THE ECOLOGICAL SOCIETY OF AMERICA

Frontiers in Ecology and the Environment

Issue No 4 Volume 14 May 2016

Mammals in the Chernobyl Exclusion Zone

Avian scavengers and supplementary feeding

Ecological intensification of agriculture

esa

Supplementary feeding and endangered avian scavengers: benefits, caveats, and controversies

Ainara Cortés-Avizanda[1,2]*, Guillermo Blanco[3], Travis L DeVault[4], Anil Markandya[5], Munir Z Virani[6,7], Joseph Brandt[8], and José A Donázar[2]

Large avian scavengers are among the most vulnerable vertebrates, and many of their populations have declined severely in recent decades. To help mitigate this marked reduction in abundance, supplementary feeding stations (SFS; colloquially termed "vulture restaurants") have been created worldwide, often without consideration of the scientific evidence supporting the suitability of the practice. SFS have been effective and important tools for conservation and reintroduction of avian scavengers. However, negative consequences can result from large aggregations of individual birds, disrupting intraguild processes and promoting density-dependent decreases in productivity. At the community level, SFS favor the congregation of predators (ie facultative scavengers), increasing predation risk on small- and medium-sized vertebrates in the vicinity of the SFS. These feeding stations might also affect processes of natural selection and even render populations maladapted to their natural environments. We also examine future scenarios for avian scavengers in relation to ecosystem services, to changes in agro-grazing economies and in land uses, and ultimately to rewilding landscapes where SFS play a controversial role.

Front Ecol Environ 2016; 14(4): 191–199, doi:10.1002/fee.1257

Carcasses are pulsed resources, often appearing randomly within landscapes and providing large amounts of food for a short period of time (Yang *et al.* 2008). Large herbivore carcasses, in particular, are prized resources for an extremely wide range of organisms, from bacteria to arthropods and vertebrates (DeVault *et al.* 2003). Although many animals use carrion at least occasionally (eg during periods of famine), strict scavenging specialization among vertebrates inhabiting terrestrial ecosystems is limited to large-bodied avian scavengers (Old World vultures [Accipitridae] and New World vultures [Cathartidae]). These species search large areas by sharing social information (Ruxton and Houston 2004; Cortés-Avizanda *et al.* 2014) and are characterized by complex interspecific facilitation processes (eg local enhancement and trophic advantage; see below for details and also DeVault *et al.* 2003; Cortés-Avizanda *et al.* 2012).

In a nutshell:

- Worldwide effort and investment have been devoted to creating supplementary feeding stations (SFS) in attempts to reverse or reduce observed declines of large avian scavengers
- Declines in avian scavenger populations disrupt food web functioning and the provision of ecosystem services
- SFS can increase survival of individual birds and help to maintain neighboring breeding populations
- However, supplemental feeding may also exert undesirable impacts within target populations and on non-target species and communities
- Ecological knowledge based on interdisciplinary research and stakeholder collaboration could provide solutions under an adaptive management framework

Avian scavengers in some East African areas still depend on migratory ungulates, mostly concentrated in protected areas, where herbivore populations have increased in some cases (Figure 1; Virani *et al.* 2011). Worldwide, however, the availability of wild ungulate carcasses has gradually decreased as a result of the replacement of wild ungulates by livestock (Figure 1). As a consequence, the diet of many avian scavengers is now based largely on domestic species (Lambertucci *et al.* 2009; Ogada *et al.* 2012). Yet especially during the past century, the availability of domestic carrion has been unstable because of rapidly changing agro-grazing economies and increasing sanitary regulations that may require burial or burning of livestock carcasses. As a result, in the late 1960s, conservationists created "vulture restaurants" or supplementary feeding stations (SFS) to increase the availability of food resources in southern Europe and southern Africa (Bijleveld 1974). At the end of the 20th century, the appearance of

[1]*Infraestruturas de Portugal Biodiversity Chair CIBIO-InBIO, Campus Agrário de Vairão, Vairão, Portugal* *(cortesavizanda@gmail.com); [2]*Department of Conservation Biology, Estación Biológica de Doñana, CSIC, Sevilla, Spain;* [3]*Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain;* *continued on last page*

M Virani

I Anton

Figure 1. *(a) In Africa, avian scavengers like vultures still depend on many of the vast herds of migratory ungulates such as the wildebeest populations in the Mara–Serengeti ecosystem. During the dry period between July and September each year, wildebeest experience high mortality as they cross the Mara River in the Masai Mara Reserve, which forms the northern part of the Serengeti. (b) Conversely, in Europe, vultures have become dependent on the carcasses of livestock animals after the gradual decrease of native wild ungulates.*

Bovine Spongiform Encephalopathy in Europe led to regulations that prohibited the abandonment of domestic ungulate carcasses in the field. With this crisis, the conservation of large avian scavengers was focused again on the creation of new SFS in Mediterranean countries (Donázar *et al.* 2009a, 2009b).

Supplementary feeding programs have also been considered as a key tool to provide micronutrients and to reduce ingestion of toxic compounds such as the veterinary pharmaceutical diclofenac by the birds; use of this drug nearly caused the extinction of once-abundant Indian vulture populations (see Panel 1; WebTable 1; Gilbert *et al.* 2007). Finally, the establishment of SFS is commonly proposed as a key management action for scavenger reintroduction efforts, often attracting considerable funding at both local and regional scales (see below).

To counteract real or perceived factors that constrain vulture populations, conservation initiatives have frequently included the establishment of SFS, where food is almost constantly, consistently, and predictably available (Figure 2; WebTable 1). SFS are popular for conservation and reintroduction of avian scavengers. Despite their demonstrated importance, the ecological consequences of intentionally supplied surplus food have traditionally received little attention (see also Robb *et al.* 2008). Although some research on SFS for avian scavengers has been conducted during the past decade, no synthesis is available thus far that can guide the work of scientists and managers. Here, we present an overview of SFS and the positive and negative effects that these practices may have on avian scavengers, from individuals to guilds (groups of species that exploit the same resources), as well as on non-target species and communities. We also discuss future research avenues and outline ways to optimize management of carrion resources, including supplementing food to maintain viable populations, functional guilds, and the ecosystem services they provide.

■ Pros and cons of supplementary feeding: ecological consequences

Enhancing demographic parameters

Supplementary feeding is often intended to enhance individual survival and thus provide immediate conservation benefits (WebTable 1). Long-term monitoring programs based on capture–recapture approaches have shown that SFS do improve survival for some fraction of the population, and may therefore facilitate population recovery in the long term, as was seen in the bearded (*Gypaetus barbatus*) and Egyptian (*Neophron percnopterus*) vultures in the Pyrenees and southern France, respectively (Panel 1; WebTable 1; Oro *et al*. 2008; Lieury *et al*. 2015). Moreover, food provided at SFS may distract vultures from consuming toxic carcasses of predators and other animals that have been illegally poisoned (Margalida *et al*. 2014). This scenario may also apply to other New and Old World scavenger populations in which higher survival rates have been observed in subadults, such as those of reintroduced griffon vultures (*Gyps fulvus*) in France (WebTable 1; Le Gouar *et al*. 2008). Documented increases in survival of long-billed vultures (*Gyps indicus*) and their

Panel 1. Case studies

Little is known about the lasting effects of supplementary feeding on populations of avian scavengers, mainly because of the difficulty in obtaining long-term data and because these practices often do not occur within well-established programs with clear scientific supervision. Several species-specific studies and conservation-based experiences shed light on the effectiveness of this management tool.

California condor

The California condor, rendered extinct in the wild, has been successfully reintroduced and three distinct populations have been established in California/Arizona/Utah (southwestern US) and Baja California (Mexico). In each population, captive-reared individuals continue to be released annually. Supplemental feeding plays an important role in successfully releasing the 1- to 2-year-old captive-reared condors because it acts as a substitute for the up to 18 months' worth of parental care that fledgling condors would typically receive in the wild. Additionally, supplementary feeding is necessary to capture and release wild condors to monitor blood lead levels, to treat condors that have been recently exposed to lead, and to fit condors with tracking devices. Unlike many other supplemental feeding programs for avian scavengers, food provisioning for the California condor is not related to food scarcity. It is believed that there is currently an adequate resource base available for condors without supplemental feeding; observations indicate that condors have less reliance on supplemental food sources given that their populations have increased and their range has expanded (WebTable 1; Kelly *et al.* 2014).

Indian vultures

Several populations of various Indian vulture species (see Figure 2) were substantially affected by use of the highly toxic, non-steroidal, anti-inflammatory drug (NSAID) diclofenac to treat livestock. Vultures were exposed when they scavenged carcasses of livestock treated with diclofenac shortly before death. Diversionary feeding with diclofenac-free carcasses – one of the mitigation policies that was implemented in Nepal (WebTable 1; Prakash *et al.* 2012) – has been shown to reduce but not eliminate vulture mortality from diclofenac poisoning, and uncertainty regarding the ranging behavior of Asian *Gyps* vultures makes it difficult to measure the effectiveness of such measures (Pain *et al.* 2008). Birds have been tagged with satellite transmitters in various parts of their distribution, not only to improve understanding of their movements, foraging range, and site fidelity, but also to aid the development of suitable conservation strategies; however, the cost effectiveness of these measures has not been determined.

Bearded vulture

The bulk of the European population of bearded vultures is located in the Pyrenees Mountains between France and Spain. To contribute to the recovery of the last remaining 40 pairs, from 1988 to 2002 as many as 25 SFS were created, providing up to 15,000 kg of bone per year, a practice that is still active (Margalida *et al.* 2014). As a result, the pre-adult survival rate has improved and the population has recovered markedly (Oro *et al.* 2008). On the other hand, large SFS appear to promote aggregation of bearded vulture breeding pairs, as well as a decrease in breeding success of vultures in territories near the feeding stations, perhaps due to the greater probability of interactions between breeding adults and non-breeding birds (Carrete *et al.* 2006a). Additionally, overabundant food resources at SFS have likely contributed to overcrowding within the central Pyrenean bearded vulture population, leading to observed changes in mating systems (appearance of polyandrous trios) that are causing further reductions in breeding success (Carrete *et al.* 2006b; Margalida *et al.* 2014). Relocating SFS toward the periphery of the species' breeding range has been recommended to encourage vulture colonization on neighboring mountains, but regional governments are reluctant to do so because these feeding stations are popular with local wildlife managers and birdwatchers in their existing locations.

African vultures

Scavenging birds have depended on predictable food resources – including village abattoirs and rural butcheries – across Africa for centuries. At some highland sites in East Africa, as many as seven species of vultures routinely congregate at sites where offal is dumped. Currently, supplementary feeding is increasingly used to help counter abrupt declines in the abundance of these carrion-eaters. Mainly because of the use of poisons, seven species of vultures have experienced population decreases at rates exceeding 80% over three generations, and therefore qualify for uplisting to "Critically Endangered" on the IUCN Red List of Threatened Species. Surplus food schemes have a long tradition in South Africa, where nearly 200 SFS have been established for vultures and have been an effective conservation tool despite management challenges (A Botha, pers comm); some of these challenges include ensuring that disposed carcasses are free of chemicals (poisons and veterinary drugs) and are safe from predators and humans. Wing tagging of vultures at feeding stations has yielded vital and cost-efficient movement data for tagged birds that are reported through a network of observers. These feeding stations, such as the one in Giant's Castle National Park, have also provided important revenue through photographic tourism. In East Africa, one feeding station was developed at Hell's Gate National Park, where colonies of Ruppell's vultures (*Gyps rueppellii*) breed. However, because of a lack of oversight, the effectiveness of this feeding station remains in question.

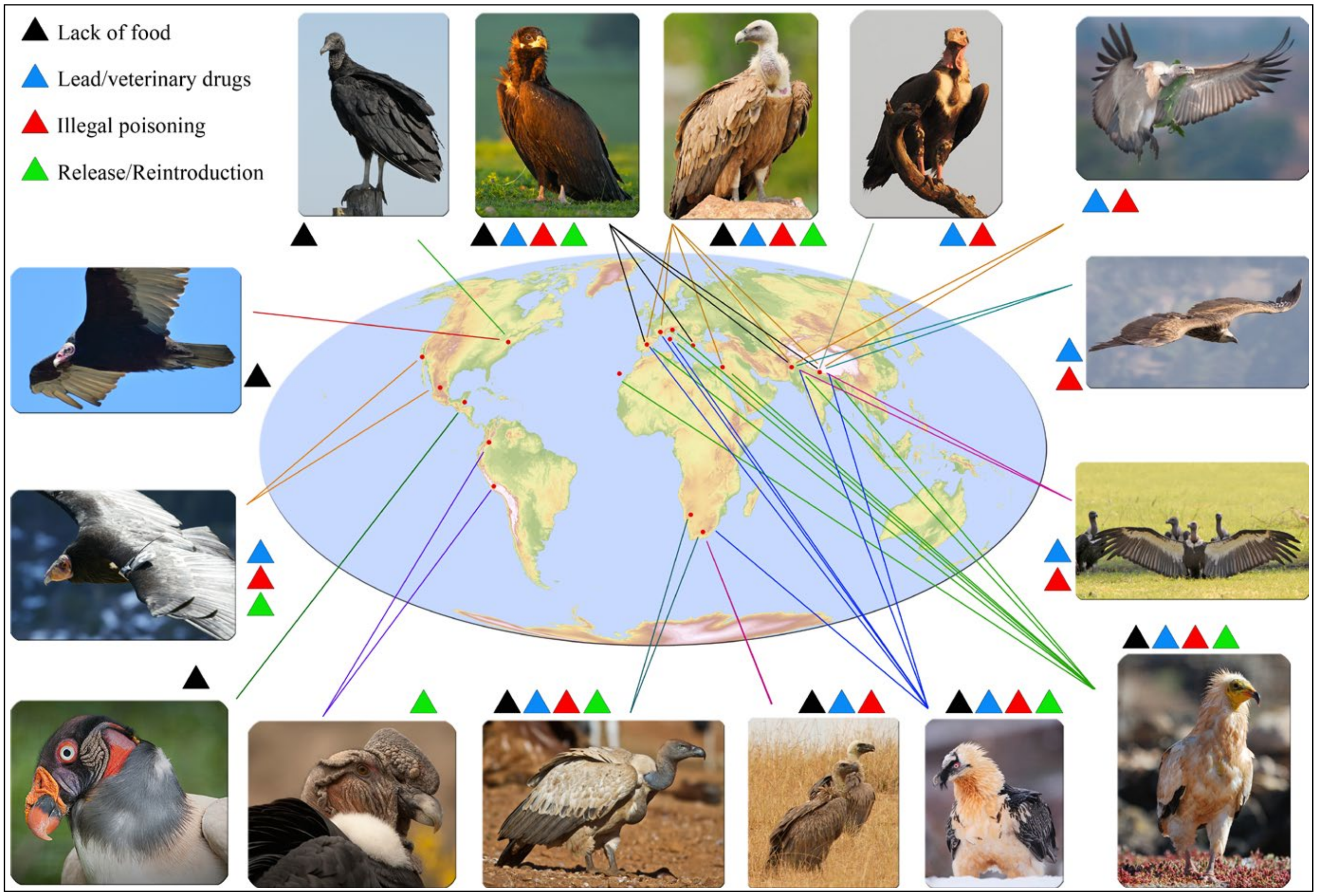

Figure 2. *World map of the distribution of supplementary feeding programs, focal target species, and most important drivers of population declines (based on data in WebTable 1). Clockwise – Old-World vultures: cinereous vulture (*Aegypius monachus*), griffon vulture (*Gyps fulvus*), red-headed vulture (*Sarcogyps calvus*), long-billed vulture (*Gyps indicus*), Himalayan griffon vulture (*Gyps himalayensis*), white-rumped vulture (*Gyps bengalensis*), Egyptian vulture (*Neophron percnopterus*), bearded vulture (*Gypaetus barbatus*), African white-backed vulture (*Gyps africanus*), Cape griffon vulture (*Gyps coprotheres*). New-World vultures: Andean condor (*Vultur gryphus*), king vulture (*Sarcoramphus papa*), California condor (*Gymnogyps californianus*), Turkey vulture (*Cathartes aura*), black vulture (*Coragyps atratus*). For image credits, see WebPanel 1.*

subsequent slight population recovery have also been attributed to SFS as well as to the ban on diclofenac (Figure 2; WebTable 1; Gilbert *et al.* 2007; Balmford 2013). SFS are also playing a key role in the reintroduction of California condors (*Gymnogyps californianus*) in North America, mitigating the effects of lead poisoning that nearly brought the species to extinction (Panel 1; WebTable 1; Snyder and Snyder 2005; references in Kelly *et al.* 2014).

SFS have often been used to increase reproductive success, especially during reintroduction programs, but its effectiveness in this regard is controversial. In fact, the breeding success of Egyptian and griffon vultures had purportedly been linked to long-term changes in the sanitary restrictions governing feeding programs (eg Grande *et al.* 2009; Margalida and Colomer 2012; WebTable 1). Yet these assertions were based on circumstantial evidence, and at least for some regions such as the Mediterranean countries, the recovery of birds of prey was more likely derived from the cessation of their historical persecution against a backdrop of overall food availability, far above the needs of the populations (Parra and Tellería 2004). However, experimental approaches offer contradictory results; although some researchers claimed that SFS have probably aided reproduction of facultative and specialist scavengers (González *et al.* 2006; Ferrer *et al.* 2014), other authors did not find a similar relationship (Blanco 2006; Oro *et al.* 2008; Margalida 2010).

Favoring aggregation of birds: a double-edged sword

Proximity to predictable feeding sites favors the establishment of communal roosts where immature birds gather; the creation of SFS is therefore often considered a useful management tool for attracting individuals that will disperse to isolated and declining populations (Donázar *et al.* 2009b; Lieury *et al.* 2015; and see WebTable 1). These concentrations increase the probability of long-term territory occupancy, enhancing population viability (Grande *et al.* 2009). Conversely, the aggregation of non-breeding birds at SFS might contribute to reduced reproductive success in breeding birds with territories located near the feeding stations, perhaps due to increased interactions between breeding adults and non-breeding birds, and to crowding of breeding populations (Carrete *et al.* 2006a, 2006b).

Unintended effects: health effects among individuals, communities, and ecosystems

Avian scavengers can be susceptible to pathogens that infect humans and domestic animals. This risk may depend primarily on two factors: farming practices involving the consumed livestock species coupled with the sanitary management of SFS. Provisioning of carrion from intensively reared and medicated livestock such as poultry and swine could be detrimental due to the potential ingestion of veterinary drug residues and harmful multidrug-resistant pathogens (Blanco 2014, 2015; Blanco *et al.* 2016). Apart from the diclofenac crisis in South Asia (Watson *et al.* 2004) and unintended poisoning from pentobarbital-euthanized carcasses, there is little knowledge about the impact of (1) secondary poisoning and subtle intoxication with veterinary drugs and (2) infections with pathogens acquired from carrion. Specifically, no research is currently available on the interaction between food availability and carcass nutritional quality, the content of veterinary drugs and disease agents in carcasses obtained from different livestock farming practices, and how these influence mortality rates and survivor health in avian scavengers (WebTable 2).

SFS have unintended effects on the structure and functioning of feeding guilds. The predictability of carcasses at SFS and other consistent sources of carrion favors the most social and dominant species (griffon vultures in Europe, black vultures [*Coragyps atratus*] in South America), which monopolize food to the detriment of less competitive and often more threatened scavengers (Figure 3; Carrete *et al.* 2010; Cortés-Avizanda *et al.* 2010, 2012). Moreover, the predictability (in space and time) of the resources found in SFS reduces diversity of the guild and disrupts interspecific facilitation (ie small-sized facultative scavengers landing earlier at carcasses would increase the chances of carcass detection by larger vultures [local enhancement], and dismemberment of carcasses by large vultures will allow smaller scavengers to profit from the resource [trophic advantage]; Cortés-Avizanda *et al.* 2012).

Non-scavenging members of vertebrate communities may also be negatively affected by the existence of predictable and concentrated carrion in SFS. Facultative scavengers (or avian and mammal predators; Selva and Fortuna 2007; Cortés-Avizanda *et al.* 2009a, 2009b; WebTable 1) consume carcasses less efficiently and more slowly than obligate scavengers and thus remain gathered near clumped food resources for longer periods (Ogada *et al.* 2012). As a result, predation on other small- and medium-sized prey species living in the same areas might increase. Facultative scavengers exert predation pressure on passerine birds and herbivorous mammals in the vicinity of SFS and other carcass accumulations (WebTable 1; Cortés-Avizanda *et al.* 2009a, 2009b; Yarnell *et al.* 2014), a situation that may be more pronounced where cold temperatures suppress microorganism and invertebrate activity and where obligate scavengers, which quickly deplete carrion, are not present (DeVault *et al.* 2003; Cortés-Avizanda *et al.* 2009a; Donázar *et al.* 2009b and references therein).

Social and economic perspectives

Ecosystem services provided by vultures have been recognized as a type of mutualism with humans (DeVault *et al.* 2016; see below). By removing carcasses, vultures hamper growth in species that are potentially harmful to humans (including some microorganisms, rodents, and feral dogs) that prosper with local food abundance (Markandya *et al.* 2008; Ogada *et al.* 2012). These services are supplied by the birds at no cost when carcasses of free-range livestock are left undisturbed in the countryside (Morales-Reyes *et al.* 2015). A similar scheme can be found when livestock carcasses are abandoned by farmers near their farms (so-called "light feeding stations"; WebTable 2; Monsarrat *et al.* 2013). However, large SFS specifically designed to feed vultures frequently require major investments such as road construction, fencing, and carcass management (transport from distant sources, such as slaughterhouses). In France and Spain, the creation of a new feeding station costs between €20,000 ($21,900) and €50,000 ($54,700), plus additional maintenance fees of €20,000 ($21,900) per year (Donázar *et al.* 2009b).

Vultures have been the subject of historical fascination (including spiritual roles; Figure 4) among humans for over 12,000 years. This is likely one of the reasons why direct observation of scavenging birds is yielding economic benefits to rural economies within developing regions in Europe, Africa, and the Americas (DeVault *et al.* 2016). SFS may therefore help maintain cultural services (DeVault *et al.* 2016), but their net economic value has not yet been evaluated.

Ongoing research and perspectives

Despite recognition of the limitations of SFS in avian scavenger conservation, an exhaustive study of their advantages and disadvantages has only recently become possible (see above), mainly because the increased number and extended duration of SFS now provide adequate information to allow quantitative analysis. Managers currently have a better understanding of how

Figure 3. *Socially dominant, specialist scavengers can monopolize carcasses when they are abundant and when feeding resources are predictable. In regions within the Mediterranean Basin, (a) griffon vultures (*G fulvus*) congregate by the hundreds at feeding stations, whereas small-body-sized scavengers (b) red kite (*Milvus milvus*) and Egyptian vulture (*N percnopterus*) are able to obtain more benefits from unpredictable resources (Cortés-Avizanda* et al. *2012). In Patagonia, accumulation of resources though human activities favors the expansion of (c) black vultures (*C atratus*) to the detriment of (d) Andean condors (*V gryphus*). Condors are much larger than black vultures, but the latter may be found in very high numbers in populated regions where they exclude condors from ungulate carcasses (Carrete* et al. *2010).*

avian scavengers respond not only to carcass size and type but also to variation in SFS timing and location (Panel 2; Cortés-Avizanda *et al.* 2010, 2012; Moreno-Opo *et al.* 2015). Future research challenges include discerning how individuals respond to similar ecological scenarios and which factors determine variability between them. In particular, a study of inter-individual variability may provide practical insights into how and when to best deploy SFS. Likewise, as described in other avian groups (van Overveld and Matthysen 2010), investigating how individual avian scavengers modulate their food-searching strategies and social behavior in response to SFS-based changes in food predictability warrants further scrutiny (Ruxton *et al.* 1995; Cortés-Avizanda *et al.* 2014). Special attention should be paid to examining what influences individual foraging strategies. Satellite tagging evidence shows that when food location is predictable, some individuals tend to concentrate their movements within and search efforts on these areas (Monsarrat *et al.* 2013). However, more detailed research is needed (eg tracking of scavengers captured at SFS may reflect an overreliance on this type of resource; López-López *et al.* 2014). Asymmetric individual responses to clumped food resources may also have evolutionary implications. Predictable food sources could increase the survival of individuals that would otherwise disappear as a result of selective processes (Blanco 2006; Donázar *et al.* 2009b; García-Heras *et al.* 2013; Oro *et al.* 2013). As such, human-provided, predictable food patches may represent an artifact that could lead to an uncertain future for populations, functional guilds, and, ultimately, communities.

From a practical point of view, managers must determine how to establish SFS sites in relation to the spatial distribution of scavengers. Clearly, because the probability of visiting feeding stations is inversely related to the distance from breeding sites (García-Heras *et al.* 2013; see also López-López *et al.* 2014), spatial constraints should be considered in feeding programs. Additionally, site-specific assessments are required because guild

Figure 4. *A long-billed vulture* (G indicus) *at the sacred cenotaphs of Orchha in the state of Madhya Pradesh in India. Old World vultures have been revered in cultures for more than 12,000 years, with the earliest documented rock drawings of vultures found in Göbekli Tepe, an archaeological site at the top of a mountain ridge in southeastern Turkey. It is believed that in the early Neolithic culture of Anatolia, the recently deceased were deliberately exposed in order to be consumed by vultures and other avian scavengers. This would represent an early form of "sky burials", as still practiced by Buddhists in Tibet and by Zoroastrians (Parsees) in Iran and India. In Hindu mythology, Jatayu – the vulture god – sacrificed his life to save the goddess Sita from the evil ten-headed demon Ravana. In Maasai culture, vultures are considered goodwill messengers showing where missing cattle are located. In ancient Egypt, Nekhbet, the vulture, along with the cobra, symbolized the unity of Upper and Lower Egyptian civilizations.*

structure (determined by the presence and relative abundance of each scavenger species) may vary between regions. Thus, the benefits potentially obtained by a species may differ, depending on whether dominant competitors are present. Much research remains to be done on this topic. To date, most studies have focused on scavenger guilds of the Mediterranean Basin; less information is available concerning scavenger communities from other Old World regions and from locations in the New World.

Finally, we note that human populations are declining in some rural areas of Europe, providing an opportunity for future rewilded scenarios (Navarro and Pereira 2012). The current decline of traditional agro-grazing practices (numbers of livestock have fallen by 25% between 1990 and 2010; Navarro and Pereira 2012) could result in a substantial reduction of food resources for vultures. Conversely, landscape abandonment by humans may drive the expansion of wild ungulate populations (Donázar *et al.* 2009b) and large carnivores such as wolves, providing a regular supply of randomly distributed carcasses (Selva and Fortuna 2007). Such a scenario would also add stability to trophic networks by buffering the oscillations linked to temporally pulsed events (Wilmers and Getz 2005). This situation may have counterparts in the Old and New Worlds, where livestock raising could be offset by recovering wild herbivore populations (Madhusudan 2004). However, such an offset cannot be generalized to densely human-populated regions, where the dependence of scavengers on farming activities and supplementary feeding schemes may be the rule (eg Margalida *et al.* 2011; Ogutu *et al.* 2011).

Panel 2. Management recommendations

(1) **Focusing on target species**
- Preferentially establish SFS at suitable and (eventually) at variable locations, based on the distribution and seasonal movements of the less abundant and less dominant scavenger species.
- Manage the spatiotemporal predictability and abundance of disposed carrion according to requirements of target species.
- Promote the use of SFS by threatened facultative scavengers as opposed to abundant and dominant vultures by providing small carcasses and small pieces of carrion remains rather than large quantities of livestock carcasses.

(2) **Controlling adequacy of food resources**
- Ensure safety of provisioned carcasses by avoiding veterinary pharmaceuticals, lead bullets in game species, and other dangerous materials (eg plastics, rope, metal pieces).
- Improve nutritional quality by avoiding the exclusive use of particular livestock species (eg swine) or by-products (eg viscera and offal).
- Implement sanitary controls of carcasses to avoid the transmission of livestock pathogens to scavengers. Because such transmission may occur more frequently within birds, poultry should be banned.

(3) **Designing and monitoring SFS**
- Prioritize multiple small and dispersed, rather than few and large, SFS.
- Avoid environmental contamination and risk to scavengers by establishing SFS in suitable places.
- Implement strict monitoring schemes for supplied food and scavenger use throughout the year, and eventually adapt carrion provisioning based on scientifically rigorous and adaptive approaches.

Conclusions

Since vulture restaurants were first implemented over half a century ago, supplemental feeding of vultures and other threatened scavengers has been widely accepted as an effective management tool among conservationists and managers. From an ecological perspective, SFS supplied with large amounts of carrion represent a major modification of the natural distribution of resources, the consequences of which may even reach the ecosystem level, potentially influencing vegetation (Melis *et al.* 2007) and abiotic components such as soil nutrients and water (reviewed in Donázar *et al.* 2009b).

In the short and medium terms, conservation of vultures and other avian scavengers requires a balance between four factors: the recovery of wild ungulates in rural areas; the maintenance of traditional healthy agro-grazing practices (where economically and socially feasible); the modification of laws related to sanitary regulations and to the banning of lead ammunition and disposal of medicated livestock carcasses; and public education and outreach, especially in developing countries (Ogada *et al.* 2012). Accordingly, SFS may be useful for achieving specific conservation goals under adaptive management and strict monitoring (Panel 2). Likewise, it may be possible to exploit opportunities for tourism and other ecosystem services provided by scavengers by requiring beneficiaries to pay for the relevant services. Such payments for ecosystem service (PES) schemes have been successful in other contexts and could be applied to this domain (Barbier and Markandya 2012). However, considerable research will be needed, to estimate the willingness of different groups to pay, and to determine what types of institutional arrangements would support various PES schemes.

Acknowledgements

This work was funded by the projects CGL2012-40013-C01, CGL2010-15726, and RNM-1925. ACA was supported by a postdoctoral grant FCT-SFRH/BPD/91609/2012. I Afán (LAST-EBD) and M de la Riva assisted with map and Figure 2 creation, respectively.

References

Balmford A. 2013. Pollution politics and vultures. *Science* **339**: 653.

Barbier EB and Markandya A (Eds). 2012. A new blueprint for a green economy. New York, NY: Routledge.

Bijleveld M. 1974. Birds of prey in Europe. London, UK: Macmillan.

Blanco G. 2006. Natural selection and the risks of artificial selection in the wild: nestling quality or quantity from supplementary feeding in the Spanish imperial eagle. *Ardeola* **53**: 341–51.

Blanco G. 2014. Can livestock carrion availability influence diet of wintering red kites? Implications of sanitary policies in ecosystem services and conservation. *Popul Ecol* **56**: 593–604.

Blanco G. 2015. Multiresistant *Salmonella* serovar Typhimurium monophasic in wintering red kites *Milvus milvus* in Segovia, central Spain. *J Raptor Res* **49**: 339–41.

Blanco G, Junza A, Segarra D, *et al.* 2016. Wildlife contamination with fluoroquinolones from livestock: widespread occurrence of enrofloxacin and marbofloxacin in vultures. *Chemosphere* **144**: 1536–43.

Carrete M, Donázar JA, and Margalida A. 2006a. Density-dependent productivity depression in Pyrenean bearded vultures: implications for conservation. *Ecol Appl* **16**: 1674–82.

Carrete M, Donázar JA, Margalida A, *et al.* 2006b. Linking ecology behaviour and conservation: does habitat saturation change the mating system of bearded vultures? *Biol Lett* **2**: 624–27.

Carrete M, Lambertucci SA, Speziale K, *et al.* 2010. Winners and losers in human-made habitats: interspecific competition outcomes in two Neotropical vultures. *Anim Conserv* **13**: 390–98.

Cortés-Avizanda A, Selva N, Carrete M, *et al.* 2009a. Effects of carrion resources on herbivore spatial distribution are mediated by facultative scavengers. *Basic Appl Ecol* **10**: 265–72.

Cortés-Avizanda A, Carrete M, Serrano D, *et al.* 2009b. Carcasses increase the probability of predation of ground nesting birds: a caveat regarding the conservation value of vulture restaurants. *Anim Conserv* **12**: 85–88.

Cortés-Avizanda A, Carrete M, and Donázar JA. 2010. Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. *Biol Conserv* **143**: 1707–15.

Cortés-Avizanda A, Jovani R, Carrete M, *et al.* 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology* **93**: 2570–79.

Cortés-Avizanda A, Jovani R, Donázar JA, and Grimm V. 2014. Bird sky networks: how do avian scavengers use social information to find carrion? *Ecology* **95**: 1799–808.

DeVault TL, Rhodes OE, and Shivik JA. 2003. Scavenging by vertebrates: behavioral ecological and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* **102**: 225–34.

DeVault TL, Beasley JC, Olson ZH, *et al.* 2016. Ecosystem services provided by avian scavengers. In: Şekercioğlu CH, Wenny DG, and Whelan CJ (Eds). Why do birds matter? Avian ecological function and ecosystem services. Chicago, IL: University of Chicago Press.

Donázar JA, Margalida A, Carrete M, *et al.* 2009a. Too sanitary for vultures. *Science* **326**: 664.

Donázar JA, Margalida A, and Campión D (Eds). 2009b. Vultures feeding stations and sanitary legislation: a conflict and its consequences from the perspective of conservation biology. San Sebastián, Spain: Sociedad de Ciencias Aranzadi.

Ferrer M, Newton I, Muriel R, *et al.* 2014. Using manipulation of density-dependent fecundity to recover an endangered species: the bearded vulture *Gypaetus barbatus* as an example. *J Appl Ecol* **51**: 1255–63.

García-Heras S, Cortés-Avizanda A, and Donázar JA. 2013. Who are we feeding? Asymmetric individual use of surplus food resources in an insular population of the endangered Egyptian vulture (*Neophron percnopterus*). *PLoS ONE* **8**: e80523.

Gilbert M, Watson RT, Ahmed S, *et al.* 2007. Vulture restaurants and their role in reducing diclofenac exposure in Asian vultures. *Bird Conserv Int* **17**: 63–77.

González LM, Margalida A, Sánchez R, *et al.* 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (*Aquila adalberti*). *Biol Conserv* **129**: 477–86.

Grande JM, Serrano D, Tavecchia G, *et al.* 2009. Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. *Oikos* **118**: 580–90.

Kelly TR, Grantham J, George D, *et al.* 2014. Spatiotemporal patterns and risk factors for lead exposure in endangered California condors during 15 years of reintroduction. *Conserv Biol* **28**: 1721–30.

Lambertucci SA, Trejo A, Di Martino S, *et al.* 2009. Spatial and temporal patterns in the diet of the Andean condor: ecological replacement of native fauna by exotic species. *Anim Conserv* **12**: 338–45.

Le Gouar P, Robert A, Choisy J-P, *et al.* 2008. Roles of survival and dispersal in reintroduction success of griffon vulture (*Gyps fulvus*). *Ecol Appl* **18**: 859–72.

Lieury N, Gallardo M, Poncho C, *et al.* 2015. Relative contribution of local demography and immigration in the recovery of a geographically-isolated population of the endangered Egyptian vulture. *Biol Conserv* **191**: 349–56.

López-López P, García-Ripollés C, and Urios V. 2014. Food predictability determines space use of endangered vultures: implications for management of supplementary feeding. *Ecol Appl* **24**: 938–49.

Madhusudan MD. 2004. Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *J Appl Ecol* **41**: 858–69.

Margalida A. 2010. Supplementary feeding during the chick-rearing period is ineffective in increasing the breeding success in the bearded vulture (*Gypaetus barbatus*). *Eur J Wildlife Res* **56**: 673–78.

Margalida A and Colomer MA. 2012. Modelling the effects of sanitary policies on European vulture conservation. *Sci Rep* **2**: 753.

Margalida A, Colomer MA, and Oro D. 2014. Man-induced activities modify demographic parameters in a long-lived species: effects of poisoning and health policies. *Ecol Appl* **24**: 436–44.

Margalida A, Colomer MA, and Sanuy D. 2011. Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. *PLoS ONE* **6**: e20248.

Markandya A, Taylor T, Longo A, *et al.* 2008. Counting the cost of vulture decline – an appraisal of the human health and other benefits of vultures in India. *Ecol Econ* **67**: 194–204.

Melis C, Selva N, Teurlings I, *et al.* 2007. Soil and vegetation nutrient response to bison carcasses in Bialowieza Primeval Forest, Poland. *Ecol Res* **22**: 807–13.

Monsarrat S, Benhamou S, Sarrazin F, *et al.* 2013. How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers. *PLoS ONE* **8**: e53077.

Morales-Reyes Z, Pérez-García JM, Monleón M, *et al.* 2015. Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. *Sci Rep* **5**: 7811.

Moreno-Opo R, Trujillano A, Arredondo Á, *et al.* 2015. Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. *Biol Conserv* **181**: 27–35.

Navarro LM and Pereira HM. 2012. Rewilding abandoned landscapes in Europe. *Ecosystems* **15**: 900–12.

Ogada DL, Torchin ME, Kinnaird MF, *et al.* 2012. Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conserv Biol* **26**: 453–60.

Ogutu JO, Owen-Smith N, Piepho H-P, *et al.* 2011. Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977–2009. *J Zool* **285**: 99–109.

Oro D, Margalida A, Carrete M, *et al.* 2008. Testing the goodness of supplementary feeding to enhance population viability of an endangered vulture. *PLoS ONE* **3**: e4084.

Oro D, Genovart M, Tavecchia G, *et al.* 2013. Ecological and evolutionary implications of food subsidies from humans. *Ecol Lett* **16**: 1501–14.

Pain DJ, Bowden CGR, Cunningham AA, *et al.* 2008. The race to prevent the extinction of South Asian vultures. *Bird Conserv Int* **18**: S30–S48.

Parra J and Tellería JL. 2004. The increase in the Spanish population of griffon vulture *Gyps fulvus* during 1989–1999: effects of food and nest site availability. *Bird Conserv Int* **14**: 33–41.

Prakash V, Bishwakarma MC, Chaudhary A, *et al.* 2012. The population decline of *Gyps* vultures in India and Nepal has slowed since the veterinary use of diclofenac was banned. *PLoS ONE* **7**: e49118.

Robb GN, McDonald RA, Chamberlain DE, *et al.* 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front Ecol Environ* **6**: 476–84.

Ruxton GD and Houston DC. 2004. Obligate vertebrate scavengers must be large soaring fliers. *J Theor Biol* **228**: 431–36.

Ruxton G, Hall SJ, and Gurney WSC. 1995. Attraction toward feeding conspecifics when food patches are exhaustible. *Am Nat* **145**: 653–60.

Selva N and Fortuna MA. 2007. The nested structure of a scavenger community. *P R Soc B* **274**: 1101–08.

Snyder N, Snyder HA. 2005. Introduction to the California condor. California Natural History Guides No 81. Berkeley and Los Angeles, CA: University of California Press.

van Overveld T and Matthysen E. 2010. Personality predicts spatial responses to food manipulations in free-ranging great tits. *Biol Lett* **6**: 187–90.

Virani MZ, Kendall C, Njorogeb P, *et al.* 2011. Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. *Biol Conserv* **144**: 746–52.

Watson RT, Gilbert M, Oaks JL, *et al.* 2004. The collapse of vulture populations in South Asia. *Biodiversity* **5**: 3–7.

Wilmers CC and Getz WM. 2005. Gray wolves as climate change buffers in Yellowstone. *PLoS Biol* **3**: e92.

Yang LH, Bastow JL, Spence KO, *et al.* 2008. What can we learn from resource pulses? *Ecology* **89**: 621–34.

Yarnell RW, Phipps WL, Dell S, *et al.* 2014. Evidence that vulture restaurants increase the local abundance of mammalian carnivores in South Africa. *Afr J Ecol*; doi:10.1111/aje.12178.

Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.1257/suppinfo

[4]*US Department of Agriculture, National Wildlife Research Center, Sandusky, OH;* [5]*Basque Centre for Climate Change, Bilbao, Spain;* [6]*The Peregrine Fund, Boise, ID;* [7]*Ornithology Section, Department of Zoology, National Museums of Kenya, Nairobi, Kenya;* [8]*US Fish and Wildlife Service, California Condor Recovery Program, Hopper Mountain National Wildlife Refuge, Ventura, CA*