Bioinspired models for assessing the importance of transhumance and transboundary management in the conservation of European avian scavengers

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Abstract

The assessment of temporal and spatial availability of food resources is an important prerequisite in developing improved management tools for effective conservation action. It is especially useful in the conservation of avian scavengers inhabiting regions where livestock move on a regular basis (transhumance). Important management decisions can be taken on the basis of theoretical analyses that need to be regularly checked. In this case study, we consider models of Griffon vulture *Gyps fulvus*, Egyptian vulture *Neophron percnopterus* and bearded vulture *Gypaetus barbatus* populations in a part of Spain with one of the highest densities of scavenging birds, and where traditional farming practices remain. We applied bioinspired Population Dynamic P System models (PDP) to assess these species' population trends against the distribution, quantity and availability of carrion for food. We show asymmetries in the availability of food resources, which are substantially higher in summer due to transhumant movements. In the study area, a lack of food resources in winter leads to a seasonal reduction in food supplies to levels unable to meet the energetic requirements of the most abundant vulture species, the Griffon vulture. Our results suggest that regardless of active management (e.g. supplementary feeding sites) and the birds' use of other potential food resources not included in the model, Griffon vultures are able to find important alternative food resources in more remote areas. We show the importance of variations at spatio-temporal scales in the objective forecasting of population trends, and in the correct application of management actions. Because of the importance of robust assessments for management applications, we discuss the advantages and limitations of ecological modelling for avian scavengers, highlighting the importance of transhumance processes and transboundary approaches.

Key-words: livestock movements, obligate scavengers, food requirements, PDP models, population dynamics, simulation model**.**

1. Introduction

Successful conservation action rests upon harmonizing the best available knowledge with management actions appropriate to the prevailing political and economic situation (Linnell et al., 2016). To this end, conservationists and managers must adapt their activities to administrative and regional scales, and be increasingly aware of the importance both of large scale ecological processes and transboundary cooperation (Butchart et al., 2010; Wiens and Bachelet 2010; Rands et al., 2010; Rüter et al., 2014, Lim 2016; Linnell et al., 2016). The need for, and the benefits arising from, transboundary cooperation in managing wildlife populations beyond simple administrative and jurisdictional limits has led to the emergence of wider scale approaches as a major conservation paradigm, and these are being increasingly applied in many locations (Fleurke & Trouwborst 2014, Chapron et al., 2015).

Because large avian scavengers have extensive foraging ranges, their management and conservation requires transboundary approaches (Margalida et al., 2013, Lambertucci et al., 2014, Arrondo et al., 2018). Because of their specialized diet based mainly on the carcasses of domestic and wild ungulates, the assessment of food resource availability for these species, and its spatio-temporal distribution, is key and provides an important management tool in improving their conservation status (Margalida & Colomer 2012, Cortés-Avizanda et al., 2015, Kane et al., 2015). The health of vulture populations are good indicators of habitat modification and unsustainable land management at large spatial scales. Therefore, quantitative assessments of trophic availability, in conjunction with information regarding vulture food preferences and selection (Moreno-Opo et al., 2015, 2016) provide useful information about territory quality and can be used to estimate carrying capacity. Such information can also help to develop guidelines regarding the need for, and form of, supplementary feeding programs and the suitability of particular habitats for vulture reintroduction projects.

Spain is home to 90% of the European Union’s avian scavenger population, and conservation management actions carried out there are fundamental for the Europe-wide scavenging bird metapopulation. In contrast with other scavenging bird populations worldwide (e.g. Ogada et al., 2016), Spanish vulture populations have shown moderate and/or important increases in recent years (Donázar et al., 2009). Transhumance is characteristic of many Spanish ecosystems. It is a traditional farming practice whereby livestock are regularly moved between winter and summer pastures, maximizing the exploitation of grazing resources (Ruiz and Ruiz, 1986; Fernández-Giménez & Fillat 2012). This was a common practice in many European countries, but is now in decline elsewhere (Vicente-Serrano et al., 2004; Oteros-Rozas et al., 2013). Vultures make use of the food resources from transhumant livestock during at least a third of the year, and this is particularly useful for Griffon vulture management (Olea & Mateo-Tomás 2009). Because larger scale ecosystem management is important for biodiversity conservation, political or administrative boundaries, which divide ecosystems and apply different rules and guidelines, pose special problems for ecological processes and conservation efforts (Zbicz 1999, Papadopoulou & Sitsoni 2012). These issues were highlighted in Spain during the outbreak of bovine spongiform encephalopathy in 2001, when changes in sanitary regulations suddenly reduced the food available to vultures provided by livestock carcasses (Tella 2001, Donázar et al., 2009). The various Spanish regions applied different sanitary policies, each affecting the distribution and availability of animal carrion biomass. After this, a network of protection areas for the feeding of scavengers in Spain was designated, but the criteria adopted to manage carrion resources differed among regions (Morales-Reyes et al., 2017).

Clearly, it is therefore important to determine whether the available food resources are sufficient to cover the energetic requirements of an avian scavenger assemblage and whether spatio-temporal variations in food availability may affect their population levels and trends. This information allows managers and policy-makers to anticipate and forecast the effects of food shortages, or changes in their spatio-temporal distribution, on scavenger populations, and enable management and conservation measures to minimize such effects (Margalida & Colomer 2012). The use of bioinspired models (PDP Systems) allows the assessment of the influence of spatio-temporal changes in food availability on the population dynamics (e.g. Colomer et al., 2011, Cortés-Avizanda et al., 2015, Kane et al., 2015). These estimates, based on data collected in the field, allow the modeling of hypothetical scenarios that can enable managers to anticipate decision-points regarding conservation measures such as the provision of Supplementary Feeding Sites (SFS) or “vulture restaurants”. However, the different scenarios provided by modeling approaches are subject to degrees of uncertainty, and to minimize bias in the results it is necessary to estimate the sensitivity of any model to changes in the parameters involved, and the degrees of causality between them.

Considering the important ecosystem services provided by vultures (Dupont et al., 2012, Moleón et al., 2014, Morales-Reyes et al., 2015) and the lack of empirical data on the influence of transhumance effects, we undertook a case study on three vulture species (Egyptian vulture *Neophron percnopterus,* Eurasian Griffon vulture *Gyps fulvus* and bearded vulture *Gypaetus barbatus*), all of which are obligate scavengers, in a part of Spain with one of the highest avian scavenger population densities (Navarra, N Spain). Our goals were: i) to estimate the carrying capacity of the ecosystem based on the availability of trophic resources; ii) to quantify the spatio-temporal distribution of these resources and their relationship to transhumance practices, in order to determine how the distribution of food impacts vulture population dynamics; iii) to examine the advantages and limitations of ecological modelling in the management of carrion and its effects on ecosystem services provided by vultures, to assess the usefulness of modelling as a decision making tool for managers and policy-makers.

2. Material and Methods

2.1.Model building and assumptions

Using a Population Dynamic P System (see Supporting information) we built a model to study the ecosystem dynamics in an area subdivided into five zones and four peripheral zones surrounding the main study area (Figure 1). PDP models are computational methods that are analogous to the machinery of cells (Colomer *et al*., 2013). The cells of the model correspond to the physical space of the environment. Animals (which along with things such as resources, are represented by model ‘objects’) will feed, reproduce, develop, etc… within an environment which is accounted for by a set of mathematical rules describing these behaviours in the model (Colomer et al., 2011). The application of PDP models constitute an effective computational tool to model a complex problem, because these bioinspired models are characterized by the ability to work in parallel (simultaneously interrelating different processes, for example combining demographic parameters with energetic requirements), being modular and with a high computational efficiency,

The subdivision of the study area has been based on climatic, topographic, landscape and ecological criteria (see Elósegui & Pérez-Ollo 1982). This area of 10 391 km^2 is inhabited by three avian scavenger species: seven bearded vulture pairs, 129 Egyptian vulture pairs, and 2798 Eurasian Griffon vulture pairs.

Regarding carrion provided by wild species, we considered the Pyrenean chamois (*Rupicapra pyrenaica*), the red deer (*Cervus elaphus*), the roe deer (*Capreolus capreolus*) and the wild boar (*Sus scrofa*). Carrion provided in the study area by domestic ungulates, mainly comprises sheep (*Ovis aries*), cows (*Bos taurus*) and horses (*Equus caballus*), occurring either naturally after death (*in situ*) or artificially at the network of supplementary feeding sites (SFS) (Table 1, Table S1). The study area contains 10 SFS, where farmers and administrators provide carcasses and bone remains (Table S1). In addition, we added the contribution of alternative carrion from other species such as birds, small mammals, rodents, and lagomorphs (see Supporting information). These constitute a very important part of the diet of the Egyptian vulture (see Donázar 1993, Margalida et al., 2012) and complement the trophic spectrum of the bearded vulture (Margalida et al., 2006, 2009).

The study area is characterized by husbandry related seasonal movements of livestock (transhumance). Two periods are defined annually according to the use of the grasslands and the variations in certain biological parameters throughout the year: ‘summer or non-reproductive period’ (hereafter *summer* - the months between June and September), and ‘winter or reproductive period’ (hereafter *breeding* - the period between October and May). Since livestock are man-managed, we considered their spatio-temporal distribution to be seasonally fixed and the model takes this effect of transhumance into account. Humans also partially manage the feeding of scavengers artificially by placing bones and meat at the SFS. Some of these SFS are specifically targeted at the bearded vulture (for which lamb carrion is the only food offered), while others are more generic, in which any type of carcass is provided and the entire scavenging vulture guild can feed at them. In addition, some wild ungulates are hunted (some selectively for trophies), so that humans manage the number of animals killed through decisions based on the quarry population sizes or through the issue of hunting permits.

2.2.Annual energetic requirements

To estimate regular foraging ranges, we constructed circular areas around the nesting site based on the maximum distance that a bird will fly in a straight line from the nest in search of food: Griffon vulture 90 km, bearded vulture 40 km, Egyptian vulture 15 km (for more details see Margalida & Colomer 2012). We used an extension of the central place forager theory known as the foraging radius concept at which every individual is energetically constrained in terms of the spatial range they can cover while foraging (Sinclair & Norton-Griffiths 1995). As central place foragers, breeding individuals must return to their breeding sites after they forage every day. The energetic requirements of the three avian scavengers according to food type (bones and meat) and period (summer vs breeding) were estimated following Donázar (1993). Eurasian Griffon vultures need 404 kg/pair/year, Egyptian vultures 100 kg and bearded vultures 308 kg (Table S7).

In addition to including the natural and non-natural mortality rates of ungulates, the model assumes that an animal dies of starvation when it exceeds the carrying capacity of the habitat. In defining the model, a directed network table of avian scavenger movement was specified following the rationale given in Table S2.The model predicts that as a mean foraging range (Table S2), a species will move to a nearby zone if food resources become insufficient at its current location, and that it returns to the starting point (nesting area) if there are food limitations but no space (density) limitations. In this sense, we do not consider the large metabolic cost that result from the requirement to move greater distances. Accordingly, an individual colonizes a new area if insufficient space is available at its current location. Scavengers can choose between more than one available destination if they need to move, and the model assumes that they select one at random. If the new area selected also lacks resources, this random sampling continues until resources are found. If an individual cannot find sufficient resources after the process of random sampling, it will move to another area subject to the maximum density of each species in each zone. If space is not a limiting factor, it will return to its original location, or otherwise colonize a new area.

When feeding resources are insufficient in an avian scavenger’s usual home range, birds move to the peripheral zones (A, F, E, R-CL) in search of food, assuming they can obtain the same food resources found in the neighboring areas (Table S3). The model assumes that floater individuals can obtain a part of the resources available in the study area. However, the model does not take into account the use of the resources by neighboring individuals, including obligate and facultative scavengers.

The model takes into account the fact that each species uses the resources closest to their nesting area first, and then widens the radius of search as these deplete. The amount of meat and bones consumed by scavengers depends on the season. Excess meat disappears from the ecosystem at the end of each period (breeding or summer). The model assumes that 20% of the unconsumed bones remain available in the ecosystem in spring, as a consequence of bone preservation (Margalida & Villalba 2017). In addition, because not all carrion remains available due to its location (i.e. it lies in forested areas), we reduced the food actually available for scavengers by applying a correction factor (Tables S8, S9).

The bone remains of large bovine ungulates and equines are rarely consumed by bearded vultures (Margalida et al., 2009) and simply counting them would therefore overstate their importance, so we reduced their quantification by applying a factor according the size of the various bones (Table S9).

Population growth is restricted due to limitations on physical space imposed by each species foraging range and the food available to cover their energetic requirements. This informs the habitat carrying capacity used in the model (Table S4). Running the model requires input of initial parameters (such as reproduction, mortality and feeding), which are entered before generating the output. The model is first run for each individual and then again simultaneously for all individuals. Therefore, the system operates in parallel, allowing for competition when birds of the same or different species share resources. In this regard, the bearded and Egyptian vultures are the first to arrive at the carrion and/or to feed with respect to the griffon vulture (see Supporting information).

The values of the parameters used in the model were derived from published sources (for more details see Colomer et al., 2011, Margalida et al., 2011, Margalida & Colomer 2012; see also Supporting information).

2.3.Food availability scenarios

Three possible scenarios were studied to test the impact of different food availability regimes based on different livestock mortality rates, to examine their potential effects on population projections over time. The *Medium food availability scenario* represents the estimated food available in a normal year based on average domestic ungulate mortality rates (Table 2). The *High* scenario models the situation where available food increases relative to an average year (optimistic scenario). The *Low* scenario simulates an ecosystem where the food available is less than average (conservative scenario). The scavenger population trends were simulated on the basis of the demographic parameters typical of each species (Table S5) and the availability of biomass provided by the different domestic ungulate mortality scenarios, plus the biomass provided by wild ungulates and feeding stations (see Supporting information).

2.4.PDP model

We used PDP models to build the ecosystem model. These are probabilistic computational models inspired by studies of body cell function, and can perform a high number of simultaneous and perfectly-synchronized processes. These models resemble multi-agent models, although they have some special characteristics which enable them to model complex processes (see Colomer et al., 2013, 2014, Fondevilla et al., 2015). The integrated data on food availability, food requirements and population dynamics of the avian scavenging guild and the ungulate populations of the study area (Figure 1 and Supporting Information) try to determine if carcass availability could meet the demands of the avian scavenger population over a 20-year period. The conceptual bases of the models are given in Figure 2.

The parameters used are defined in Table S10 and the model is thoroughly described in the Supporting information. The model was executed using MeCoSim (a free software under license) developed by the Computation Group at the University of Sevilla (GNU GPL; htpp://www.p-lingua.org).

3. Results

3.1. Food availability

The availability of animal biomass (meat and bones) was estimated for the three scenarios considered (low, medium and high availability of food resources), during two periods (summer and breeding). In all scenarios, the meat and bone biomass available to scavenging birds was higher in summer than during breeding (low-meat: 787,823 vs 325,854 kg; low-bones: 144,448 vs 34,377 kg; medium-meat: 1,005,630 vs 416,021 kg; medium-bones: 195,563 vs 46,024 kg; high-meat: 1,339,084 vs 585,049 kg; high-bones: 247,220 vs 58,292 kg) , with sheep providing the most domestic meat and bone biomass in all the scenarios considered (meat range: 34.80% - 42.11%; bones range: 65.40% - 77.39%). During the breeding period, the sheep is also the domestic ungulate that provides the most amount of meat and bone biomass (meat range: 34.57% - 39.96%; bones range: 60.35% - 74.05%) (Figure 3).

Regarding the wild species, wild boar and red deer provided in a similar way the highest amount of meat biomass (summer meat range: 9.87% - 5.80% and 7.76% - 4.61% for wild boar and red deer respectively; breeding meat range: 6.09% - 3.38% and 5.91% - 3.27% for wild boar and deer respectively) while deer provided the most amount of bones biomass (summer bones range: 13.70% - 8.01%; breeding bones range: 17.19% - 10.14%) (Figure 3).

3.2. Temporal availability of food resources to cover energetic requirements under different scenarios

Comparing the total meat trophic resources available (green bars) with the total energy requirements of the avian scavenger species (red bars), the food available is substantially greater than requirements in the summer, in the medium and high scenarios (Figure 4). On the contrary, during breeding in all three scenarios, the food available is insufficient to cover the energy requirements of the scavenging species assemblage.

When the total bone trophic availability (green column) is compared with the energy requirement (red column), the availability of bones is clearly much higher than needed to cover the energy requirements of the breeding bearded vulture population, even in the low food availability scenario (Figure 5).

3.3. Population trends in the Eurasian Griffon, Bearded and Egyptian vultures according to the carrying capacity

In the case of the Griffon vulture, the model forecasts significant differences among scenarios ($F_{2, 60} = 19.45$, $P < 0.0001$). The differences were found between the low and the rest of scenarios. In the high and medium food availability scenario the population grows and stabilizes at 3900 pairs after 20 years, whereas in the low food availability scenarios the trend is different. In this scenario, the model predicts that the population stabilizes at 3500 pairs after 20 years (Figure 6).

Regarding the bearded vulture, the results suggest oscillations between the current seven pairs and a maximum of 8, stabilizing over the following 20 years, with no significant differences between years ($F_{2, 60} = 1.126$, $P = 0.331$, Figure 6).

Considering the Egyptian vulture, the results show a positive population trend in all three scenarios with no significant differences between years ($F_{2, 60} = 0.149$, $P = 0.862$, Figure 6). The model predicts an increase of c. 11 pairs in the first six years, before rising later and stabilizing at 143 pairs after 20 years, in all three scenarios with no significant differences between them.

4. Discussion

The availability of resources limits the population size of an animal species, and sets the carrying capacity of an area (Hanski et al., 1993, Turchin 2001). In the case of avian scavengers, the availability of food provided by wild ungulate carcasses has gradually decreased as a result of their replacement by domestic ungulates (Lambertucci *et al.*, 2009; Margalida et al., 2011, Ogada *et al.*, 2012). Livestock is man-managed and this makes it easy to obtain accurate data on numbers of animals and their demographic parameters, as well as their spatio-temporal distribution and its effect on the amount of food that they provide for scavengers. This quality of information makes it possible to assess the precise carrying capacity of an environment and to forecast scavenger population trends based on estimates of food availability. Modeling this information can help managers and policy-makers to make decisions regarding reintroduction projects, conservation measures, and to assess the impact of policy decisions regarding health and sanitation regulations on scavenger population dynamics (Sarrazin & Legendre 2000, Hirzel et al., 2004, Margalida & Colomer 2012). As this study shows, it is imperative to have good datasets in order to model population trends or assess carrying capacity because the sensitivity of some demographic parameters can have a significant impact on the results obtained. As we show, even a 1-2% change in livestock mortality can substantially modify the assessment of carrion available and the effects on scavenger population dynamics. For example, with respect to the differences between the low vs medium food availability scenario, in the case of the griffon vulture the model forecasts a difference of 384 pairs after 20 years (Figure 6). Therefore, even small errors in livestock mortality estimates could lead to serious mistakes in management measures, with important conservation repercussions. However, it is important to remark that predictions were only different significantly among the three scenarios for the griffon vulture but not for Egyptian and bearded vultures.

We show that asymmetries exist in the availability of food resources during the year, emphasizing the importance of estimating food availability over the full annual cycle (Marra et al., 2015). According to our results, although the overall annual availability of carrion for the scavenger populations studied is enough to cover their energetic requirements, when we separate the breeding from the summer period (when transhumance occurs) the results suggest that seasonal food shortages do exist in our study area (Figure 4), at least for the most abundant species, the Griffon vulture. An additional issue which suggests that results are conservative is that some facultative scavengers and breeding pairs inhabiting outside the study area can take advantage of the carrion present (Moreno-Opo et al., 2016). The quantification of the impact of biomass consumption by these facultative carrion eaters (birds and mammals) is difficult and will require future approximations to improve the models. However, the progressive increase in the griffon vulture population size (from 312 pairs in 1979 to 2783 in 2009, Del Moral 2009), suggests that an important proportion of their food is obtained from zones peripheral to the core area, or even from more distant areas, possible because of the high mobility of these species (Monsarrat et al., 2013). Therefore, as has been shown for other large birds of prey, home ranges vary according to prey density and individual reproductive status, with habitat quality serving to regulate their use of space (Fernández et al., 2009, Pérez-García et al., 2013). Spatial scales are therefore important to assess correctly available feeding resources and to understand the relevance of transboundary agreements between regional administrations to develop, coordinate and apply conservation measures for species with extensive foraging areas (Lambertucci et al., 2015, Margalida et al., 2013, 2016, Morales-Reyes et al., 2017, Arrondo et al., 2018). This is the case of our study area that, as the results show, do not provides enough resources to cover the energetic requirements of the griffon vulture population being dependent of the availability and management of food in neighbouring areas. Accordingly, species with large foraging areas, like griffon vultures, are difficult to implement on computational models as a consequence of the use of alternative food resources from far-away areas.As a result, the coordination between different Spanish administrations and countries (France and Portugal) regulating health policies are necessary.

From a temporal perspective, we show that the availability of carrion is substantially higher in summer because of the increased numbers of livestock in mountain pastures. Mountain areas are the main zones which benefit from livestock seasonal movements, as occurs in the Pyrenean and MW regions. Sheep provide most of the carrion biomass, and constitute 50% of the food available. Therefore, transhumance, mainly of sheep, is important in increasing food availability in mountain ecosystems and this practice plays an important role in the conservation of avian scavengers and other wild species (Olea & Mateo-Tomás 2009, Bernués et al., 2011, López-Santiago et al., 2014, Tyrrell et al. 2017). However, transhumance practice is suffering a progressive decline (Olea & Mateo-Tomás 2009) that can have important consequences for biodiversity conservation (Mateo-Tomás & Olea 2010, Carmona et al., 2013,). Therefore, any conservation measure which facilitates extensive sheep husbandry should be a priority from a conservation point of view. However, this is compromised by the fact that the critical energetic shortfall for this avian scavenger guild occurs during the breeding period (winter-spring). At this time, the constraints of breeding limit the foraging movements at a time of reduced hours of daylight, adverse weather conditions, and the increased energetic requirements due to feeding chicks. We show that evident food shortages exist during the breeding period. The network of special feeding sites for avian scavengers (ZPAEN) recently established by Spanish administrations (Morales-Reyes et al., 2017) therefore play an important role for breeding birds inhabiting regions with limited food resources, or which are affected by sanitary regulations which remove carcasses from the landscape (Donázar et al., 2009). From a management perspective, the location of SFS should be related to the spatio-temporal distribution of natural resources and the avian scavenger population. Only by taking these into account can managers optimize the value of SFS, always considering the controversial pros and cons of this widespread conservation management tool (Moreno-Opo et al., 2015, Cortés-Avizanda et al., 2016).

Given that all the scenarios modelled show a deficit of food resources in the breeding season, our results suggest that a high proportion of the trophic resources available to the nesting population in the study area are obtained from: i) peripheral zones outside the study area; and/or ii) the exploitation of other sources of food not considered in this study (e.g. landfills, intensive farms, e.g. Plaza & Lambertucci 2017, Tauler-Ametller et al., 2017). The first explanation can be confirmed by satellite tracking results obtained from several breeding individuals that exploited resources located far from nesting sites, such as certain areas in Extremadura, located 600 km from their breeding colony (C. Fernández, unpubl. rep.). Regarding the second explanation, Griffon vultures have been observed exploiting other resources such as garbage dumps following food shortages (Donázar et al., 2010, Plaza & Lambertucci 2017). Therefore, models which assess food resource availability should consider larger spatial areas and every possible source of scavenger food. In contrast, specialized and less abundant species such as the bearded or Egyptian vulture do not seem limited by food resources. This is probably due to the small size of their breeding populations and the diet plasticity of both species, suggesting that trophic availability is not a limiting factor either for the establishment of new territories or the geographic expansion of these species. This agrees with previous studies (Margalida & Colomer 2012, Margalida et al., 2017) suggesting that, quantitatively, food is not a limiting factor for Egyptian and bearded vultures. The results suggest that the available food is still substantially more than is needed by the breeding birds. For example, in the case of bearded vultures, while we included the smaller items of carrion from horses and cows, these are only rarely selected by this species (Margalida et al., 2009), and even considering only sheep remains, the potential food available each year in a medium food availability scenario is 175 000 kg, sufficient to sustain 568 bearded vulture breeding pairs. Therefore, the geographical expansion of bearded vultures does not seem to be limited by food resources, and limiting factors are more likely to be other aspects of habitat quality (e.g. disturbance, habitat modification), non-natural mortality factors (i.e. illegal poisoning) and the potential overcrowding with conspecifics attracted to the supplementary feeding sites established in the Pyrenees (Carrete et al., 2006, Margalida et al., 2008, Margalida et al., 2017).

Among the 23 Old World vulture species, 81% are globally threatened or near threatened and most of these species are declining, particularly in Africa and Asia, as a consequence of anthropogenic activities such as the illegal use of poisons, landscape transformation, health policies and ingestion of toxic veterinary drugs (Ogada et al., 2012). These threats persist and continue to increase, despite the fact that vultures provide important ecosystem services (Moleón et al. 2014a). Regarding the projected population estimates, changes in spatial dynamics and distribution of the different species will be governed by factors such as: i) the maximum carrying capacity of the region (density); ii) the availability of suitable nesting sites; iii) the availability of food; and iv) to a lesser extent, longer distance movements of individual birds. Data regarding the increase in the breeding population of the Spanish Griffon vulture suggests that there is no density-dependent regulation of numbers, since the population grew more steadily in the more densely occupied provinces (Parra & Tellería 2004). However, this large-scale result does not preclude the possibility of local regulatory processes in more densely occupied zones, where decreased breeding success has been observed (see Fernández et al., 1996). In the case of the bearded vulture, its population dynamics will depend fundamentally on management measures carried out in the rest of the Pyrenean range. During the last 20 years, there has been hardly any geographic expansion and this is attributable to the effect that supplementary feeding points have in attracting this species (Margalida et al., 2013). The large concentrations of individuals at these sites probably reduce geographic expansion of this species westwards, as evidenced by the lack of movement of pre-adult individuals beyond these areas (Margalida et al., 2013, Margalida et al., 2016). There is an abundant trophic supply and limiting factors could be the quality of available nesting sites and the population density (Donázar et al., 1993;

Margalida et al., 2008). With respect to Griffon vultures, following an exponential growth in numbers during the last 30 years (Del Moral et al., 2009), the indications are of reduced growth leading to a possible stabilization of the population. Recent changes in sanitary policies have modified the behavior and diet of this species (Donázar et al., 2009, 2010, Margalida et al., 2011) and probably affected demographic parameters in similar ways to those noted for bearded vultures (Margalida et al., 2014). Finally, with respect to Egyptian vultures, the models suggest a population increase because its dietary plasticity allows it to utilize a wide spectrum of different prey. Consequently, the primary factor limiting the population viability of this species appears to be illegal poisoning (Hernández & Margalida 2009, Ogada 2014, Sanz-Aguilar *et al*., 2016).

Because each region/country may make independent decisions and work according to their own specific interests and conservation policies, approaches based on large spatial scales are essential to generate effective conservation measures based on transboundary approaches (Bischof et al., 2015). This approach is also required for avian scavengers where management centers on the provision of SFS or “vulture restaurants” at which surplus resources modify the quality of a habitat and provide predictable food resources that might affect spatial distribution and breeding density. Accordingly, the economic costs of providing SFS and their effects on ecological processes (see Donázar et al., 2009, Cortés-Avizanda et al., 2010, Dupont et al., 2012, Cortés-Avizanda et al., 2016) should force managers and policy-makers to assess the natural food provided by the ecosystem and to carefully evaluate the usefulness of supplementary feeding sites (Kane et al., 2015). The identification of optimal areas (i.e. those with abundant food resources and nesting-sites) could provide conservation tools to identify priority areas for reintroduction projects. It is important to consider large spatial scales in order to manage species with large foraging areas and to apply the correct management and conservation measures.

Pros and cons of computational models in ecology

Bioinspired models, such as PDP systems that work in parallel, are more flexible and enable the consideration of the heterogeneity of the population and the environment. These models allows to capture the randomness of the natural environmental processes using stochastic strategies based on Gillespie’s kinetics (Gillespie 1976) and the semantics defined by using probabilistic functions (Colomer et al., 2011, Colomer et al., 2013). However, modeling complex systems in which several environments and species interact competing for resources requires experienced researchers familiarized with these models. Although their complexity could limit the use of this tool, PDP systems allows modelling of demographic parameters with regard to food resources, and provides an effective tool in conjunction with other considerations (Colomer et al., 2013). PDP models are a complementary approach to be used when the classical modeling approaches fail (Colomer et al., 2011), and can aid in conservation planning for species of concern where available trophic spectra can be assessed objectively, and should be used to combine trophic resource measurements with demographic parameters to improve the effectiveness of conservation management. However, as a result of the limitations in computational models, replication of the models seems necessary to increase credibility and efficiency to facilitate theory development (Thiele & Grimm 2015) and, as occurs in the case of threatened species, to optimize management and conservation actions.

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References

Arrondo, E., Moleón, M., Cortés-Avizanda, A., Jiménez, J., Beja, P., Sánchez-Zapata, J.A. & Donázar, J.A. 2018. Invisible barriers: Differential sanitary regulations constrain vulture movements across country borders. *Biological Conservation* 219, 46-52.

Bernués, A., Ruiz, R., Olaizola, A., Villalba, D. & Casasús, I. 2011. Sustainability of pasture-based livestock farming systems in the European Mediterranean context: Synergies and trade-offs. *Livestock Science* 139, 44–57.

Cardinale, B.J., Hillebrand, H., Harpole, W.S., Gross, K. & Ptacnik, R. 2009. Separating the influence of resource ‘availability’ from resource ‘imbalance’ on productivity–diversity relationships. *Ecology Letters* 12, 475–487.

Carmona, C.P., Azcárate, F.M., Oteros-Rozas, E., González, J.A. & Peco, B. 2013.

Assessing the effects of seasonal grazing on holm oak regeneration: Implications for the conservation of Mediterranean dehesas. *Biological Conservation* 159, 240–247.

Carrete, M., Donázar, J.A. & Margalida, A. 2006. Density-dependent productivity depression in Pyrenean bearded vultures: implications for conservation. *Ecological Applications* 16, 1674-1682.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D. *et al*., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346, 1517–1519.

Colomer, M.A., Margalida, A. & Pérez-Jiménez, J.J. 2013. Population dynamic P system (PDP) models: a standardized protocol for describing and applying novel bio-inspired computing tools. *PLoS ONE* 8, e60698.

Colomer, M.A., Margalida, A., Sanuy, D. & Pérez-Jiménez, M.J. 2011. A bio-inspired computing model as a new tool for modelling ecosystems: the avian scavengers as a case study. *Ecological Modelling* 222, 34-47.

Cortés-Avizanda, A., Blanco, G., DeVault, T.L., Markandya, A., Virani, M.Z. *et al*., 2016. Supplementary feeding and endangered species: benefits, caveats and controversies. *Frontiers in Ecology and the Environment* 14, 191-199.

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.

Del Moral, J.C. 2009. *El buitre leonado en España: población reproductora en 2008 y método de censo*. SEO/BirdLife. Madrid.

Donázar, J.A. 1993. *Los buitres ibéricos: biología y conservación*. J.M. Reyero Editor. Madrid.

Donázar, J.A., Margalida, A. & Campión, D. 2009. *Vultures, feeding stations and sanitary legislation: a conflict and its consequences from the perspective of conservation biology*. Munibe 29, Sociedad de Ciencias Aranzadi, San Sebastián.

Donázar, J.A., Margalida, A., Carrete, M. & Sánchez-Zapata, J.A. 2009. Too sanitary for vultures. *Science* 326, 664.

Dupont, H., Mihoub, J.B., Bobbe, S. & Sarrazin, F. 2012. Modelling carcass disposal practices: implications for the management of an ecological service provided by vultures. *Journal of Applied Ecology* 49, 404-411.

Elósegui, J. & Pérez Ollo, F. 1982. *Navarra naturaleza y paisaje*. Caja de Ahorros de Navarra. Pamplona.

Fernández, C., Azcona, P. & Donázar, J. A. 1996. Density-dependent effects on productivity in the Griffon Vulture *Gyps fulvus*: then role of interference and habitat heterogeneity. *Ibis* 140, 64–69.

Fernández, M., Oria, J., Sanchez, R., Gonzalez, L. M. & Margalida, A. 2009. Space use of adult Spanish Imperial Eagles (*Aquila adalberti*). *Acta Ornithologica* 44, 17–26.

Fernández-Giménez, M.E. & Fillat, F. 2012. Pyrenean pastoralists' ecological knowledge: documentation and application to natural resource management and adaptation. *Human Ecology* 40, 287–300.

Fleurke, F.M. & Trouwbors, A. 2014. European regional approaches to the transboundary conservation of biodiversity: the Bern Convention and the EU Birds and Habitats Directives. In: Kotze L, Marauhn T, editors. Transboundary governance of biodiversity. Leiden/Boston: Martinus Nijhoff Publishers. Pp. 128–62.

Gillespie, D.T. 1976. A general method for numerically simulating the stochastic time evolution of coupled chemical reactions. *Journal of Computational Physics* 22, 403-434.

Hirzel, A. H., Posse, B., Oggier, P. A., Crettenand, Y., Glenz, C. *et al*., 2004. Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. *Journal of Applied Ecology* 41, 1103-1116.

Kane, A., Jackson, A.L., Monadjem, A., Colomer, M.A. & Margalida, A. 2015. Carrion ecology modelling for vulture conservation: are vulture restaurants needed to sustain the densest breeding population of the African White-backed Vulture? *Animal Conservation* 18, 279-286.

Lambertucci, S.A., Alarcón, P.A.E., Hiraldo, F., Sánchez-Zapata, J.A., Blanco, G. *et al*., 2014. Apex scavenger movements call for transboundary conservation policies. *Biological Conservation* 170, 145-150.

Lim, M. 2016. Governance criteria for effective transboundary biodiversity conservation. *International Environment Agreements* 16, 797–813

Linnell, J.D.C., Trouwborst, A., Boitani, L., Kaczensky, P., Huber, D. *et al*., (2016) Border security fencing and wildlife: the end of the transboundary paradigm in Eurasia? *PLoS Biology* 14, e1002483.

López-Santiago, C., Oteros-Rozas, E., Martín-López, B., Plieninger, T., González, E. *et al*., 2014. Using visual stimuli to explore the social perceptions of ecosystem services in cultural landscapes: the case of transhumance in Mediterranean Spain. *Ecology & Society* 19, 27.

Margalida, A., Benítez, J.R., Sánchez-Zapata, J.A., Ávila, E., Arenas, R. *et al*., 2012. Long-term relationships between diet and breeding success in a declining population of Egyptian Vulture *Neophron percnopterus*. *Ibis* 154, 184-188.

Margalida, A., Bertran, J. & Heredia, R. 2009. Diet and food preferences of the endangered Bearded vulture *Gypaetus barbatus*: a basis for their conservation. *Ibis* 151, 235-243.

Margalida, A., Campión, D. & Donázar, J.A. 2011. European vultures' altered behaviour. *Nature* 480, 457.

Margalida, A., Carrete, M., Hegglin, D., Serrano, D., Arenas, R. *et al*., 2013. Uneven large-scale movement patterns in wild and reintroduced pre-adult bearded vultures: conservation implications. *PLoS ONE* 8, e65857.

Margalida, A. & Colomer, M.A. 2012. Modelling the effects of sanitary policies on European vulture conservation. *Scientific Reports* 2, 753.

Margalida, A., Colomer, M.A. & Oro, D. 2014. Man-induced activities modify demographic parameters in a long-lived species: effects of poisoning and health policies. *Ecological Applications* 24, 436-444

Margalida, A., Colomer, M.A. & 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.

Margalida, A., Donázar, J.A., Carrete, M. & Sánchez-Zapata, J.A. 2010. Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology* 47, 931-935.

Margalida, A., Pérez-García, J.M., Afonso, I. & Moreno-Opo, R. 2016. Spatial and temporal movements in Pyrenean bearded vultures (*Gypaetus barbatus*): Integrating movement ecology into conservation practice. *Scientific Reports* 6, 35746.

Margalida, A., Pérez-García, J.M. & Moreno-Opo, R. 2017. European policies on livestock carcasses management did not modify the foraging behavior of a threatened vulture. *Ecological Indicators* 80, 66-83.

Margalida, A. & Villalba, D. 2017. The importance of the nutritive value of old bones in the diet of bearded vultures *Gypaetus barbatus. Scientific Reports* 7, 8061.

Marra P.P., Cohen E.B., Loss, S.R., Rutter, J.E. & Tonra, C.M. 2015. A call for full annual cycle research in animal ecology. *Biology Letters* 11, 20150552.

Mateo-Tomás, P. & Olea, P.P. 2010. Diagnosing the causes of territory abandonment by the Endangered Egyptian vulture *Neophron percnopterus*: the importance of traditional pastoralism and regional conservation. *Oryx* 44, 424–433,

Moleón, M., Sánchez-Zapata, J.A., Margalida, A., Carrete, M., Owen-Smith, N. & Donázar, J.A. 2014. Humans and scavengers: evolution of interactions and ecosystem services. *BioScience* 64, 394-403.

Monsarrat, S., Benhamou, S., Sarrazin, F., Bessa-Gomes, C., Bouten, W. & Duriez, O. 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, J.M., Moleón, M., Botella, F., Carrete, M. *et al*., 2017. Evaluation of the network of protection areas for the feeding of scavengers (PAFs) in Spain: from biodiversity conservation to to greenhouse gas emission savings. *Journal of Applied Ecology* 54, 1120-1129.

Morales-Reyes, Z., Pérez-García, J.M., Moleón, M., Botella, F., Carrete, M. *et al*., 2015. Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. *Scientific Reports* 5, 7811.

Moreno-Opo, R., Trujillano, A., Arredondo, A., González, L.M. & Margalida, A. 2015. Manipulating size, amount and appearance of food inputs to optimize supplementary feeding programs for European vultures. *Biological Conservation* 181, 27–35.

Moreno-Opo, R., Trujillano, A. & Margalida, A. 2016. Behavioral coexistence and feeding efficiency drive niche partitioning in European avian scavengers. *Behavioral Ecology* 27, 1041-1052.

Ogada, D. L. 2014. The power of poison: pesticide poisoning of Africa's wildlife. *Annals of the New York Academy of Sciences* 1322, 1-20

Ogada, D.L., Keesing, F. & Virani, M.Z. 2012. Dropping dead: causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences* 1249, 57–71

Ogada, D.L., Torchin, M.E., Kinnaird, M.F., Ezenwa, V.O. 2012. Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conservation Biology* 26, 453–60.

Ogada, D., Shaw, P., Beyers, R.L., Buij, R., Murn, C., *et al*., 2016. Another continental vulture crisis: Africa's vultures collapsing toward extinction. *Conservation Letters* 9, 89-97.

Olea, P.P. & Mateo-Tomás, P. 2009. The role of traditional farming practices in ecosystem conservation: the case of transhumance and vultures. *Biological Conservation* 142, 1844-1853.

Oteros-Rozas, E., Ontillera-Sánchez, R., Sanosa, P., Gómez-Baggethun, E., Reyes-García, V. *et al*., 2013. Traditional Ecological Knowledge among transhumant pastoralists in Mediterranean Spain: learning for adaptation to global change. *Ecology & Society* 18, 33.

Oteros-Rozas, E., Martín-López, B., González, J.A., Plieninger, T., López, C.A. *et al*., 2014. Socio-cultural valuation of ecosystem services in a transhumance social-ecological network. *Regional Environmental Change* 14, 1269–1289.

Papadopoulou, S.D. & Sitsoni, K.T. (2012) The potential for transboundary cooperation towards the conservation of the avifauna in the Voras Mountain Range (Greece / F.Y.R.O.M). *GlobalNEST Journal* 15, 102-110.

Parra, J., & Tellería, J.L. 2004. The increase in the Spanish population of Griffon Vulture *Gyps fulvus* during 1989–1999: Effects of food and nest site availability. *Bird Conservation International* 14, 33-41.

Pérez-García, J. M., Margalida, A., Afonso, Ferreiro, E., Gardiazábal, A., *et al*., 2013. Interannual home range variation, territoriality and overlap in breeding Bonelli's eagles (*Aquila fasciata*) tracked by GPS satellite telemetry. *Journal of Ornithology* 154, 63–71.

Plaza, P. I., & Lambertucci, S. A. 2017. How are garbage dumps impacting vertebrate demography, heath, and conservation?. *Global Ecology and Conservation* 12, 9-20.

Rands, M. R. W., Adams, W. M., Bennun, L., Butchart, S. H. M., Clements, A. *et al*., 2010. Biodiversity conservation: challenges beyond. *Science* 329, 1298.

Rüter, S., Vos, C. C., van Eupen, M., & Rühmkorf, H. 2014. Transboundary ecological networks as an adaptation strategy to climate change: The example of the Dutch-German border. *Basic and Applied Ecology* 19, 639–650.

Sarrazin, F., & Legendre, S. (2000) Demographic approach to releasing adults versus young in reintroductions. *Conservation Biology* 14, 488-500.

Sinclair, A.R.E. & Norton-Griffiths, M. 1995. *Serengeti: dynamics of an ecosystem*. Chicago: University of Chicago Press.

Tauler-Ametller, H., Hernández-Matías, A., Pretus, J.L. & Real, J. (2017) Landfills determine the distribution of an expanding breeding population of the endangered Egyptian Vulture *Neophron percnopterus*. *Ibis* 159, 757-768.

Tella, J.L. 2001. Action is needed now, or BSE crisis could wipe out endangered birds of prey. *Nature* 410, 408.

Thiele, J. C., & Grimm, V. 2015. Replicating and breaking models: good for you and good for ecology. *Oikos*, 124, 691-696.

Tyrrell, P., Russell, S., & Western, D. 2017. Seasonal movements of wildlife and livestock in a heterogenous pastoral landscape: Implications for coexistence and community based conservation. *Global Ecology and Conservation* 12, 59-72.

Vicente-Serrano, S., Lasanta, T. & Romo, A. 2004. Analysis of spatial and temporal evolution of vegetation cover in the Spanish Central Pyrenees: role of human management. *Environmental Management* 34, 802-818.

Wiens, J. A., & Bachelet, D. 2010. Matching the multiple scales of conservation with the multiple scales of climate change. *Conservation Biology* 24, 51–62.

Zbicz, D. 1999. Transboundary cooperation between internationally adjoining protected areas. In: David Harmon, Hancock, Mich eds. On the Frontiers of Conservation: Proceedings of the 10th Conference on Research and Resource Management in Parks and on Public Lands. The George Wright Society, Hancock, Michigan: 199-204.

Zupo, V., Alexander, T.J. & Edgar, G.J. 2017. Relating trophic resources to community structure: a predictive index of food availability. *Royal Society open science* 4, 160515.

Table 1. Population of domestic and wild ungulates (individuals) in each zone in the study area. Non-transhumant animals are those that are not moved by farmers and remain in the same place year round. R.p. *Rupicapra pyrenaica*; C.e. *Cervus elaphus*; C.c. *Capreolus capreolus*; S.s. *Sus scrofa*; O.a. *Ovis aries*; B.t. *Bos taurus*; E.c. *Equus caballus*.

Zones	***R. p.***	***C. e.***	***C. c.***	***S. s.***	***O. a.***	***B. t.***	***E. c.***
NW							
No transhumants	0	153	4668	2564	130 429	14 893	7982
Summer	0	0	0	0	0	0	0
Breeding	0	0	0	0	10 800	700	975
MW							
No transhumants	0	0	1556	2177	38 651	1291	2662
Summer	0	0	0	0	15 800	1250	1520
Breeding	0	0	0	0	0	0	0
Pyrenees							
No transhumants	260	4132	3917	4456	71 099	8697	2660
Summer	0	0	0	0	28 000	0	0
Breeding	0	0	0	0	0	0	0
ME							
No transhumants	0	41	3908	5252	58 176	4005	1858
Summer	0	0	0	0	0	0	0
Breeding	0	0	0	0	3200	550	545
Ribera							
No transhumants	0	0	0	0	221 972	7588	5820
Summer	0	0	0	0	0	0	0
Breeding	0	0	0	0	20 800	0	0

Table 2. Annual mortality of domestic ungulates according to the different food availability scenarios, age classes and the two temporal periods. Scenario variation indicates the annual mortality variation in the low and high scenarios regarding the medium scenario.

Juveniles		**Annual**	**Summer**	**Breeding**	**Scenario variation**
Low	*O. aries*	0.100	0.067	0.033	-0.05
	B. taurus	0.050	0.033	0.017	-0.01
	E. caballus	0.020	0.013	0.007	-0.01
Medium	*O. aries*	0.150	0.100	0.050	0
	B. taurus	0.060	0.040	0.020	0
	E. caballus	0.030	0.020	0.010	0
High	*O. aries*	0.200	0.133	0.067	0.05
	B. taurus	0.070	0.042	0.028	0.01
	E. caballus	0.040	0.040	0	0.01

Adults		**Annual**	**Summer**	**Breeding**	**Scenario variation**
Low	*O. aries*	0.020	0.013	0.007	-0.01
	B. taurus	0.040	0.024	0.016	-0.01
	E. caballus	0.009	0.009	0.000	-0.01
Medium	*O. aries*	0.030	0.02	0.01	0
	B. taurus	0.050	0.03	0.02	0
	E. caballus	0.010	0.01	0	0
High	*O. aries*	0.040	0.027	0.013	0.1
	B. taurus	0.060	0.036	0.024	0.1
	E. caballus	0.020	0.020	0	0.1

Figure legends

Figure 1. Location of study area in northern Spain showing the five zones considered within the study area (surrounded by orange) and the peripheral zones (surrounded by grey) in which scavengers can obtain alternative resources. The regular foraging ranges were estimated based on the maximum distance that a bird will fly in a straight line from the nest in search of food (see Material and Methods).

Figure 2. Conceptual basis and sequencing of the processes considered in the PDP model. The model takes into account two periods (summer and breeding) and the processes of reproduction, mortality, feeding and the carrying capacity. When food is insufficient in the foraging area, the scavenger birds forage in peripheral areas . If they find food they return to their nesting site. On the contrary, when food is also insufficient in peripheral areas, the individual disappear from the study area. Two executions of a loop are equivalent to the passage of one year in the ecosystem.

Figure 3. Food availability (meat and bone biomass) provided by the different domestic and wild ungulates in the study area.

Figure 4. Temporal availability of food resources (green column) compared with the energetic requirements of the scavenging species assemblage (red column) in the three trophic availability scenarios: a) low, b) medium and c) high.

Figure 5. Bone biomass available (green column) in the study area with respect to the energetic requirements necessary (red column) for the breeding bearded vulture population in a low trophic availability scenario.

Figure 6. Predicted population trends for the three avian scavengers in the study area, for each of the three scenarios tested (low, medium and high), expressed as the percentage of domestic and wild ungulate carcasses available in the ecosystem. Note the different y-axis scales.

Supporting Information

Additional Supporting Information may be found in the online version of this article.