



Modelling the effects of sanitary policies on European vulture conservation

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Biodiversity losses are increasing as a consequence of negative anthropogenic effects on ecosystem dynamics. However, the magnitude and complexity of these effects may still be greatly underestimated. Most Old World vultures have experienced rapid population declines in recent years. In Europe, their immediate conservation depends on changes in health regulations affecting the availability of food provided by domestic carcasses. Information is lacking on the effects of a hypothetical food shortage on the population dynamics of vultures, and is necessary to assess the potential impacts of policy decisions on future changes in biodiversity and ecosystem services. A novel computational model (P-systems) was used to model these effects, forecasting a rapid decline in the Eurasian griffon vulture (*Gyps fulvus*). By contrast, vulture species with greater plasticity in their dietary range appeared less sensitive to declining food availability. This study extends our understanding of vulture ecosystem services, which have social and economic implications.

During the last decade, the relationship between biodiversity and ecosystem function has emerged as an important issue due to the strong connection between the ecological mechanisms that maintain biodiversity in a community and their ecological consequences for ecosystem function^{1–3}. However, few ecosystem service assessment approaches have direct utility in political, social and ecological decision-making. Ecosystem services are natural processes that benefit humans, with birds contributing to four of the service types (provisioning, regulating, cultural, and supporting services) recognised by the UN Millennium Ecosystem Assessment^{4–6}.

Avian scavengers are part of the detrital food web of ecosystems and they provide the important ecological service of recycling carrion biomass to prevent the accumulation of dead biomass, thereby contributing to waste removal, disease regulation, and nutrient cycling⁷.

At the start of the 21st century, European avian scavenger communities were one of the few exceptions to the global decline in Old World avian scavenger birds^{8–12}. Asian and, to a lesser degree African, vulture populations declined as a consequence of ingestion of veterinary drugs and due to illegal poisoning^{8–12}. On the contrary, European vulture populations maintained or increased their numbers¹³. However, the detection of variant (vCJD) and new variant (nvCJD) Creutzfeldt-Jakob disease in humans, which was acquired from cattle infected by bovine spongiform encephalopathy (BSE), led to sanitary legislation (Regulation CE 1774/2002) that greatly restricted the use of animal by-products that were not intended for human consumption. Thus, all carcasses of domestic animals had to be collected from farms and transformed or destroyed in authorised plants, although only 80% of domestic carcasses are currently recovered by specialised companies¹³. In Spain, since 2006 supplementary feeding points for vultures, supplied by intensive farming, have also greatly diminished (–80%) as a consequence of sanitary regulations¹⁴. The disparity between sanitary and environmental policies, i.e., to eliminate corpses versus to conserve scavenger species^{3,15,16}, led to several European dispositions that regulated the use of animal by-products as food for necrophagous birds^{13,16}. Revised regulations on the use of animal by-products that are not intended for human consumption were made by the end of 2011 and they will be applied during 2012¹⁷. However, there has been no assessment of food availability or of the effects of different trophic scenarios on the population dynamics of European vultures. Recently, as a consequence of food shortages, several demographic warning signals have been documented, including a halt in population growth, decreased breeding success, and an apparent increase in mortality among younger age classes¹⁸. However, empirical analyses of the relationships between vulture population dynamics and food availability have only assessed the role of wild ungulates¹⁹. Modelling the effects of sanitary laws on population trends may provide evidence that can inform the design of policies that are compatible with vulture conservation. Multi-agent models are necessary for modelling population dynamics relative to demographic parameters and food availability²⁰ such as P Systems, which is a

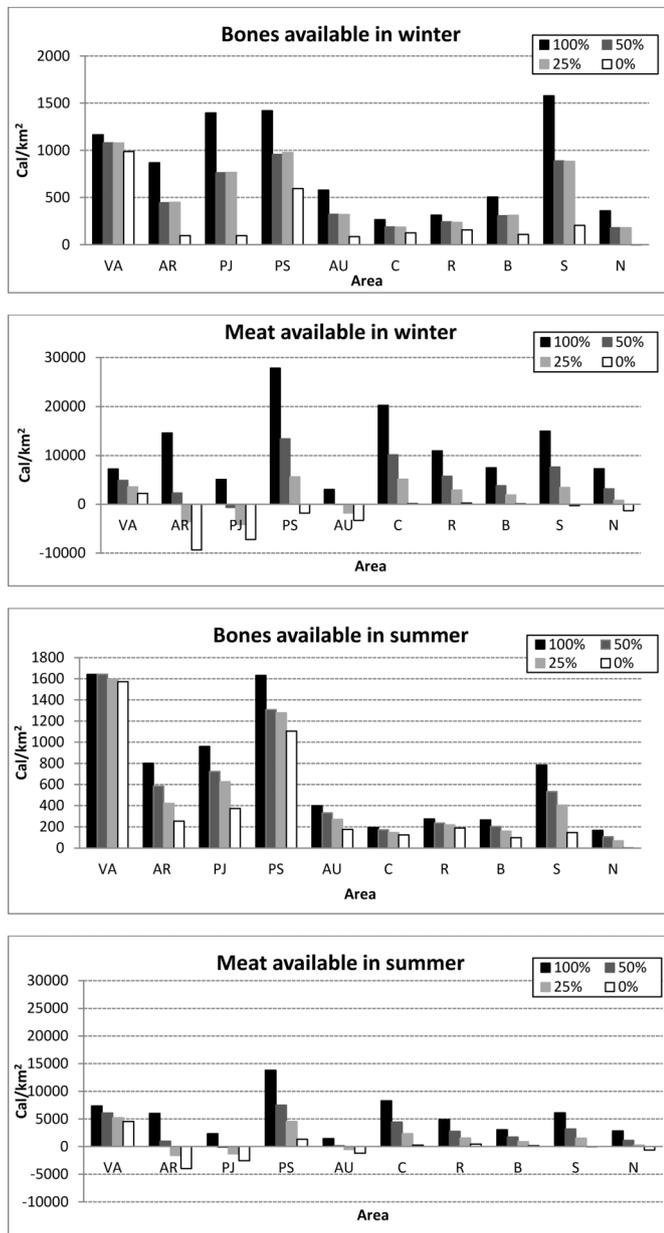


Figure 1 | Spatial and temporal estimate of the difference between the biomass estimated by the model and the energetic requirements for the current avian scavenger population standardized by surface unit (expressed in calories per km²) in the ecosystem, for each of 10 municipalities in Catalonia, Northern Spain, according to the four scenarios of food availability considered (100%, 50%, 25% and 0% of food provided by domestic ungulates).

computational modelling paradigm that was inspired by the functioning of cells working in parallel^{21,22}. This technique was applied recently in several approaches to modelling the dynamics of scavenger species^{19,23,24}. However, these studies did not consider future trends in vulture populations under different trophic scenarios. They also failed to take into account the temporal distribution of feeding resources in different breeding seasons (i.e., winter vs. summer)²⁵ and the spatial scale of areas where the resources were homogeneously distributed. This theoretical approach is valid, but the results obtained are limited from an ecological viewpoint because the models failed to detect spatial changes in species distributions or temporal limitations in food availability. Managers and conservationists require more detailed data to accurately determine parameters for optimising investment in the management of resources. These parameters

include the carrying capacity, suitable areas with potential for re-colonisation, or the benefits of supplying supplementary feeding sites.

The present study used P systems to test the effects of variable levels of food availability over 21 years, on the population viability and conservation of four European vultures (the Eurasian griffon vulture *Gyps fulvus*, the Egyptian vulture *Neophron percnopterus* and the cinereous vulture *Aegypius monachus* considered as meat-eaters and the bearded vulture *Gypaetus barbatus*, considered a specialized bone-eater) as a consequence of sanitary regulations (see Methods). Taking into account a well-studied region in northern Spain (with 10 subareas) inhabited by the four European vulture species, we model the effects of available domestic carcasses (testing four initial scenarios of 100%, 50%, 25%, and 0% of domestic carcasses available in the field and separating meat and bone remains available as a consequence of the different dietary habits between meat and bone consumers) on their population dynamics. The 100% scenario represents conditions before the outbreak of BSE (<2002) while the 0%–25% scenarios represent the current conditions, depending on the area considered, as food limitations progressively worsened between 2006 and 2012. Future changes to the sanitary legislation may modify the availability of domestic carcasses and will probably progressively increase food availability, shifting conditions from 0–25% to 50% and expected to ultimately reach pre-outbreak conditions (100% of domestic carcasses available).

Spain contains the most important European vulture populations (approximately 95% of their total numbers) and the results may have particularly important conservation applications in the assessment of their ecosystem services, the function of supplementary feeding sites, the carrying capacity, or the feeding resources available in an ecosystem during future reintroduction projects. The hypothetical effects of sanitary restrictions on vulture conservation were estimated and this method provides a computational tool that could be applied in other countries.

Results

Temporal and spatial food availability in different management scenarios. Meat was predicted to be the major factor limiting the survival of avian scavengers during winter and summer (Figure 1). In the breeding season (winter), the available food was predicted to be insufficient to cover energetic requirements in two areas with half the domestic carcasses available (PJ and AU), which increased to three (also AR) with a quarter of the domestic carrion available (current situation) and six (also PJ, N and S) without domestic carcasses available (with insufficient bone biomass in N). In the summer scenario, food availability was predicted to be higher due to transhumance. However, the food available was also predicted to be insufficient in one area (PJ) with half the domestic carcasses, increasing to three areas (also AR and AU) with a quarter of the domestic carrion available to vultures and five (also N and S) without domestic carcasses. From a population perspective, these three areas (AR, PJ and AU) were the most important for the avian scavenger guild because the areas with a quarter of the domestic carcasses available contain 59% of the bearded vulture population, 56% of Egyptian vultures, 71% of griffon vultures, and 100% of cinereous vultures in the study area.

Population dynamics in different management scenarios. The population trends of bearded, Egyptian and cinereous vultures were predicted to increase in relation to the current situation and were similar across the four scenarios considered (bearded vulture: $F_{3,83} = 2.61$, $P = 0.057$; Egyptian vulture: $F_{3,83} = 0.12$, $P = 0.95$; cinereous vulture: $F_{3,83} = 0.71$, $P = 0.55$, Figure 2) except for the griffon vulture, for which significant differences were found ($F_{3,83} = 117.54$, $P = 0.0001$). The model predicted differences in the groups formed with 50% and 100% of domestic carcasses available

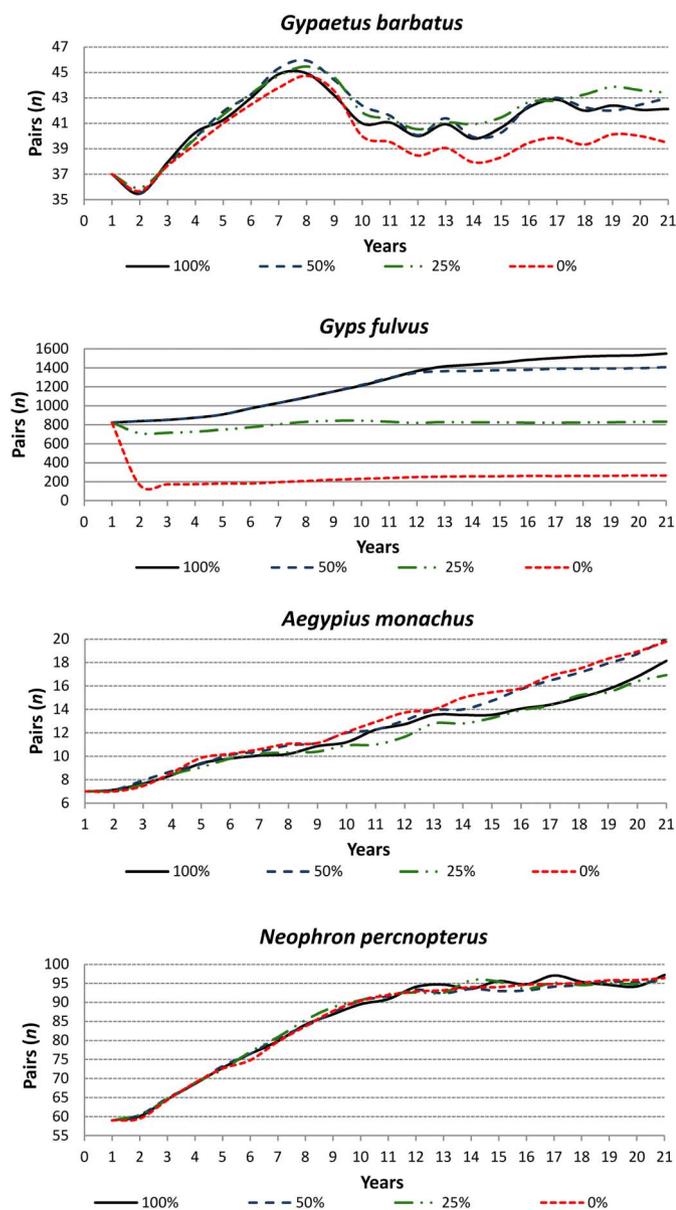


Figure 2 | Predicted population trends for the four avian scavengers in the study area, for each of the four scenarios tested, expressed as the percentage of domestic ungulate carcasses available in the ecosystem. Note the different y-axis scales.

compared to the 25% and 0% scenarios (Duncan's test, $P < 0.05$). With a quarter of domestic carcasses available, a 14% reduction in the griffon vulture population was forecast during the first year, after which their numbers were expected to become stable. In contrast, without domestic carcasses (0% scenario) a sudden decrease is expected with a reduction of 80% in griffon vulture populations, stabilizing at around 200–250 pairs. However, no global differences were found between 100% and 50% domestic carcass availability ($P = 0.44$), although the model indicated that statistically significant differences would be detected after the 12th year ($F_{1,268} = 603.60$, $P < 0.0001$) when there would be a reduction in the population growth of griffon vultures.

Assuming the network movements estimated in the study area (Figure 3), the predicted response of griffon vulture populations to the different scenarios studied is shown in Figure 4. With 25% or 0% of domestic carcasses available, a significant reduction of the population was forecasted in all study areas. The decrease was especially important in populated areas (AR, PJ and AU). A decrease of 50% in the contributions of domestic carcasses was predicted to promote

movement of animals between neighbouring areas (Figure 3). It was predicted that most individuals would not colonize new areas, so the population balance of the species in each area was not predicted to be affected (a trend similar to the 100% scenario) and only some individuals could colonize unoccupied areas such as VA and C. The growth trend with 50% domestic carcass availability is similar to 100% availability during the first 12 years. After this time, the food resources in the receiving areas (VA, C, B and N) were predicted to be insufficient for all pairs such that there is a significant decrease in griffon vulture populations in areas AR, PJ and AU and population stability only occurred with an increase in the biomass provided by wild ungulate populations.

Benefits of vulture ecological services. On average, the Spanish vulture populations were estimated to remove 133.6–200.5 t of bones and 5,550.7–8,326 t of meat each year. The corresponding economic savings of natural carrion removal were estimated at a minimum of 907,679–1,488,719 EUR, while vulture populations throughout the entire European Union may contribute an annual cost reduction of 972,915–1,595,715 EUR. The animal biomass consumed by avian scavengers and removed from the ecosystem in the study area (assuming 50–75% of the diet is based on domestic ungulates) was estimated at 4.23–6.38 t of bones and 176.73–265.10 t of meat. This constituted annual benefits estimated at 28,900–47,400 EUR for farmers and authorities.

Discussion

Sudden changes in the availability of food may cause changes in the population dynamics of species²⁶. The current study highlights the consequences of different levels of food availability on the population dynamics of an avian scavenger guild, indicating the halt and subsequent decline in population growth of the most meat-dependent species, i.e., the griffon vulture. The model predicted meat biomass to be the major limiting factor whereas the dietary plasticity of the other species allowed them to avoid declining population trends, as did their specific dietary habits (small animals for the Egyptian vulture and bones for the bearded vulture) and low densities. From a conservation perspective, these results suggest that the population growth of the most endangered species (Egyptian, cinereous, and bearded vultures) will continue in the current scenario, despite sanitary legislation that limits food resources^{13,16}, given that a quarter of domestic ungulates are available in the ecosystem. However, this trend may be reversed by an increased effect of non-natural mortality when considering the effects of factors, such as illegal poisoning or lead poisoning, on breeding success and survival^{27–31}. These problems currently affect the threatened bearded vulture and they appear to have stabilised their populations via non-natural mortality effects on adult survival²⁹. In addition, given the difficult nature of assessing the numbers and age structure of the non-breeding population for modelling demographic trends and movements, and because these individuals mainly feed at supplementary feeding sites³², our model only considered the immature population (chicks reared). Thus, we can consider our model conservative because a portion of available food could benefit other non-breeding individuals.

In recent years, the Spanish griffon vulture population has experienced decreases in their breeding parameters and changes in the spatial distribution of the breeding and non-breeding population, while there have also been increases in their number of aggressive interactions with live livestock and an increase in the mortality of their young^{18,33}. By contrast, other species have increased their populations, although illegal poisoning has affected some subpopulations^{27,30}. It is speculated that these changes were due to food shortages, although no empirical evidence is presented to support this hypothesis. For the first time, the current study suggests that food limitations mainly affect griffon vultures. According to the model, vultures might respond to food shortages by shifting their spatial distribution leading to population decline (in the case of the 0% and 25%

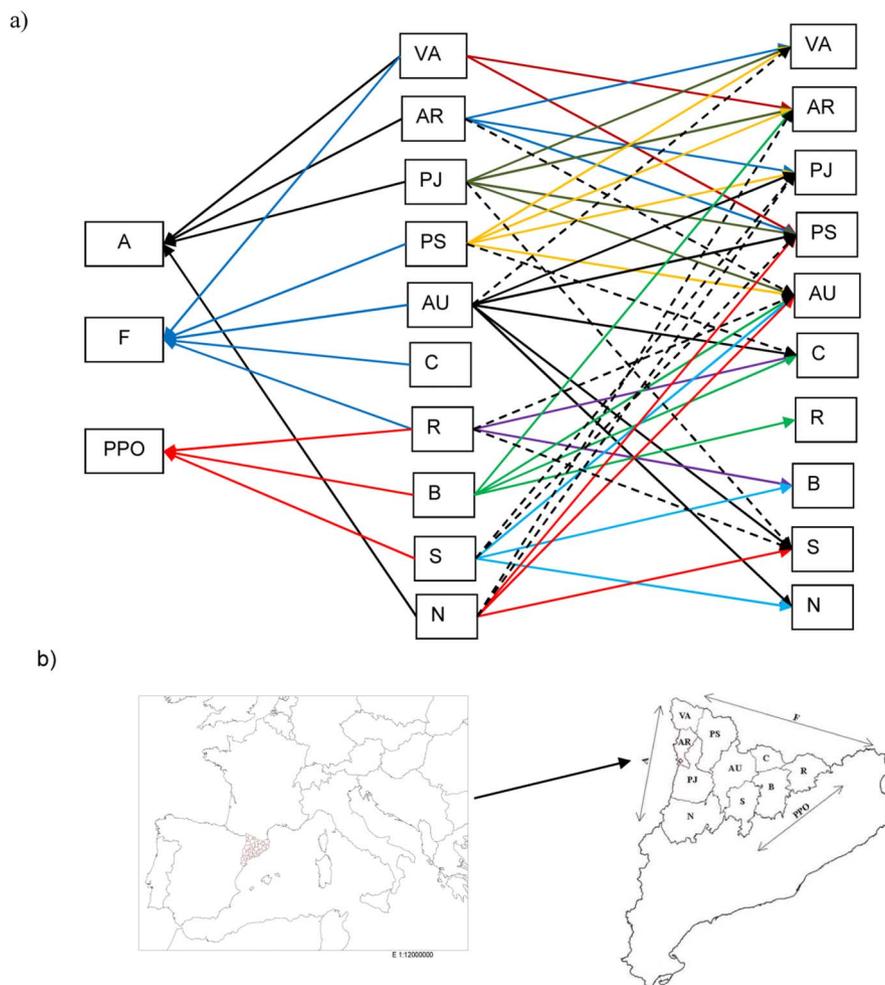


Figure 3 | (a) Possible avian scavenger foraging movements between areas, when there is a lack of resources. The continuous lines are the possible movements of the bearded vulture (*Gypaetus barbatus*), Egyptian vulture (*Neophron percnopterus*), and cinereous vulture (*Aegypius monachus*). The dashed line represents the Eurasian griffon vulture (*Gyps fulvus*). (b) Distribution of the ten areas considered in the study: VA: Val d’Aran; AR: Alta Ribagorça; PJ: Pallars Jussà; PS: Pallars Sobirà; AU: Alt Urgell; C: Cerdanya; R: Ripollès; B: Berguedà; S: Solsonès; N: Noguera. A, F, and PPO correspond to peripheral areas (alternative environments in the model) in which the population might obtain alternative food resources outside of the study area (see more details in Methods).

scenarios) and these effects could accelerate in coming years if food limitations continue. These regressive scenarios suggested by the model do not imply an increase in mortality. Instead, individuals were predicted to abandon the ecosystem to search for suitable alternative areas where food and breeding sites are available, when food resources are insufficient and the carrying capacity at small spatial scales approaches the maximum levels. From an ecological perspective, griffon vultures are the dominant species of the avian scavenger guild in a competitive scenario because they can monopolise resources to the detriment of other species¹⁴. This suggests that the provision of supplementary feeding sites as a stopgap measure to meet food deficits would mainly favour this species. However, other ecological effects on the ecosystem of a population decline are unknown and the consequences may be a new concern for managers and policy-makers³⁴. The ecological services provided by vultures have an important role and the regular use of feeding stations by these species could reduce ecological service provision in terms of scavenging^{18,25,35}. In addition, the role of griffon vultures as facilitator species preparing carrion for other facultative and obligate scavengers is unknown but may have cascade effects within the ecosystem.

A more advisable management measure would be to reduce the amount of food provided at large feeding stations and promote the creation of smaller sites that simulate a trophic scenario by more

closely resembling actual ecosystems, thereby preventing behavioural changes or any negative effects on population dynamics^{19,34,36,37}. Based on the carrying capacity and the population trend observed, supplementary feeding programs appear to be unnecessary in hypothetical scenarios where half and 100% of domestic carcasses are available. The latter scenario corresponds to that present in the period before the establishment of sanitary regulations (progressively applied since 2006), which could be representative of most Mediterranean populations that are characterised by widespread grazing and the food resources provided by wild ungulates^{19,38}. Thus, this study should be taken into account by managers and conservationists if the sanitary legislation is amended in the future. In fact, the presence of carcasses in the field as a consequence of extensive grazing is considered to be the most useful and economic method of managing avian scavenger populations^{13,17}. This is an important issue for managers and policy-makers because solutions to the management of European vulture populations are based on an assumption that food shortages due to sanitary regulations should be compensated for with supplementary feeding sites. This management approach may have detrimental consequences because a patchy distribution of resources can artificially modify the habitat quality, with subsequent negative effects on population dynamics^{36,39}. Thus, the carrying capacity should be regulated by feeding resources provided in the

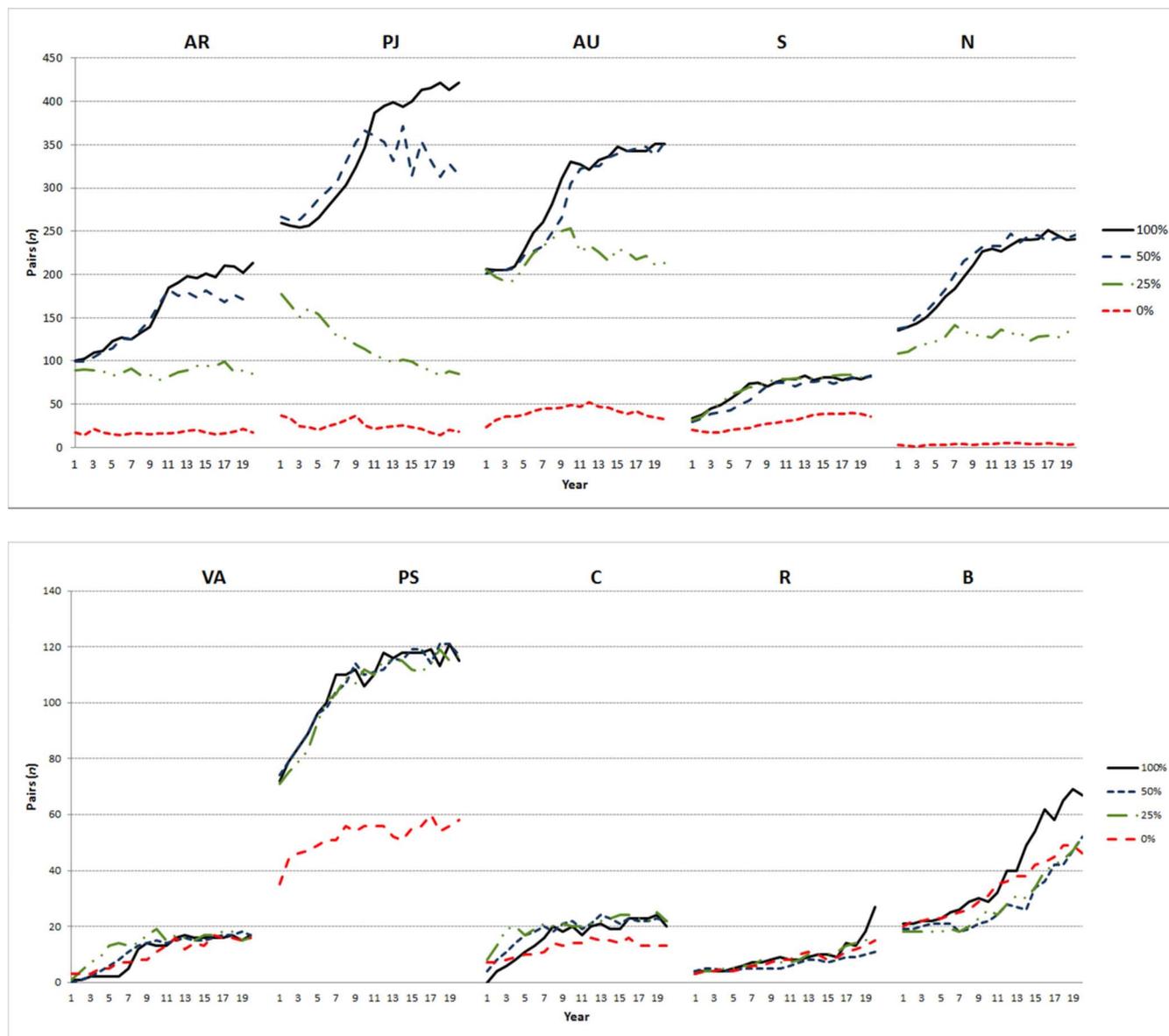


Figure 4 | Predicted population trend of the Eurasian griffon vulture in the different areas, according the four scenarios of domestic carcasses available. The population increase in several areas in which the species is initially absent (VA and C) or of low densities is a consequence of spatial changes related with food shortages or maximum carrying capacity.

ecosystem despite the long tradition in several countries of artificial food handling via supplementary feeding sites¹⁸. However, the sensitivity of some species (several threatened) in terms of demographic parameters, such as adult survival^{29,40,41} due to the presence of non-natural mortality factors (mainly illegal poisoning)⁴², could increase mortality rates and destabilise populations. Given that supplementary feeding increases pre-adult survival²⁸, this method may continue to favour the most endangered species, especially if the quantity supplied is reduced and its unpredictability is increased.

The results of this study are relevant to future reintroduction and conservation projects. Our model is capable of identifying the spatial and temporal distribution of feeding resources, thereby facilitating the planning and optimisation of the most appropriate management approach, including supplementary feeding activities, to support the most food-poor areas where necessary. The application of this model to reintroduction projects demonstrates that calculations of food availability can provide guidelines when establishing the carrying capacity to optimise economic investment. In the case of avian scavengers, food availability studies can identify problems prior to

reintroduction projects, thereby allowing managers to improve the success rate of reintroductions. This is particularly important for avian scavengers because they are highly dependent on carrion resources, the availability of which can be modified by humans by direct management, e.g., hunting of wild ungulates, the sanitary legislation for domestic ungulates, or the establishment of a network of supplementary feeding sites. Given the global decline affecting Old World vultures⁸, the availability of robust tools can help managers to optimise the investment of economic resources^{43,44} and to identify the most appropriate conservation measures.

Methods

Model building and assumptions. Using a Population Dynamic P System (see Supplementary Information) we defined a model allowing the study of the ecosystem dynamics in a zone subdivided into 10 areas inhabited by four avian scavengers whose diet depends on the food provided by the carcasses of wild and domestic ungulates. For the validation of the model^{19,24}, we used census data obtained in the study area between 1994 and 2008^{24,25} taking into account the inter-annual variation in demographic parameters and density-dependent effects affecting the population trends observed.

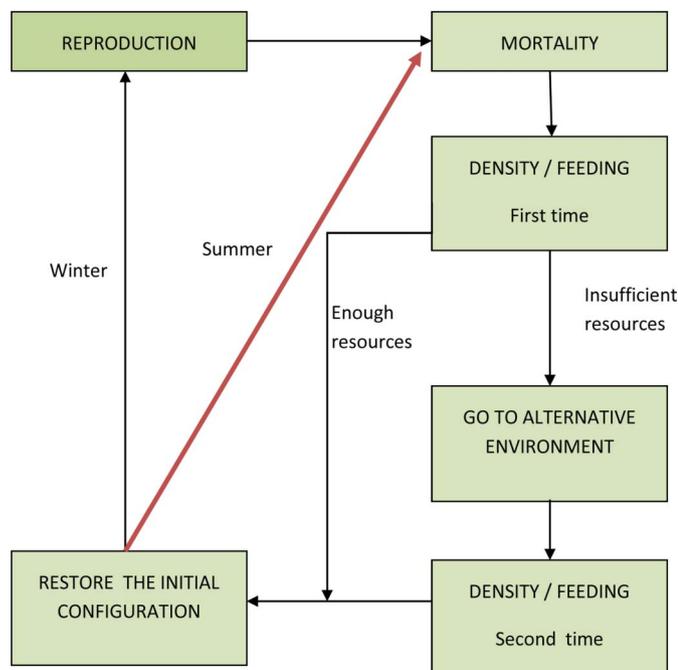


Figure 5 | Scheme of the model. The model takes into account two periods (summer and winter) and the basic processes of reproduction, mortality, and feeding. The scavenger birds forage in others areas when insufficient resources are available (i.e., they move). If food is scarce, the animals take the food and return to their initial area. They change territory if space is scarce. The carrying capacity of each area is limited and it is necessary to control the number of animals present. Before repeating the loop, it is necessary to restore the initial configuration. Two executions of a loop are equivalent to the passage of one year in the ecosystem.

The model consists of a loop with six modules (Figure 5). One year in the ecosystem involves running the loop twice, i.e., once for the summer period (four months) and once for the winter season (eight months). The model starts with the run of the reproduction module. The species are modelled with only one reproductive period each year. While the population of wild animals is a dynamic system conditioned by environmental and ecological factors, domestic animals are controlled by humans such that there are significant fluctuations in the population between the summer and winter as a consequence of transhumant movements.

In the reproduction module, all breeding age females can reproduce successfully in a probabilistic way. After the application of reproduction rules, the mortality module is carried out; there are two possible causes of death, i.e., natural mortality (e.g., senescence or accidents) and non-natural mortality (e.g., hunting or illegal poisoning). In most ungulate species (except wild boar), hunting practices are focused on males, producing variations in the sex-ratio. The model takes into account temporal and sex-ratio mortality variations influencing population growth and the biomass provided. In the following module the model takes into account whether food and carrying capacity are sufficient in the environment occupied to maintain their presence.

For each vulture species we obtained parameters on breeding, demography and energetic requirements according to their metabolism⁴⁶ (Supplementary Information Table S2), mortality and the biomass that dead wild ungulates provided in the field, separating bone and meat remains in accordance with the different dietary habits of the species¹⁹. The diet of avian scavengers is complemented by external inputs through supplementary feeding sites and in smaller quantities by other small species such as birds, reptiles and small mammals and micromammals^{19,24,46–49}. Available grass biomass is enough to cover the energetic requirements of wild and domestic ungulates^{50,51} and has not been considered as a limiting factor.

With respect to the interspecific hierarchies in the access and exploitation of carrion, we consider that Egyptian and cinereous vultures are the first species to access the carrion and griffon and bearded vultures the last (A.M. unpubl. data). Intraspecific age hierarchies are not differentiated in access to food, since the behavioral patterns observed at feeding sites^{52–54} may differ from the random distribution of food in the wild.

When resources are limited, they are distributed randomly according to the number of individuals of each species competing for the same type of food and according to the amount of resources they need. The model also takes into account the presence of a non-breeding population (Table S2) consisting of fledglings produced by the breeding population. These are counted individually and when they reach breeding maturity, two individuals become a breeding pair occupying a new territory.

Besides natural and non-natural mortality, the model assumes that an ungulate dies when it lacks physical space as a consequence of its carrying capacity. In the case of avian scavengers, if a species has insufficient resources it moves to nearby areas. It returns to the starting point if there are food limitations but no space limitations. An individual colonises a new area if insufficient space is available. Scavengers can choose from more than one destination if they need to move, and they select one randomly. If the alternative area selected lacks resources, this random sampling continues until resources are found, leaving the ecosystem if resources are not found.

If there is an avian scavenger who lacks sufficient resources after carrying out the rules of feeding and controlling for the maximum density of each species, it will move to another environment, running the feeding process and/or density previously unrealized for this animal. If space is not a limiting factor, they will return to the source environment or otherwise colonize a new area.

When defining the model, a directed network-graph of avian scavenger movement is specified (Figure 3). The avian scavengers move to search for food in the peripheral areas (A, F, PPO) when feeding resources in the regular home ranges are insufficient. For the foraging areas, we consider the maximum linear foraging movement from the nest for the griffon vulture to be 90 km, 40 km for the bearded vulture, 15 km for the Egyptian vulture and 60 km for the cinereous vulture⁴⁶ (A.M. unpubl. data). The model takes into account that each species takes advantage of the resources close to their nesting area and widens the radius of their movements as they deplete. The amount of meat and bones consumed by scavengers depends on the season. The excess meat disappears from the ecosystem at the end of each period (summer or winter). The model assumes that 20% of the unconsumed bones remain available in the ecosystem, because bones can be preserved for up to 10 times longer than meat⁵⁵. Populations of animals will generally grow exponentially if they have sufficient resources, although this growth is restricted due to limitations in physical space, which supports the maximum carrying capacity used in the model (Table S1). The objective of the final module is to restore the initial configuration to restart the loop. Running the model requires some initial parameters, so these are entered before returning an output. The evolution rules used by the model are run for each individual and they are executed simultaneously for all individuals. Thus, the system operates in parallel, which means there can be competition when animals of the same or different species share resources. The values of the parameters used in the model were derived from the bibliography^{19,24}. The running model is detailed in Supplementary Information.

Management scenarios. Several possible scenarios were modelled by testing the impact of different food availability regimes to elucidate their potential effects on population projections over time. Four initial scenarios were considered that depended on the hypothetical biomass provided by domestic ungulates. Thus, the 100% scenario represented the ecosystem function prior to the application of sanitary regulations^{13,16} where all domestic and wild ungulate carcasses were available to the avian scavenger guild. The 50% scenario represented a scenario where only half of the hypothetical food resources provided by domestic carcasses were available. The 25% scenario might reflect a scenario that is similar to the current situation because approximately 80% of carcasses are recovered and destroyed by specialist companies. Finally, the 0% scenario simulates an ecosystem where food is provided only by wild ungulates.

First, the biomass was calculated provided for each subzone by subtracting the megalocalories available from the energetic requirements of the avian scavengers inhabiting each subzone. This provided a picture of the surplus or constraints on food availability from a spatial perspective. Second, the population trend was simulated with consideration for the demographic parameters of hypothetical growth in each species (see Supplementary Information) and the availability of biomass provided by the different scenarios plus the biomass provided by wild ungulates and feeding stations. Data used for the a posteriori statistical analyses were obtained by using the model to simulate the population dynamics (21 years and a total of 50 replicates) in a probabilistic manner, which reflected the random behaviour of the natural situation.

Quantifying carrion removal vs. vulture ecological services. To estimate the potential biomass that avian scavengers can remove from the ecosystem, the annual energetic requirements of each individual and species were determined based on their standard metabolism^{48,56,57}, and then multiplied by the number of individuals present in the ecosystem. It was estimated that 50–75% of the diet of avian scavengers was composed of domestic ungulate remains, which was based on the animal biomass range (its natural removal from the ecosystem). To compare the results, this estimate of the ecological services provided by the Spanish vulture population was added to the total for the European population¹⁶. The cost of removing this carrion for farmers and authorities was calculated as the cost for the removal and transport of each ton of carrion: an average of 89 EUR, and the cost of disposal in authorised plants, 76.3 EUR⁵⁸. This allowed the economic estimate of the ecological services performed by avian scavengers to be compared with the cost of carrion removal.

Statistical analyses. Normality of the data was confirmed using the Kolmogorov–Smirnov test, before a one-way ANOVA to compare the annual population trend of avian scavengers obtained in different management scenarios. This analysis took into account the animal biomass as a dependent variable while the species were factors. When ANOVA tests were significant, a further test of homogeneity was performed using Duncan's test to identify inter-group differences.

1. Loreau, M., Naeem, S. & Inchausti, P. *Biodiversity and ecosystem functioning: synthesis and perspectives*, Oxford University Press, 2002.



2. Loreau, M. Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philos. Trans. R. Soc. B* **36**, 49–60 (2010).
3. Naeem, S. *et al.* *Biodiversity, ecosystem functioning and human wellbeing: an ecological and economic perspective*, Oxford University Press, 2009.
4. Sekercioglu, C. H., Daily, G. C. & Ehrlich, P. R. Ecosystem consequences of bird declines. *Proc. Natl. Acad. Sci. USA* **101**, 18042–18047 (2004).
5. Whelan, C. J., Wenny, D. G. & Marquis, R. J. Ecosystem services provided by birds. *Ann. New York Acad. Sci.* **1134**, 25–60 (2008).
6. Wenny, D. G. *et al.* The need to quantify ecosystem services provided by birds. *Auk* **128**, 1–14 (2011).
7. DeVault, T. L., Rhodes, O. E. & Shvilk, J. A. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* **102**, 225–234 (2003).
8. Oaks, L. *et al.* Diclofenac residues as the cause of vulture population declines in Pakistan. *Nature* **427**, 630–633 (2004).
9. Green, R. E. *et al.* Diclofenac poisoning as a cause of vulture population declines across the Indian subcontinent. *J. Appl. Ecol.* **41**, 793–800 (2004).
10. Thiollay, J. M. Raptor declines in West Africa: comparisons between protected, buffer and cultivated areas. *Oryx* **41**, 322–329 (2007).
11. Naidoo, V., Wolker, K., Cuthbert, R. & Duncan, N. Veterinary diclofenac threatens Africa's endangered vulture species. *Regul. Toxicol. Pharm.* **53**, 205–208 (2009).
12. Virani, M. Z., Kendall, C., Njoroge, P. & Thomsett, S. Major declines in the abundance of vultures and other scavenging raptors in and around the Masai Mara ecosystem, Kenya. *Biol. Conserv.* **144**, 746–752 (2011).
13. Donazar, J. A., Margalida, A., Carrete, M. & Sánchez-Zapata, J. A. Too sanitary for vultures. *Science* **326**, 664 (2009).
14. Cortés-Avizanda, A., Carrete, M. & Donazar, J. A. Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. *Biol. Conserv.* **143**, 1707–1715 (2010).
15. Tella, J. L. Action is needed now, or BSE crisis could wipe out endangered bird of prey. *Nature* **410**, 408 (2001).
16. Margalida, A., Donazar, J. A., Carrete, M. & Sánchez-Zapata, J. A. Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. *J. Appl. Ecol.* **47**, 931–935 (2010).
17. Margalida, A., Carrete, M., Sánchez-Zapata, J. A. & Donazar, J. A. Good news for European vultures. *Science* **335**, 284 (2012).
18. Donazar, J. A., Margalida, A. & Campión, D. *Vultures, feeding stations and sanitary legislation: a conflict and its consequences from the perspective of conservation biology*. Sociedad de Ciencias Aranzadi 2009.
19. Margalida, A., Colomer, M. A. & Sanuy, D. 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 (2011).
20. Bousquet, F. C. & Le Page, C. Multi-agent simulations and ecosystem management: a review. *Ecol. Model.* **176**, 313–332 (2004).
21. Páun, G. Computing with membranes. *J. Comp. Syst. Sci.* **61**, 108–143 (1998).
22. Páun, G., Rozenberg, G. & Salomaa, A. *The Oxford Handbook of Membrane Computing*, Oxford University Press, 2010.
23. Cardona, M. *et al.* Modelling ecosystems using P Systems: The Bearded Vulture, a case study. *Lect. Notes Comput. Sc.* **5391**, 137–156 (2009).
24. Colomer, M. A., Margalida, A., Sanuy, D. & Pérez-Jiménez, M. J. A bio-inspired computing model as a new tool for modeling ecosystems: the avian scavengers as a case study. *Ecol. Model.* **222**, 33–47 (2011).
25. Dupont, H., Mihoub, J. B., Becu, N. & Sarrazin, F. Modelling interactions between scavenger behaviour and farming practices: Impacts on scavenger population and ecosystem service efficiency. *Ecol. Model.* **222**, 982–992 (2011).
26. Ostfeld, R. S. & Keasing, F. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol. Evol.* **15**, 232–237 (2000).
27. Hernández, M. & Margalida, A. Pesticide abuse in Europe: effects on the Cinereous vulture (*Aegypius monachus*) population in Spain. *Ecotoxicology* **7**, 264–272 (2008).
28. Gangoso, L. *et al.* Long-term effects of lead poisoning on bone mineralization in vultures exposed to ammunition sources. *Environ. Pollut.* **157**, 569–574 (2009).
29. Oro, D. *et al.* Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. *PLoS One* **3**, e4084 (2008).
30. Hernández, M. & Margalida, A. Poison-related mortality effects in the endangered Egyptian Vulture (*Neophron percnopterus*) population in Spain: conservation measures. *Eur. J. Wildl. Res.* **55**, 415–423 (2009).
31. Hernández, M. & Margalida, A. Assessing the risk of lead exposure for the conservation of the endangered Pyrenean bearded vulture (*Gypaetus barbatus*) population. *Environ. Res.* **109**, 837–842 (2009).
32. Margalida, A., Oro, D., Cortés-Avizanda, A., Heredia, R. & Donazar, J. A. Misleading population estimates: biases and consistency of visual surveys and matrix modelling in the endangered Bearded Vulture. *PLoS One* **6**, e26784 (2011).
33. Margalida, A., Campión, D. & Donazar, J. A. European vultures' altered behaviour. *Nature* **480**, 457 (2011).
34. Olson, Z. J., Beasley, J. C., DeVault, T. L. & Rhodes, E. jr. Scavenger community response to the removal of a dominant scavenger. *Oikos* **121**, 77–84 (2011).
35. Deygout, C., Sarrazin, F., Gault, A. & Bessa-Gomes, C. Modeling the impact of feeding stations on vulture scavenging service efficiency. *Ecol. Model.* **220**, 1826–1835 (2009).
36. Carrete, M., Donazar, J. A. & Margalida, A. Density-dependent productivity depression in Pyrenean Bearded Vultures: implications for conservation. *Ecol. Appl.* **16**, 1674–1682 (2006).
37. Dupont, H., Mihoub, J. B., Bobbe, S. & Sarrazin, F. Modelling the consequences of farmer's carcass disposal practices on scavengers' ecological service. *J. Appl. Ecol.* **49**, 404–411 (2012).
38. Olea, P. & Mateo-Tomás, P. The role of traditional farming practices in ecosystem conservation: the case of transhumance and vultures. *Biol. Conserv.* **142**, 1844–1853 (2009).
39. Robb, G. N., McDonald, R. A., Chamberlain, D. E. & Bearhop, S. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.* **6**, 476–484 (2008).
40. Le Gouar, P. *et al.* Roles of survival and dispersal in reintroduction success of Griffon vulture (*Gyps fulvus*). *Ecol. Appl.* **18**, 859–872 (2008).
41. Grande, J. M. *et al.* Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. *Oikos* **118**, 580–590 (2009).
42. Margalida, A. Poison baits and funding cuts: a deadly mix. *Science* (In press).
43. Sutherland, W. J. & Freckleton, R. P. Making predictive ecology more relevant to policy makers and practitioners. *Philos. Trans. R. Soc. B* **367**, 322–330 (2012).
44. Wilson, H. B., Joseph, L. N., Moore, A. L. & Possingham, H. P. When should we save the most endangered species? *Ecol. Lett.* **14**, 886–890 (2011).
45. Cardona, M. *et al.* A P-System based model of an ecosystem of some scavenger birds. *Lect. Notes Comput. Sc.* **5957**, 182–195 (2010).
46. Donazar, J. A. *The Iberian Vultures. Biology and Conservation*, J.M. Reyero Editor, 1993.
47. Margalida, A., Bertran, J. & Heredia, R. Diet and food preferences of the endangered Bearded vulture *Gypaetus barbatus*: a basis for their conservation. *Ibis* **151**, 235–243 (2009).
48. Margalida, A. *et al.* Long-term relationship between diet and breeding success in a declining population of Egyptian Vulture. *Neophron percnopterus Ibis* **154**, 184–188 (2012).
49. Donazar, J. A., Cortés-Avizanda, A. & Carrete, M. Dietary shifts in two vultures after the demise of supplementary feeding stations: consequences of the EU sanitary legislation. *Eur. J. Wildl. Res.* **56**, 613–621 (2010).
50. Fillat, F. Gestión semi-extensiva de prados y pastos europeos ricos en especies: caso particular de los Pirineos españoles. *Pastos* **33**, 171–215 (2006).
51. García-Martínez, A., Olaizola, A. & Bermués, A. Trajectories of evolution and drivers of change in European mountain cattle farming systems. *Animal* **3**, 152–165 (2009).
52. Bosè, M. & Sarrazin, F. Competitive behaviour and feeding rate in a reintroduced population of Griffon Vultures. *Gyps Fulvus Ibis* **149**, 490–501 (2007).
53. Bosè, M., Duriez, O. & Sarrazin, F. 2012 Intra-specific competition in foraging griffon vultures: 1. The dynamics of feeding in groups. *Bird Study* **59**, 182–192 (2012).
54. Duriez, O., Herman, S. & Sarrazin, F. 2012 Intra-specific competition in foraging griffon vultures: 2. the influence of supplementary feeding management. *Bird Study* **59**, 193–206 (2012).
55. Houston, D. C. & Copesey, J. A. Bone digestion and intestinal morphology of the Bearded Vulture. *J. Raptor Res.* **28**, 73–78 (1994).
56. Prinzing, E. *et al.* Energy metabolism and body temperature in the Griffon Vulture (*Gyps fulvus*) with comparative data on the Hooded Vulture (*Necrosyrtes monachus*) and the White-backed Vulture (*Gyps africanus*). *J. Ornithol.* **143**, 456–467, (2002)
57. King, J. R. & Farner, D. S. Energy metabolism, thermoregulation and body temperature. In, Marshall, J. A. (Ed.) *Biology and comparative physiology of birds* Vol. II New York: Academic Press, pp. 215–288, 1961.
58. Boumellasa, H. *Rapaces nécrophages: concilier conservation de l'espèce et minimisation des dépenses, vers un renforcement du lien Agriculture-Environment*. University Paris X 2004.

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Author contributions

A.M. and M.A.C. designed the experiment, collected all the data, performed analysis of the data, and wrote the manuscript. Both the authors discussed the results and commented on the manuscript.

Additional information

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Supplementary Information

Modelling the effects of sanitary policies on European vulture conservation

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Supplementary Materials and Methods

Study area

The study area was in northeastern Spain, where breeding sites occur for all four European vulture species, i.e., Eurasian griffon vulture (*Gyps fulvus*), cinereous vulture (*Aegypius monachus*), Egyptian vulture (*Neophron percnopterus*), and bearded vulture (*Gypaetus barbatus*). This region contains an important vulture population representative of southwestern Europe, which made it possible to test the potential effects of changes in food availability on European vulture population dynamics. An abundance of grazing livestock are found in this area, mainly sheep (*Ovis aries*), goats (*Capra hircus*), cattle (*Bos taurus*), and horses (*Equus caballus*) (see <http://www.marm.es>), while six wild ungulate species are also present, namely red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), mouflon (*Ovis musimon*), southern chamois (*Rupicapra pyrenaica*), and wild boar (*Sus scrofa*).

The study area was divided into 10 subareas of which detailed data censuses of avian scavengers and wild and domestic ungulates are available. Wild and domestic ungulates are herbivores (except the omnivorous wild boar) and their remains form the basic food source for the avian scavenger guild (>80% of the diet is based on these species [44]).

The study area contains a total of 19 feeding stations in which food is provided principally during the breeding season. Of these supplementary feeding stations, 10 are specific for bearded vultures (remains are principally sheep extremities; average amount of food provided by site/year $2598.2 \pm \text{SD} = 1404.16$ kg) and the rest for the remaining avian scavengers (carcasses and meat remains; average amount of food provided by site/year: $1531.8 \pm \text{SD} = 1084.16$ kg).

Since individuals can move from one area to another depending on the resources available, the ecosystem appears to function as a single set (overall ecosystem) composed of a network of 10 subsets according to specific data obtained in each area. In this way, whenever there is a lack of food in one of the subareas or the carrying capacity reaches its peak, the individuals will move to the nearest suitable area (Figure 3). Maximum carrying capacity for wild ungulates and avian scavengers (Table S1) has been established according to the data provided by the literature and estimates are based

on the population growth observed during the previous 20 years and are used to adjust the variables of the model [24].

The subarea in which the nest is located is considered the core area and the neighbouring subareas the potential home range from which each species will obtain their energetic requirements. Thus, in our model the individuals can move from one area to the other and the ecosystem's local carrying capacity has been limited to the appropriate areas and habitats for the different species as has the maximum density that can be reached (Table S1).

Censuses, dietary habits and demographic parameters

Data on the avian scavenger and wild ungulate populations were obtained through censuses carried out by technicians from the Departament de Medi Ambient i Habitatge of the Generalitat de Catalunya, literature and personal observations from 1994-2011.

Unlike in previous work [19, 24], the year has been divided into two periods: *winter*, from October to June and *summer*, from July to September. During the winter, the reproductive period of avian scavengers takes place, during which time egg-laying occurs between December and February (except for the Egyptian vulture in April) and fledging occurs between June and August coinciding with the presence of transhumant livestock in mountain areas. During the summer period, the number of livestock in the mountain areas increases significantly as a consequence of transhumant livestock. Thus, food availability differs among seasons being greater during the summer, whereas the energetic requirements of avian scavengers are higher during the breeding season (winter and spring). In addition to population fluctuations there are also some demographic (i.e., mortality) and biological (i.e., energetic requirements) parameters that vary between the summer and winter periods (Table S2).

With respect to interspecific differences in dietary habits, the diet of the bearded vulture is based on bone remains, whereas the diet of griffons, cinereous and Egyptian vultures is based on meat provided by wild and domestic ungulates and to a lesser degree small animal carcasses. In the case of cinereous, bearded and Egyptian vultures, small mammals are also important in the diet [45-48]. Thus, we established a minimum of 3600 kg of available biomass provided by small animal carcasses as a supplement to

the diet of all avian scavengers. The remaining biomass is obtained from the food provided by the feeding stations.

Population Dynamic P System Model

This study of population dynamics used a variant of P systems, known as a *Population Dynamic P System* (PDP), i.e., a multi-environment probabilistic functional extended P system with active membranes of degree $[m,q]$ [24, 45]. P systems are computational models that are based on the structure of biological cells and one of their key characteristics is their ability to work in parallel [21-24]. The way to model a problem using PDP models depends on the type of problem itself and the strategies used by the modeler. The costs grow by increasing the number of rules. PDPs are computational models that work with objects such that description is not simple and cannot be synthesized by analytical expressions as in classic models.

A cell in PDP models is represented by membranes within which objects are located. The objects evolve according to the characteristics of the medium generating a succession of configurations associated with the dynamics of the problem studied (Figure S1).

The main components of P systems are a *membrane structure*, which is made up of an external membrane that is often referred to as a skin membrane, and additional internal membranes that can also contain membranes. The entire series of membranes forms a structure that can be represented in a hierarchical manner, where the skin membrane constitutes the roots of the tree. The membranes are labelled (this number appears in the lower part) and they can possess a charge (this number appears in the upper part) with three possible values “0”, “+”, or “-“ (Figure S1). Objects are located in areas defined throughout the membrane structure, including existing objects associated with the input of the model (e.g., individuals) and objects necessary for the correct execution and synchronization of the model (Figure S1). The objects are described using symbols or chains of symbols known as *multisets of objects*. The *evolution rules* allow objects to evolve and move to different areas, or they can be transformed and dissolved. The evolution rules that can be applied in the regions formed by membranes in a variant PDP are of the following type:

$$u[v]_i^\alpha \xrightarrow{f_r} u'[v']_i^{\alpha'}.$$

If the area formed by membrane i with charge α contains object v and the outer part of the membrane contains object u , with a probability f_r , the rule will be applied to change the charge polarity of membrane i from α to α' and objects u and v will evolve to become u' and v' . If $f_r = 1$, it is omitted.

The rules that potentially can be applied will be applied in parallel and in a maximal way to consume all the objects involved. The application of the rules causes the P system to evolve and its configuration changes (Figure S1). A P system computation is made up of a sequence of configurations obtained from previous computations via transitions.

There are different environments (q) and communication is permitted between them. When an object passes through the skin membrane, it evolves in accordance with the rules in the new environment, which are of the following type:

$$(x)_{e_j} \xrightarrow{p(x,j_1 \dots j_h)} (y_1)_{e_{j_1}} \dots (y_h)_{e_{j_h}}.$$

If object x passes from environment e_j to environment $e_{j_1} \dots e_{j_h}$ it can be modified into object $y_1 \dots y_h$, respectively.

Model used

The ecosystem modelled is composed of 10 environments, E , and 13 species of animals, N . The number of animals per species and environment as well as the biological parameters and the number of years to be simulated are the input of the model (Tables S2 and S3).

The output is formed by the number of animals of each species per year and the biomass (expressed in megacalories) that every species provides throughout the years simulated.

In order to model this ecosystem we use a PDP formed by five membranes and eleven environments, ten of which are associated with the established geographic area. The eleventh environment is used to facilitate the movement of animals between environments where resources are insufficient. This is a variant of P systems that reproduces the randomness of natural processes and assigns an environment to each of

the areas studied. The polarization of the membranes is used to show environmental changes (i.e., time of year).

The membrane structure is $\mu = [[[\]_3]_1[[\]_4]_2]_0$

Objects that appear in the initial configuration in each of the membranes are:

- Membrane labelled with 0:

$$M_0 = \{X_{ij}^{q_{kij}}, XA_{ij}^{q_{kij}}, XS_{ij}^{qs_{kij}}, d_i, co_1\}, 1 \leq k \leq E, 1 \leq i \leq N, 1 \leq j \leq g_{i,5},$$

- Membrane labelled with 1 and 2: $M_j = \{R\}, 1 \leq j \leq 2$
- Membrane labelled with 3 and 4: $M_j = \{FO_k\}, 1 \leq k \leq E, 3 \leq j \leq 4.$

In the initial configuration (Figure S2), each wild animal of species i and age j exists as an object X_{ij} . In a similar way, an object XA_{ij} represents domestic animals that spend all year in the ecosystem whereas an object XS_{ij} represents domestic animals that spend only some time in the ecosystem, the superscripts indicate the number of each type of existing object. The object co_1 is used to indicate the period (winter, co_2 , or summer, co_1), FO_k is used to generate external contributions (i.e., supplementary feeding) and food provided by small animals present in the ecosystem, while object R (counter) allows the synchronisation of the model.

The objects evolve, by evolution rules, creating new objects, dissolving, moving between membranes, etc. The set of objects that will appear in different configurations form the working alphabet of the model and in the case of the proposed model is:

$$\Gamma = \{X_{i,j}, XA_{i,j}, XS_{i,j}, Z_{i,j}, ZS_{i,j}, Z'_{i,j}, Za'_{i,j}, Zm'_{i,j}, Z''_{i,j}, W_{i,j}, ZE_{i,j,c+2,k}, ZEA_{i,j,c+2,k}, ZEm_{i,j,c+2,k}, ZE'_{i,j,c+2,k}, ZEA'_{i,j,c+2,k}, ZEm'_{i,j,c+2,k}, W'_{i,j,c+2,k}, X'_{i,j,c+2}, 1 \leq i \leq N, 0 \leq j \leq g_{i,5}, 1 \leq c \leq 2, 1 \leq k \leq E\} \cup \{H_i, C_i, H'_i, C'_i, H''_{i,c+2}, 5 \leq i \leq N, 1 \leq c \leq 2\} \cup \{B, M, S, B'_{c+2}, BE_{c+2,k}, ME_k, SE_k, BE'_{c+2,k}, ME'_k, SE'_k, BM, 1 \leq c \leq 2, 1 \leq k \leq E\} \cup \{co_i, cop_i, 1 \leq i \leq 2\} \cup \{d_i, d'_i, D_i, a_i, a'_i, e_i, 1 \leq i \leq N\} \cup \{FO_k, F_k, b, 1 \leq k \leq E\} \cup \{R, R_i, 0 \leq i \leq N\}.$$

Objects $X_{i,j}, XA_{i,j}, XS_{i,j}, Z_{i,j}, ZS_{i,j}, Z'_{i,j}, Za'_{i,j}, Zm'_{i,j}, Z''_{i,j}, W_{i,j}, ZE_{i,j,c+2,k}, ZEA_{i,j,c+2,k}, ZEm_{i,j,c+2,k}, ZE'_{i,j,c+2,k}, ZEA'_{i,j,c+2,k}, ZEm'_{i,j,c+2,k}, W'_{i,j,c+2,k}, X'_{i,j,c+2}$ are objects associated with animals during the execution of the model and are related to the processes running. Index i is associated with the species, index j is associated with

the age ($g_{i,5}$ is the average life expectancy), c is the simulated period and k the environment.

Objects

$H_i, C_i, H'_i, C'_i, H''_{i,c+2}, B, M, S, B'_{c+2}, BE_{c+2,k}, ME_k, SE_k, BE'_{c+2,k}, ME'_k, SE'_k$ represent the biomass, the objects that include letters H or B are associated with bone biomass and C, M or S with meat biomass.

$F0_k$ and F_k are used to generate external contributions (i.e., supplementary feeding). D_i is an object used to count the existing animals of species i . If a species overcomes the maximum density values, it will be regulated. Objects d_i, a_i and e_i allow us to control the maximum number of animals per species in the ecosystem (i.e., carrying capacity). When a regulation takes place, object a_i allows us to eliminate the number of animals of species i that exceeds the maximum density. b is an object used to change the charge of the membrane. The objects co_i and cop_i indicate the period in which the model is working. At the end, object R and R_i are a counter that allow the synchronization of the P system.

Some objects go the environment as they leave the skin membrane (labelled with 0); all objects that appear in different configurations of the environment are the environment alphabet and in the case of the proposed model is:

$$\Sigma = \left\{ ZE_{i,j,c+2,k}, ZEa_{i,j,c+2,k}, ZEm_{i,j,c+2,k}, ZE'_{i,j,c+2,k}, ZEa'_{i,j,c+2,k}, ZEm'_{i,j,c+2,k}, W'_{i,j,c+2,k}, X'_{i,j,c+2}, 1 \leq i \leq N, 0 \leq j \leq g_{i,5}, 1 \leq c \leq 2, 1 \leq k \leq E \right\} \cup \left\{ BE_{c+2k}, ME_k, SE_k, BE'_{c+2k}, ME'_k, SE'_k, BM_{3,k}, 1 \leq c \leq 2, 1 \leq k \leq E \right\} \cup \left\{ d_i, d'_i, a_i, e_i, 1 \leq i \leq N \right\}$$

The model has been structured in six modules (Figure 5) and is formed by 188 types of evolution rules that run within the membranes and 21 rules that are executed in the environment; all of these rules can be run in the 20 steps of the model, many of them applied in parallel. The following describes the 20 configurations involving a loop (Figure S2).

To summarize the description of the model composed of 209 rules, we only will describe the rules that correspond to the main processes.

The first rule that applies is

$$co_k []_k^0 \longrightarrow [co_k]_k^+, 1 \leq k \leq 2$$

that changes the polarization of membrane 1 (configuration 1) and activates the start of the model run.

After this step, the objects associated with animals X_{ij} and XS_{ij} enter the membrane labelled 1 with charge +; in the membrane skin we maintain copies of the objects associated with the populations of domestic animals controlled by man.

In step 3, the rules of reproduction are applied in parallel. A breeding female may or may not reproduce and if reproduction is successful new individuals are generated. The rules that allow the execution of this process are of the type:

$$\left[X_{i,j} \xrightarrow{1-\varphi(i,j)} Z_{i,j} \right]_1^0, \left\{ \begin{array}{l} g_{i,3} \leq j < g_{i,4}, \\ 1 \leq i \leq N. \end{array} \right. \quad (\text{males})$$

$$\left[X_{i,j} \xrightarrow{k_{i2} \cdot \varphi(i,j)} Z_{i,j} Z_{i0}^{k_{i3}} \right]_1^0, \left\{ \begin{array}{l} g_{i,3} \leq j < g_{i,4}, \\ 1 \leq i \leq N. \end{array} \right. \quad (\text{breeding females})$$

$$\left[X_{i,j} \xrightarrow{(1-k_{i2}) \cdot \varphi(i,j)} Z_{i,j} \right]_1^0, \left\{ \begin{array}{l} g_{i,3} \leq j < g_{i,4}, \\ 1 \leq i \leq N. \end{array} \right. \quad (\text{non-breeding females})$$

$\varphi(i, j)$ is the percentage of females of species i and age j . All objects of type X_{ij} evolved to object type Z_{ij} indicating that the process of reproduction has been carried out, while the objects associated with females that have reproduced create new objects of type Z_{i0} , the second subscript indicates the age is equal to 0.

In the same step are applied the rules that generates objects associated with annual food fixed contributions. Man makes contributions through the food provided in supplementary feeding sites (C_0 and H_0) and the ecosystem by small animals (S):

$$\left[FO_k \longrightarrow C_0^{\beta_{k,1}} H_0^{\alpha_{k,1}} M^{\beta_{k,1}} B^{\alpha_{k,c}} S^{\lambda_{\Gamma_{k,1}}} F_k \right]_3^+, 1 \leq k \leq E.$$

The subscripts associated with the objects are the contributions (expressed in kg) that are made in each period.

After the application of these rules we obtain the configuration 3. To this configuration the rules of natural mortality have been applied, removing the same objects of type Z_{ij} and ZS_{ij} , and those objects that are not removed enter the inner

membrane (configuration 4). In the case of young animals, the mortality rules are of the type:

$$Z_{i,j} []_3^+ \xrightarrow{1-m_{i,1,1}} [Z_{i,j}]_3^+, \begin{cases} 0 \leq j < g_{i,3}, \\ 1 \leq i \leq 4. \end{cases} \text{ (young animals that survive)}$$

$$Z_{i,j} []_3^+ \xrightarrow{m_{i,1,1}} []_3^+, \begin{cases} 0 \leq j < g_{i,3}, \\ 1 \leq i \leq 4. \end{cases} \text{ (young animals that die)}$$

$m_{i,1,1}$ is the probability that a young animal of the species i will die during summer.

In the following two steps the feeding and control of the density rule are applied. In the first step all the scavengers eat except the griffon vulture ($i = 4$),

$$[Z_{i,j} a_i B^{f_{i,7}} M^{f_{i,8}} \rightarrow W_{i,j}]_3^+, \begin{cases} g_{i,3} \leq j \leq g_{i,5}, \\ 1 \leq i \leq 3. \end{cases}$$

$$[Z_{i,j} a_i B^{f_{i,7}} S^{f_{i,8}} \xrightarrow{g_{i,6}} W_{i,j}]_3^+, \begin{cases} g_{i,3} \leq j \leq g_{i,5}, \\ 1 \leq i \leq 3. \end{cases}$$

$$[Z_{4,j} \rightarrow Z''_{4,j}]_3^+, 0 \leq j \leq g_{i,5}.$$

$g_{i,6}$ is equal to 1 only for Egyptian vultures whose diet is mainly based on remains of small animals, whereas for the other the scavengers it is equal to 0. $f_{i,7}$ and $f_{i,8}$ are respectively the amounts of biomass in kg of bones and meat required for each animal. $f_{i,7}$ is greater than 0 only for bearded vultures, because bones are not part of the diet of the other avian scavengers.

In the previous step the objects associated with the griffon vulture have evolved to $Z''_{4,j}$. In the following step the griffon vulture eats if enough food is available.

$$[Z''_{4,j} a_i B^{f_{i,7}} M^{f_{i,8}} \rightarrow W_{i,j}]_3^+, g_{i,3} \leq j \leq g_{i,5}.$$

If there is an object a_i for an object $Z_{i,j}$ it means that this animal has sufficient physical space; if in addition the number of objects of type B and M that can be accessed are equivalent to the energy needs, the animal has sufficient resources and evolves.

In these rules, it is determined whether there is enough food and space. Objects $Z_{i,j}$ that do not evolve into objects $W_{i,j}$ correspond to animals that did not have enough resources (configuration 6).

The next step is to send to the environment all objects associated with animals that lacked resources and all resources that are left. In a first step these objects move out of the inner membrane labelled with 3, then enter the membrane labelled with 1 (configuration 7).

$$[Z_{i,j}]_3 \rightarrow Z'_{i,j,3}[\#]_3, \begin{cases} 0 \leq j \leq g_{i,5}, \\ 1 \leq i \leq 3. \end{cases}$$

It could be the case that there was insufficient space for some wild ungulates and therefore these animals died leaving food resources; the next step is to verify whether there are resources for avian scavengers who have not eaten (configuration 8). Subsequently, objects move to the skin membrane (configuration 9),

$$[Z'_{i,j,3}]_1 \rightarrow Z'_{i,j,3}[\#]_1, \begin{cases} 0 \leq j \leq g_{i,5}, \\ 1 \leq i \leq 3 \end{cases}$$

and finally these objects move to the environment (configuration 10).

$$[Z'_{i,j,3}]_0 \rightarrow Z'_{i,j,3}[\#]_0, \begin{cases} 0 \leq j \leq g_{i,5}, \\ 1 \leq i \leq 4. \end{cases}$$

Once in the environment, they must be moved to the environment e_{11} , not associated with geographical area (configuration 11).

$$(Z'_{i,j,3})_{ei} \rightarrow (Z'_{i,j,3})_{e11}, \begin{cases} 0 \leq j \leq g_{i,5}, \\ 1 \leq i \leq 4. \end{cases}$$

The following step is to enter membrane 0 (configurations 12) and then membrane 1 (configuration and 13), and to then check whether there are objects associated with resources available to the animals that had not evolved (configuration 14). The rules that apply are the type

$$\left[ZE_{i,j,3,k} aE_{i,s} BE_{3,v}^{f_{i,7}} ME_v^{f_{i,8}} \right]_1 \xrightarrow{p_{TM_{i,kv}} p_{TM_{i,ks}}} W'_{i,j,3,s} []_1, \begin{cases} g_{i,3} \leq j \leq g_{i,5}, \\ 1 \leq k \leq E, \\ 1 \leq s \leq E, \\ 1 \leq v \leq E, \\ 1 \leq i \leq 4. \end{cases}$$

Associated with the rules, there is the probability that an animal from the environment k can access resources from s and v environments. In the rule shown, the animal finds food in the environment v and the accessible geographic space in the environment s ($aE_{i,s}$). Thus this animal leaves their original k environment to breed and lives in the environment s .

In the following configurations, objects move from the virtual environment, e_{11} , to the physical environment where the animal lives (4 steps, configurations 15-18) and

restores their initial configuration (configuration 19). These 20 configurations encompass the entire summer season in the ecosystem. Another 20 configurations similar to the previous configurations are repeated with different parameters to simulate the passage of the winter period. Hence, one year involves 40 configurations and two consecutive executions of the loop shown (Figure S2).

Supplementary Table S1. Maximum carrying capacity considered in each subset of the study area. Avian scavengers are expressed as pairs (n) whereas the rest of the species are individuals (n).

	VA	AR	PJ	PS	AU	C	R	B	S	N
<i>Gypaetus barbatus</i>	7	10	14	14	14	3	5	5	5	6
<i>Neophron percnopterus</i>	1	11	22	7	15	2	5	9	10	14
<i>Aegypius monachus</i>	0	10	20	3	10	0	0	3	3	10
<i>Gyps fulvus</i>	15	180	360	100	300	20	60	60	70	210
<i>Rupicapra pyrenaica</i>	2000	2000	600	4000	650	850	4000	2000	650	50
<i>Cervuselaphus</i>	2750	70	1250	800	1000	200	250	1000	70	20
<i>Dama dama</i>	0	30	50	950	40	0	0	0	30	0
<i>Capreolus capreolus</i>	1700	250	1000	2000	850	850	650	1300	250	150
<i>Ovis orientalis</i>	0	0	0	600	100	50	500	0	50	0
<i>Sus scrofa</i>	4500	2500	5500	8750	7500	7500	10000	12500	22500	4250

Supplementary Table S2. Values of the parameters used in the model (for more details see Supplementary Table S3 and references 19 and 24).

	$g_{i,1}$	$g_{i,2}$	$g_{i,3}$	$g_{i,4}$	$g_{i,5}$	$g_{i,6}$	$k_{i,1}$	$k_{i,2}$	$k_{i,3}$	$m_{i,1,1}$	$m_{i,1,2}$	$m_{i,2,1}$	$m_{i,2,2}$	$ht_{i,1}$	$ht_{i,2}$	hp_i	$f_{i,1}$	$f_{i,2}$	$f_{i,3}$	$f_{i,4}$	$f_{i,5}$	$f_{i,6}$	$f_{i,7}$	$f_{i,8}$	$f_{i,9}$	$f_{i,10}$
<i>Gypaetus barbatus</i>	1	1	8	20	21	1	0.7	0.5	1	0.02	0.04	0.03	0.01	0	0	0	0	0	0	0	1	1	70	24	160	54
<i>Neophron percnopterus</i>	1	1	5	24	25	1	0.75	0.57	1	0.02	0.04	0.02	0.05	0	0	0	0	0	0	0	1	1	0	40	0	20
<i>Aegypius monachus</i>	1	1	5	24	25	1	0.7	0.55	1	0.02	0.04	0.02	0.05	0	0	0	0	0	0	0	1	1	0	132	0	272
<i>Gyps fulvus</i>	1	1	5	24	25	0	0.7	0.75	1	0.02	0.04	0.02	0.05	0	0	0	0	0	0	0	1	1	0	132	0	272
<i>Rupicapra pyrenaica</i>	1	1	2	18	18	0	0.55	0.75	1	0.2	0.4	0.02	0.04	0.3	0	0	3	4	6	24	0.5	0.5	0	0	0	0
<i>Cervus elaphus</i>	1	1	2	20	20	0	0.5	0.75	1	0.11	0.23	0.02	0.04	0.3	0	1	12	15	24	96	0.6	0.6	0	0	0	0
<i>Dama dama</i>	1	1	2	12	12	0	0.75	0.55	1	0.17	0.33	0.02	0.04	0	0	0	1	14	2	37	0.25	0.25	0	0	0	0
<i>Capreolus capreolus</i>	1	1	1	10	10	0	0.67	1	1	0.19	0.39	0.02	0.04	0	0	0	1	4	1	19	0.25	0.25	0	0	0	0
<i>Ovis orientalis</i>	1	1	2	12	12	0	0.5	0.9	2	0.2	0.4	0.02	0.04	0	0	0	3	4	6	22	0.6	0.6	0	0	0	0
<i>Sus scrofa</i>	1	1	1	4	6	0	0.5	0.55	4	0.05	0.09	0.03	0.07	0.32	0.32	0	4	6	12	60	0.25	0.25	0	0	0	0
<i>Ovis aries*</i>	0	1	2	8	8	0	0.96	0.75	1	0.05	0.1	0.01	0.02	0	0	0	3	4	7	38	0.35	0.35	0	0	0	0
<i>Bos taurus</i>	0	2	2	9	9	0	0.9	0.9	1	0.02	0.04	0.02	0.03	0	0	0	10	60	6	518	0.025	0.3	0	0	0	0
<i>Equus caballus</i>	0	3	3	9	20	0	0.97	0.9	1	0.01	0.02	0	0.01	0	0	0	10	60	9	891	0.025	0.4	0	0	0	0

*Including individuals from *Capra hircus* populations

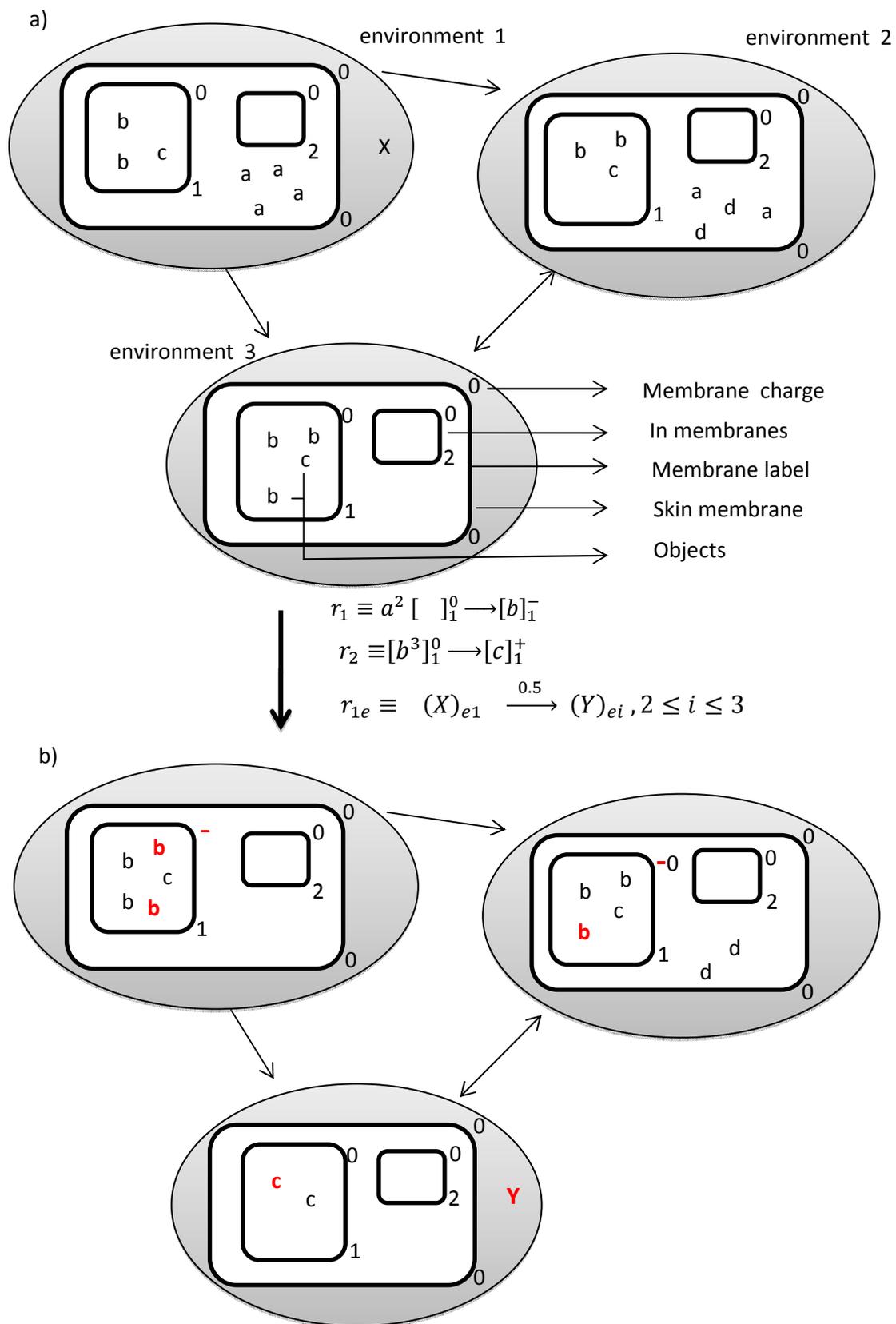
Supplementary Table S3. Description of the parameters used in the model.

Input	<p>q_{kij}: Number of animals of species i and age j in the environment k.</p> <p>N: Number of years to simulate.</p> <p>N_R: Number of repetitions per year.</p>
Parameters	<p>$g_{i,1}$: 1 for wild species and 0 for domestic species.</p> <p>$g_{i,2}$: Age at which adult size is reached. This is the age at which the animal of species i consumes an adult diet with the same energetic requirements, and at which time, if the animal dies, the amount of biomass it leaves is similar to the total left by an adult.</p> <p>$g_{i,3}$: Age at which fertility begins in species i.</p> <p>$g_{i,4}$: Age at which fertility ends in species i.</p> <p>$g_{i,5}$: Average life expectancy of species i in the ecosystem.</p> <p>$g_{i,6}$: 1 when an important proportion of the diet of species i can be based on other small species (i.e. Carnivora, Leporidae) and 0 for the remainder.</p> <hr/> <p>$k_{i,1}$: In the case of ungulates, percentage of females of the species i present in the population. For scavengers, percentage of pairs of the species i that can breed. For both scavengers and ungulates the sex-ratio at birth is considered as 1:1.</p> <p>$k_{i,2}$: Fertility ratio, proportion of fertile females that reproduce in the case of ungulates and proportion of pairs with successful breeding in the case of scavengers.</p> <p>$k_{i,3}$: Number of descendants of fertile females of species i that reproduce.</p> <hr/> <p>$m_{i,1,c}$: Natural mortality ratio in first years of species i and period c, age < $g_{i,2}$ (per one).</p> <p>$m_{i,2,c}$: Mortality ratio in adult animals of species i and period c, age < $g_{i,2}$ (per one).</p> <p>$ht_{i,1}$: Percentage of males of the species i hunted.</p> <p>$ht_{i,2}$: Percentage of females of the species i hunted.</p> <p>hp_i: 1 when after hunting the body of the animal of species i remains in the ecosystem and otherwise 0.</p>

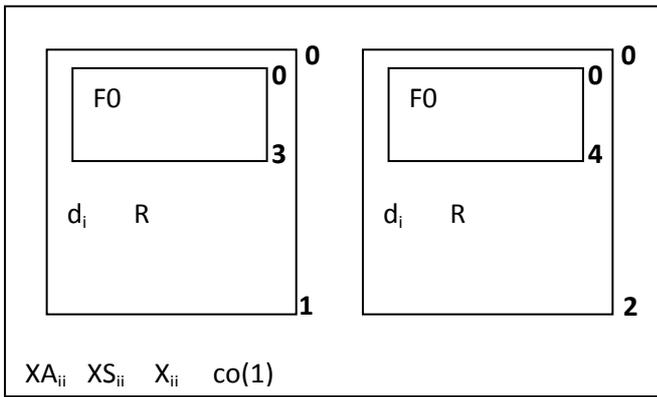
	<p> $f_{i,1}$: Amount of bones (kg) provided by young animals of species i available, age $< g_{i,2}$. $f_{i,2}$: Amount of meat (kg) provided by young animals of species i available, age $< g_{i,2}$. $f_{i,3}$: Amount of bones (kg) provided by adult animals of species i available, age $\geq g_{i,2}$. $f_{i,4}$: Amount of meat (kg) provided by adult animals of species i available, age $\geq g_{i,2}$. $f_{i,5}$: Percentage of useful bones left by species i. $f_{i,6}$: Percentage of useful meat left by species i. $f_{i,7}$: Amount of bones (kg) necessary per year and pair of the species i according to the energetic requirements of the scavenger species in the summer period. $f_{i,8}$: Amount of meat (kg) necessary per year and pair of the species i according to the energetic requirements of the scavenger species in the summer period. $f_{i,9}$: Amount of bones (kg) necessary per year and pair of the species i according to the energetic requirements of the scavenger species in the winter period. $f_{i,10}$: Amount of meat (kg) necessary per year and pair of the species i according to the energetic requirements of the scavenger species in the winter period. $\beta_{k,c}$: Amount of bones delivered to supplementary feeding sites of the environment k during the period c ($c = 1$ summer; $c = 2$ winter). $\alpha_{k,c}$: Amount of meat delivered to the feeding stations of the environment k during the period c. $\lambda_{k,c}$: Amount of meat provided by small animals delivered to the supplementary feeding sites of the environment k in the period c. $ff_{k,c,z}$: Percentage of food available for the avian scavengers in the peripheral zone z. The amount of food (kg) available is quantified with respect to the environment k in the period c. </p>
	<p> TM_i: Classification of the movements that can be made by the species i according to their foraging abilities. $P_{TM_i,k,v}$: Probability that species i will move from environment k to environment v when there is a lack of resources for the type of movement TM_i. $d_{i,k,1}$: Maximum density of species i in the environment k. </p>
Output	<p> \bar{N}_v, σ_{Ni}: Average and deviation of number of animals of species i for the year simulated. $\bar{B}_v, \sigma_{Bi}, \bar{M}_v, \sigma_{Mi}$: Average and deviation of amount of biomass, bones and meat, left for species and year simulated. </p>

Supplementary Figure S1. Representation of the structure of the *Population Dynamic P System* model, which is formed by membranes, regions, and objects. a) Initial configuration of the model formed by five membranes all with a neutral charge. The type and amount of objects can vary between environments. In this example, a possible communication between environments exists. Concretely the environment 1 can communicate with the environment 2 and 3, and the environment 2 and 3 with each other. The rules r_1 and r_2 will be applied in parallel when possible. The rule r_1 is applied if membrane 1 has a neutral charge and in the region below membrane 0 there are two objects a . The rule r_2 will be applied if there are three objects b in membrane 3 with a neutral charge. In the case of the figure the rule r_1 is applied two times in environment 1 and one time in environment 2. The second rule is only applied one time in environment 3. r_e is an environment rule, as it satisfies the conditions that were applied randomly sending an object Y to environment 2 or 3 (environment 3 in Figure 3). The rules are applied in a maximal way and we obtain configuration b).

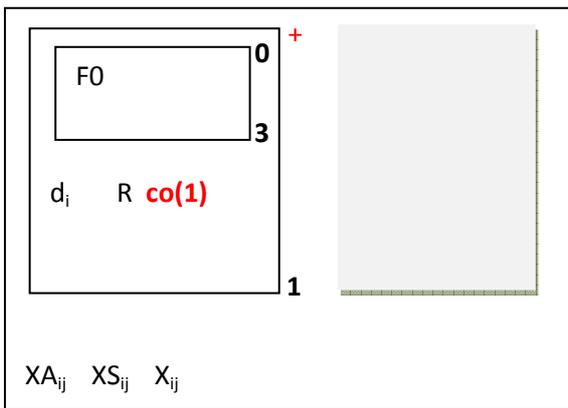
Figure S1.



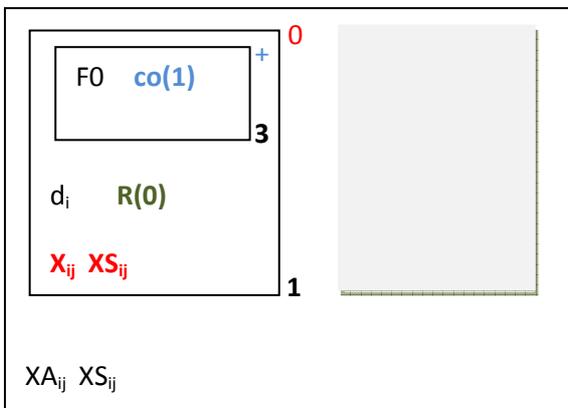
Supplementary Figure S2. PDP model proposed for the study of the dynamics of the avian scavengers is formed by six modules with 20 steps. The pass from one configuration to another is carried out by applying all possible evolution rules at each step.



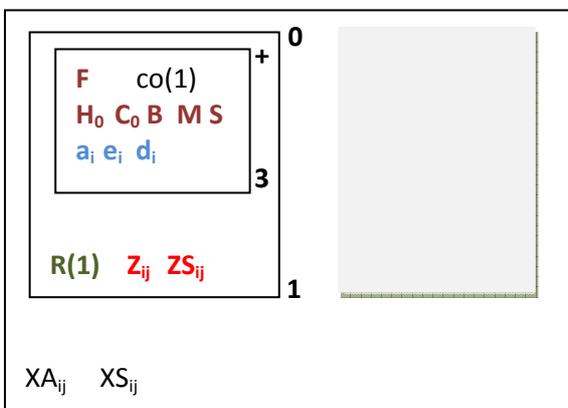
Configuration 0. X objects are associated with wild animals. XA objects with domestic animals living throughout the year in the ecosystem and the domestic XS nomads. The other objects were used to generate external inputs of food, control of animal densities and to synchronize the model. In membrane 1 and 3, summer processes are performed while in membrane 2 and 4 the winter processes are performed.



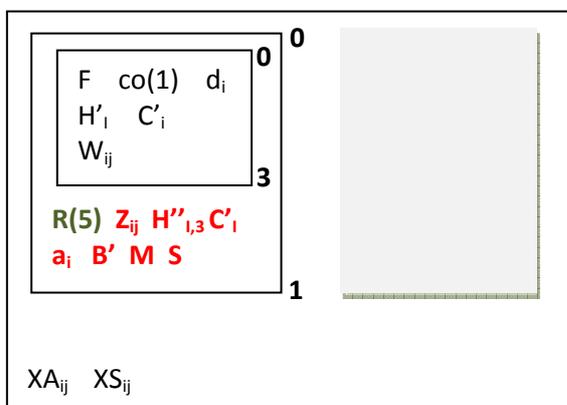
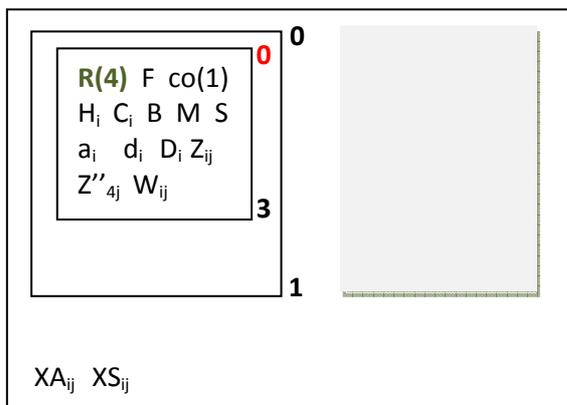
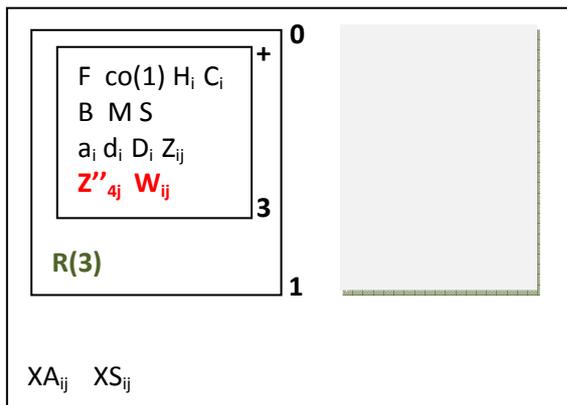
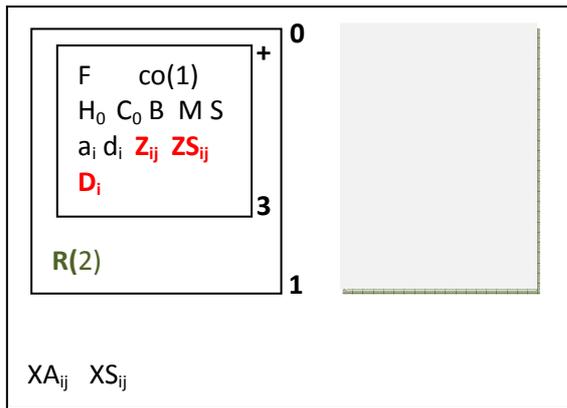
Configuration 1. The object $co(1)$, which is in skin membrane. When entering membrane 1 changes the polarization of the membrane changes to positive. This activates the execution of the processes corresponding to the model summer period.

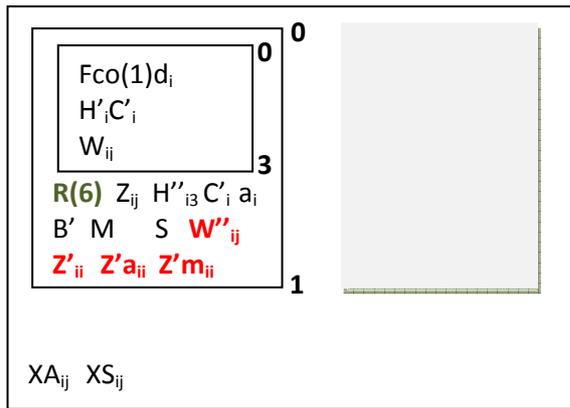


Configuration 2. The object $co(1)$ which is in membrane 1 enters membrane 3 by changing the polarization of the membrane to positive. The objects associated with animals must enter membrane 1 so they can evolve according to the processes running in the summer period. The R counter starts its evolution; this step ensures that the change of membrane charge 1 to neutral would not take place if there were no objects associated with animals

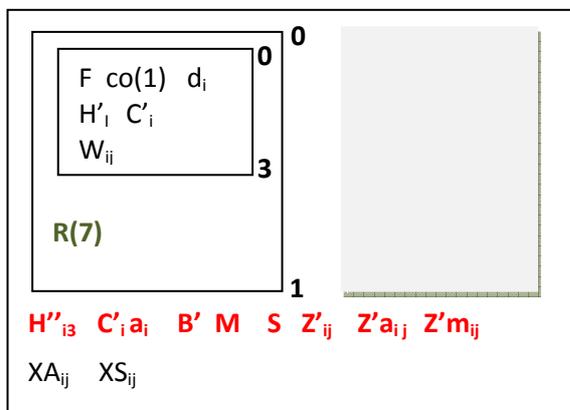


Configuration 3. The object $F0$ evolves as F object generating objects associated with food provided by humans and small animals. In the same step the object d_i enters membrane 3 generating new objects a_i and e_i that will allow control of population density of each species. In parallel runs the reproduction process evolving objects X_{ij} and XS_{ij} to Z_{ij} and ZS_{ij} respectively, generating new objects Z_{i0} and ZS_{i0} , corresponding to animals that are born.

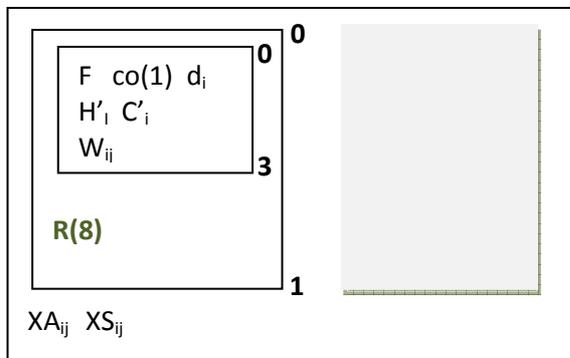




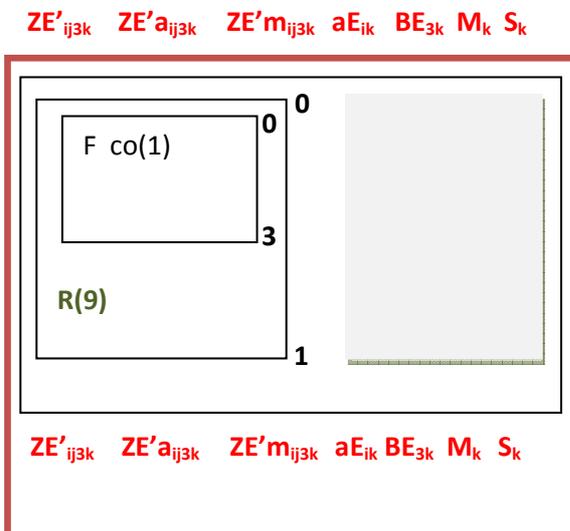
Configuration 8. Before to leave the objects Z_{ij} (membrane 1) it is checked what resource has been lacking. If the resource that is lacking is space Z'_{ij} evolves to $Z'_{m_{ij}}$. In the case of a lack of food it evolves to $Z'_{a_{ij}}$ and if both resources are lacking it evolves to W''_{ij} .



Configuration 9. In this step all objects associated with animals with a lack of resources and surplus resources exit to the membrane skin.

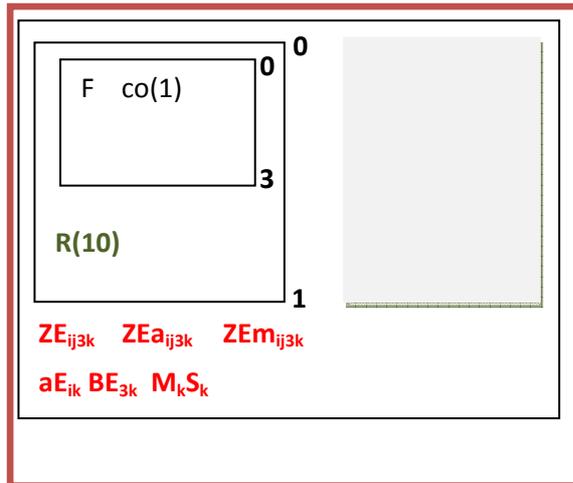


Configuration 10. In this step all objects associated with animals with a lack of resources and the objects associated with surplus resources go out to the environment. This objects keeping the environment from which they come (k) and the period of the year that is simulated (in this case 3 correspond to the summer period)

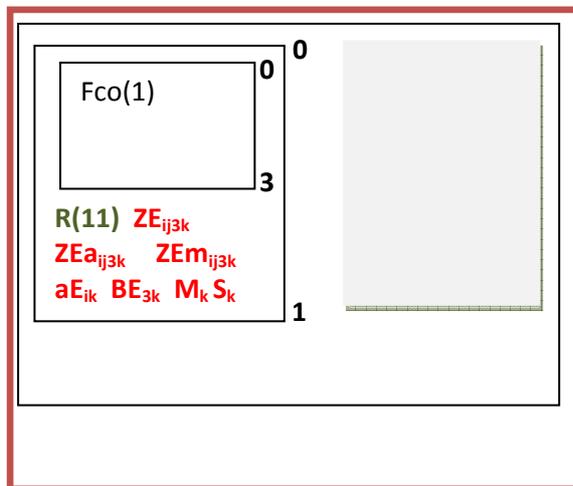


Configuration 11. In this step the objects that were in a physical environment pass to the virtual environment e_{11} . In the environment e_{11} objects associated with animals and food do not exist.

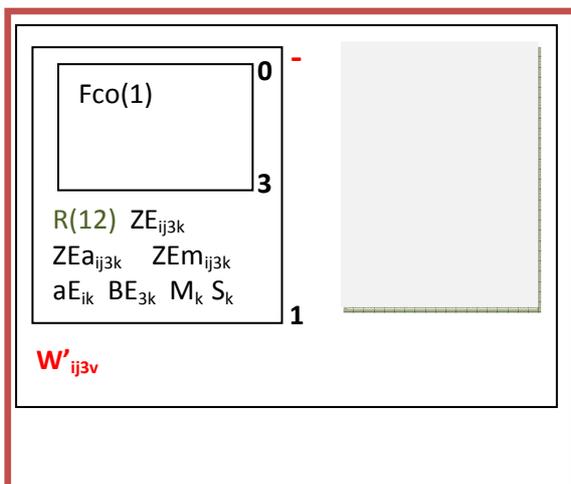
Environment e_{11}



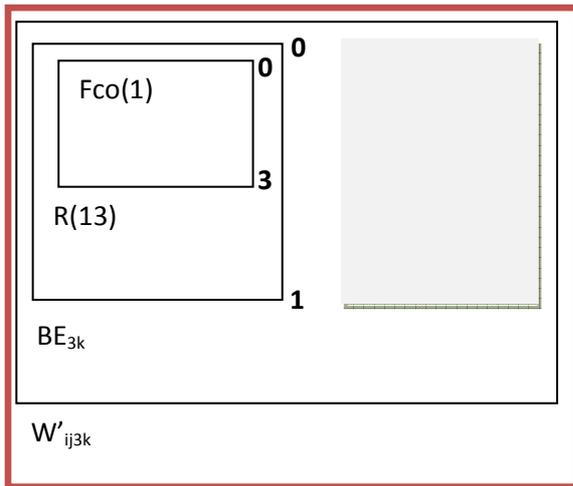
Configuration 12. The objects that are in the environment come into the skin membrane.



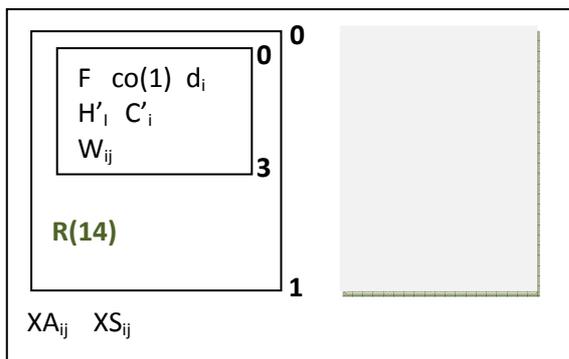
Configuration 13. In this step the objects pass to membrane 1.



Configuration 14. In membrane 3, rules related to the existence of resources are applied. Not all animals have access to all resources, only those who belong to the area in which they can move. In the case that the animals have access to the necessary resources, the associated objects evolve to objects of type W' . In the same step they arrive at the skin membrane. The membrane labeled with 1 changes the polarization indicating that the process has been completed and will be able to dissolve the remaining objects (except parts of the bones).



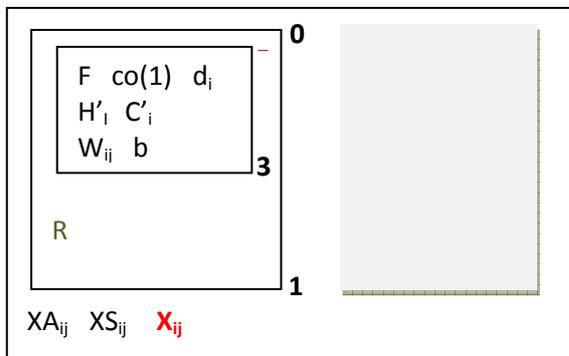
Configuration 15. The objects associated with animals that have enough resources must move to the environment in which they have physical space. The remaining objects, except part of the biomass in the form of bones, are dissolved. Some of the bones are covered by snow in the winter and serve as a food resource for Bearded vultures in the spring.



Configuration 16. In this step are the objects associated with uneaten bones found in e_{11} environment, while those associated with animals are already in the physical environment.

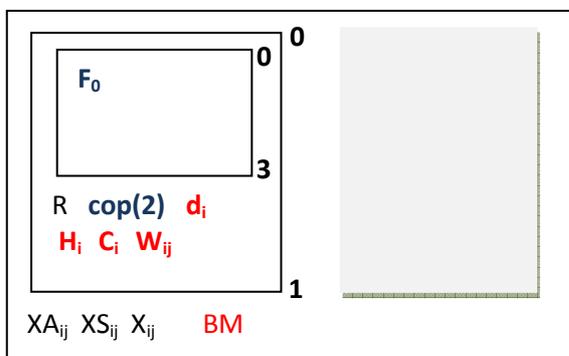
X'_{ij1}

BM_{3k}

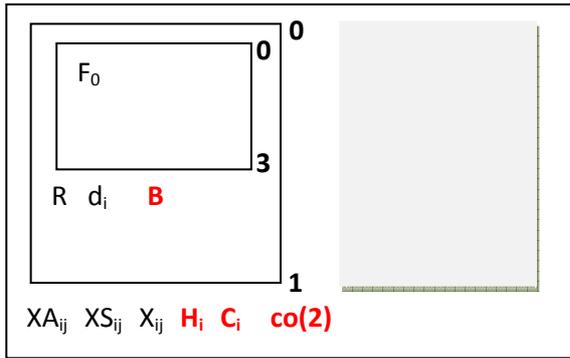


Configuration 17. This step begins the restoration of the initial configuration to start the Winter processes. The object X'_{ij} which is in the environment enters the skin membrane as X_{ij} . BM_{3k} moves to the environment e_k as BM .

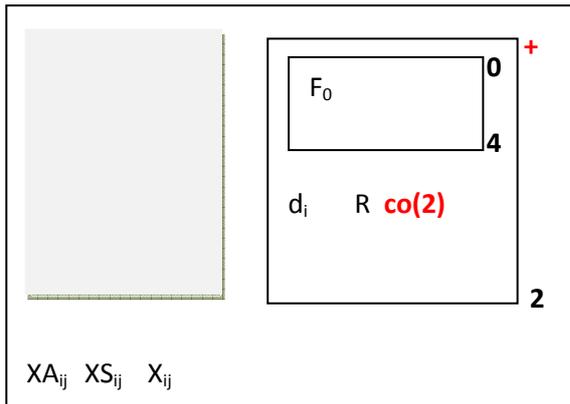
BM



Configuration 18. The object F evolves generating the object $cop(2)$ indicating that the winter period should begin simulation. The objects W_{ij} must evolve to objects X_{ij} and move to the skin membrane. Objects H'_i and C'_i hold information on the amount of biomass that leaves each species in each period, and this information will be read in the membrane skin.



Configuration 19. In this configuration the initial configuration has been restored and therefore the next step in the process is initiated for the winter period.



Configuration 20. Start of the processes for the winter period.