su dieta con la de carroñeros facultativos como el alimoche quien ha mantenido invariable sus preferencias tróficas.

5. De todos los resultados obtenidos en secciones anteriores se deduce que la concentración de alimento en puntos predecibles, en nuestro caso de estudio de carroñas en muladares, tiene efectos muy relevantes desde el punto de vista ecológico a nivel de funcionamiento del gremio de carroñeros. No independientemente de ello, la existencia de muladares tiene un efecto importante sobre la conservación de las propias carroñeras como de especies y comunidades de vertebrados asociadas espacialmente a estos puntos. No obstante, debido a las limitaciones de la normativa sanitaria europea se hace por el momento imprescindible el uso de muladares como herramienta de gestión. Por ello es necesario obtener directrices de manejo que optimicen sus resultados.

6. Un estudio dirigido a obtener estas directrices demostró que cuando los buitres leonados, la especie dominante, alcanzaban tamaños de grupo por encima de un umbral determinado el resto de aves carroñeras dejaban de estar presentes en los muladares. Ese número de buitres leonados coincide con el número máximo encontrado en las carroñas dispuestas al azar. Sin embargo, aun en este escenario de monopolización de las carroñas dispuestas en muladares hemos detectado que las especies subordinadas son capaces de desarrollar estrategias para poder acceder al alimento, por ejemplo aquellas basadas en una segregación temporal.

7. Proponemos la implementación de un manejo adaptativo de los muladares, basado en el seguimiento exhaustivo de los procesos durante el aprovechamiento que hagan las especies del alimento que permitiría la rápida detección de problemas y la toma de decisiones interactiva para resolverlos. Por otro lado, aconsejamos manejar el tipo de carroña y la hora del vertido así como establecer la gestión y ubicación sobre la base de las preferencias de las especies más amenazadas.

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