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Modelling carcass disposal practices: implications for the management of an ecological service provided by vultures

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Summary

1. In many European countries, private companies are in charge of livestock carcass disposal. In agro-pastoral systems, however, scavengers such as vultures provide an alternative ecological service for disposing of carcasses.

2. By combining interviews with farmers and ecological data from the Grands Causses region (southern France), we developed an agent-based model to assess the environmental and economic consequences of various farmers' carcass disposal strategies, involving private companies and/or vultures. The model includes 'offering' vulture feeding behaviour, as an ecological service, and farmer choices of carcass disposal system, representing the 'demand' for this service.

3. This ecological service can provide benefits through reducing monetary costs and carbon emissions associated with carcass disposal, but also represent a sanitary risk if vultures fail to remove carrion efficiently. Benefits and risks strongly depend on carcass disposal techniques and the wider strategy.

4. The most sustainable strategy to match the 'demand' and 'offer' for carcass disposal involves the adaptive use by farmers of both the ecological and the industrial services. This strategy enables the optimization of the ecological service benefits while minimizing sanitary risks by using a private company service, when carcass disposal by vultures is uncertain.

5. *Synthesis and applications*. In cases where there is a mismatch between the demand and the offer, negative feedback can occur for both humans and vultures. Preserving vulture populations and enhancing benefits from the sustainable service, they provide might henceforth be explicitly accounted for in legislation and carcass management guidance, in accordance with vulture food requirements. The agent-based modelling approach described here offers a tool that can guide management strategies and policies and support coordination among stakeholders.

Key-words: agent-based modelling, carcass disposal, conservation, ecological service, feeding station, *Gyps fulvus*, socio-ecological system, vulture

Introduction

The Millennium Ecosystem Assessment was the first worldwide interdisciplinary research programme aiming to define an integrative framework of the relationships between ecosystem processes and human needs and well-being (MEA 2005). Including ecosystem services in conservation assessment would improve the societal relevance of biodiversity conservation and should then better support their translation into effective conservation actions (Egoh *et al.* 2007). In this context, the role of the scientific community is to deliver the knowledge and tools necessary to assess the return of services on investments in nature (Daily & Matson 2008; Daily *et al.* 2009). Although the need to protect ecological processes is clearly illustrated by the ecosystem service framework, turning the conclusions from the MEA into conservation actions remains challenging (Kremen *et al.* 2008). Beyond the need for scientific research on ecological processes, interdisciplinary studies are required because the success or failure of conservation efforts mostly relies on societal choices.

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'Scavengers provide one of the most important yet underappreciated and little-studied ecosystem services of any avian group' (Şekercioğlu 2006). Vultures are specialized in scavenging (Ruxton & Houston 2004), and they have been identified as providers of ecosystem services (Şekercioğlu, Daily & Ehrlich 2004; Şekercioğlu 2006; Markandya *et al.* 2008). Recycling carcasses from livestock and wildlife, scavengers maintain energy flows higher in food webs (DeVault, Rhodes & Shivik 2003; Wilson & Wolkovich 2011). Vultures lead other scavengers to dead animals (Houston 1979) and limit the spread of diseases and of undesirable mammalian scavengers (Prakash *et al.* 2003). However, several vulture species are threatened world-wide and their populations are decreasing (Şekercioğlu 2006; IUCN 2010). Although vultures provide multiple services through carcass disposal, human practices have reduced the quantity and the safety of their trophic resources. Reduction in livestock mortality through veterinary progress, changes in agro-pastoral practices (Thiollay 2006; Olea & Mateo-Tomás 2009) or legislation dealing with organic waste and imposing their systematic destruction (Tella 2001; Camiña 2004) all reduce the quantity of food available for vultures. Moreover, livestock sanitary treatments (Oaks *et al.* 2004; Blanco *et al.* 2009) or pesticides (Virani *et al.* 2011) can result in vulture poisoning.

Supplementary feeding through the artificial provisioning of sites has been identified as a useful tool for scavenger conservation (Friedman & Mundy 1984; Oro *et al.* 2008), and it can be considered relevant especially for urgent and middle-term management (Azmanis 2009). However, in farming areas, feeding stations directly managed by farmers, called light feeding stations, seem to be more relevant for long-term vulture conservation (Dupont *et al.* 2011). In France, the first experimental trials of light feeding stations agreed by sanitary authorities have been conducted in the Grands Causses region. Thanks to the success of this experimental design, French law has institutionalized light feeding stations in 1998. Although European directive 142/2011/CE authorized the creation of light feeding stations in 2011, not all countries enforced this regulation. Since the 'mad cow' crisis caused by bovine spongiform encephalopathy in cattle, carcass disposal has been undertaken by private companies in many European countries. However, using vultures represents an alternative, sustainable ecological service. The viability of vulture populations, sanitary considerations and air quality as well as monetary costs are all influenced by carcass disposal management and farmer choices. With regard to the ecological service, carcasses made available for vultures can be considered as the demand for this ecological service, and the ability of vultures to eliminate carcasses as the offer of the service. The correspondence between the offer and the demand will affect the consequences of carcass disposal management. From an interdisciplinary framework based on an example of this socio-ecological system in the Grands Causses region (southern France), we aimed to (i) identify the decision criteria that lead farmers to use either the ecological service or the industrial service through interviews and (ii) assess the consequences of various carcass disposal strategies resulting from farmer decision criteria through agent-based modelling.

Materials and methods

SCAVENGING SYSTEM

Our study is based on the oldest and the most documented initiative involving light feeding stations in France, in the Grands Causses region, Massif Central, Southern France (448120 N, 38150 E). This site was the first place in France where the griffon vulture *Gyps fulvus* was reintroduced, with 61 vultures released from 1981 to 1986 by the Ligue pour la Protection des Oiseaux (LPO) and the Parc National des Cévennes (PNC) (Sarrazin *et al.* 1994; Terrasse *et al.* 1994, 2004). In 2010, the number of breeding pairs of this population was estimated to be above 720 (R. Néouze, personal communication). In the Grands Causses, food is provided to vultures through natural livestock mortality. Two systems of carcass disposal involve vultures: indirectly through collections by managers (LPO and PNC) and directly through the light feeding stations. From the start of the reintroduction, LPO and PNC agents have collected carcasses from farms and placed them on three main artificial feeding stations. Light feeding stations have been investigated as an alternative food supply by offering food in conditions that could help to maintain the natural feeding behaviour of vultures. In 2010, 61 farmers had legal permission from sanitary authorities to use their own light feeding stations, but many more feeding stations are used illegally (Bobbé 2006). Carcass disposal on light feeding stations is hereafter called 'vulture-mediated service'.

INTERVIEWS

In order to determine which decision criteria are involved in carcass disposal practices in the Grands Causses region, we conducted 40 semi-structured interviews with farmers located within a 50-km radius from the core nesting sites. Open-ended questions were specifically asked about: their past and current carcass disposal practices, their relationships with various stakeholders (i.e. LPO, PNC, sanitary authorities, private companies) and their perceptions of vultures. Each interview was recorded and lasted approximately two hours.

MODEL

Our goal was to assess the environmental and economic consequences of various carcass disposal strategies identified during the interviews with famers. The collections by managers were excluded from the carcass disposal options, because in reality it does not represent a sustainable system on the long term. This allowed us to assess whether farmers' preference for a given carcass disposal system can influence the sustainability and the efficiency of the ecological service when collections by managers no longer take place.

We used the CORMAS simulation platform (Bousquet *et al.* 1998), an agent-based modelling framework providing the opportunity to create spatially explicit models of socio-ecological systems (Bousquet & Le Page 2004).

Model framework

We previously developed a spatially explicit agent-based model, taking the Grands Causses as an example, to study the efficiency of carcass disposal by vultures under diverse livestock farming strategies and scenarios of carcass disposal involving the managers (Dupont *et al.* 2011). In the present study, we retained the spatial and temporal structure of this model, the farming system (including farmers, their livestock and livestock mortality process), as well as daily feeding behaviour and population dynamics of vultures. Livestock mortality is characterized by an annual rate and a seasonal distribution, which were here both calibrated from data from the Grands Causses region (S. Morio, unpublished data). The vulture population is structured in age classes to integrate intraspecific competition for food between juveniles and older individuals (Bosè & Sarrazin 2007). Vultures forage according to a central place (Xirouchakis & Andreou 2009) and optimal foraging behaviour (Pyke, Pulliam & Charnov 1977) until they satisfy their food requirements or until the depletion of the food resource. Vulture survival and productivity depends on consumed resources. For further details and an exhaustive description of the model following the standard ODD protocol, see Dupont *et al.* 2011.

We integrated the private company as a new agent and modify the carcass disposal practices of farmers according to the identified carcass disposal strategies (see section scenarios of carcass disposal strategies). As a result, the agents considered in the present model are farmers, their livestock, a vulture population and a private company. The model proceeds by daily steps. Each day, livestock mortality is computed iteratively according to the number of animals at a given farm by generating probabilistic individual mortality events. When a mortality event occurs in the herd, a farmer can either call the private company or put the carcass(es) on his own feeding station depending on the scenario. Then, vultures feed and/or the private company collects the carcass within two working days following a farmer's call. We model the carcass disposal by the private company either the same day with a probability of 0·5 or the following working day with a probability of 1. Roads are not represented and trucks that collect carrion move straight from one farm to the closest farm. As the private company collects carcasses over a larger area than the area represented by the grid, the entrance of the truck is randomly located on a boundary cell.

Outputs

Efficiency output. The efficiency of carcass disposal corresponds to the ratio between the number of removed carcasses and the number of carcasses to remove, at the annual scale. For the vulture-mediated service, a carcass is considered removed if it has been eaten within 5 days from being deposited at the feeding station.

Sanitary output. A sanitary output is also considered, reflecting the increase in sanitary risk proportionally to the duration a carcass remains in the environment. This output is measured as the average delay of carcass disposal (in days) either for vultures or for the private company.

Carbon emissions output. Carbon emissions (in tons/year) arising from carcass collection by the private company are calculated according to the distance covered by the truck weighted by a coefficient related to gross vehicle weight rating. Trucks used by private companies weigh between 11 and 17 tons (H. Fumery, personal communication), corresponding to a gross vehicle weight coefficient of 0·2409 kg equivalent carbon per km (ADEME 2005). The amount of emitted carbon is divided by the annual number of eliminated carcasses to calculate an eco-efficiency index of carcass disposal strategies (in kg equivalent carbon per eliminated carcass).

Monetary costs output. The monetary costs of carcass collection are calculated according to the mean market prices of the service provided by the companies in France, that is, 343·53 Euros per ton of carrion (E. Demange, personal communication).

The monetary costs and carbon emissions resulting from the transport of a carcass to a light feeding station have not been assessed. Indeed, the light feeding station is usually located very close to the farm, so we assumed that monetary costs and carbon emissions were negligible.

SCENARIOS DESIGN

Interviews: the choice of a carcass disposal system

The most important criteria that can explain carcass disposal practices are the certainty of carcass disposal (i.e. efficiency), the delay of carcass disposal (i.e. rapidity) and the cleanliness of the system. The appraisal of the cleanliness of the various carcass disposal systems depends on perceptions of individual farmers.

According to national sanitary laws, private companies or managers are forced to remove livestock carcasses when asked by farmers; therefore, these two carcass disposal systems are always efficient from the farmers' point of view. According to the farmers we interviewed, the vulture-mediated service is globally more fickle than the other two systems. Nevertheless, this system is always described as efficient in the vicinity of the core vulture population, and farmers are quite confident that vultures will remove a carcass once it is placed on a light feeding station. In addition, the vulture-mediated service is perceived as faster (reduced delay of removal) than carcass disposal systems involving human collectors (i.e. private companies or managers). Moreover, the light feeding station system can be appreciated because it allows farmer to be autonomous and it does not involve any intrusion of strangers onto the farm. These advantages can be sufficient to initiate the use of a light feeding station by a farmer, even if there are no other incentives to feed vultures. When the efficiency of the vulture-mediated service is perceived as uncertain, environmental concerns and the willingness to feed vultures can create a strong preference to use a light feeding station instead of being sure of carcass disposal. The interest in the cleanliness of the carcass disposal system strongly depends on a farmer's perceptions of nature, of livestock death and of vultures (Bobbé 2006; Sarrazin *et al.* 2006). For some farmers, light feeding stations are clean because it is perceived as the most natural, ecological and spontaneous system, while removal by private companies or managers can be associated with the potential contamination of livestock by the foreign elements brought in with the removal truck. Conversely, for other farmers, removal by human agents is cleanest because they consider vultures as dirty animals. Indeed, skin and bones remain after consumption of carcasses by vultures, which can be associated with death or dirtiness, and cleaning these wastes through burning can represent a burden for farmers.

Hence, the criteria used for choosing a system of carcass disposal are not exclusive and depend on farmer perceptions and motivations. Moreover, some farmers can use two different systems. For instance, a farmer who usually calls a private company can put carcasses on his feeding station because the next collection will not occur until a few days after the mortality event. Some farmers who prefer using their own feeding station may call a private company during winter because they do not observe vultures flying at that time.

Scenarios of carcass disposal strategies

The scenarios tested various stylized carcass disposal strategies inspired from realistic, traditional practices identified during the farmers' interviews. The strategies (Table 1) were based on two kinds of decision criteria used by farmers: the perception of vultures by the farmer (four strategies, see below) and the quality of the carcass disposal (three strategies, see below).

First, we considered four strategies based on the perception of vultures by the farmer, following a gradient in the use of vulture-mediated service. The *Feeding station* strategy reflects a strong preference to feed vultures or use the related ecological service. The *Compromise* strategy reflects a preference for using the ecological service while its efficiency is also an important criterion. Thus, when carcasses remain uneaten on the light feeding station, farmers switch to the industrial service only for the next livestock mortality. The *Pragmatic* strategy is based on the use of the ecological service during the private company's days off only, the industrial service being used during working days. The *Company* strategy is an exclusive use of the industrial service, farmers being motivated only by the fear of epizooties and the confidence in technology, without any concern about vulture conservation or even an aversion of avian scavengers.

Secondly, three other strategies related to the quality of the service (its efficiency and its rapidity) were considered. This enabled us to assess which of the ecological and the industrial services is preferentially selected and if both services can persist simultaneously. For the *Certain* strategy, the most important criterion is the immediate efficiency of carcass disposal. The ecological service is systematically used by all farmers as long as vultures succeed in removing carcasses. As soon as vultures fail to remove a carcass, farmers switch to using the private company. The *Fast* strategies focus on minimizing the delay in carcass disposal, assuming that farmers know which service provider is the faster. Although this assumption is not realistic, empirical and repeated observations of the use of their feeding station can help farmers to estimate the approximate delay to removal of carcasses by vultures. Since we consider a daily time step, the two service providers could both remove carcasses on a given day. We thus studied two cases of *Fast* strategies: the *FastI* strategy in which the industrial service is preferred and the *FastES* strategy in which the ecological service is preferred. These strategies represent an ideal use of the carcass disposal systems, and the results obtained by these strategies cannot be directly compared to other management strategies.

Table 1. Carcass disposal strategies

Name	Strategies based on individual preference for carcass disposal
Feeding station	Always use the vulture-mediated service.
Compromise	Use the vulture-mediated service. If a carcass remains, call the private company the next time then switch back to the vulture-mediated service
Pragmatic	Call the private company unless it is their day off, in which case use vulture-mediated service
Company	Always call the private company
Certain	Use the vulture-mediated service. If a carcass remained, switch to always calling the private company
FastI	Choose the system that removes carcasses as soon as possible, with a preference for the private company's service
FastES	Choose the system that removes the carcasses as soon as possible, with a preference for the vulture-mediated service

The model is not predictive but allows us to explore the consequences of various strategies. We assumed that preferences are homogeneous in the farmer population: simulations were performed with 500 farmers using the same strategy. The name of a scenario corresponds to the carcass disposal strategy employed by the farmers. To compare the consequences of the different strategies, the results of each scenario were compared within a given reference state, namely the carrying capacity or dynamic equilibrium of the vulture population. Outputs were then recorded as soon as the population reached the carrying capacity. Outputs are from 50 replications of each simulation at a time horizon of 30 years.

Results

VULTURE POPULATION CARRYING CAPACITY

The highest carrying capacities (mean ± standard deviation) for the vulture population were 562 (±56) and 561 (±51) individuals for the *Feeding station* and *Compromise* scenarios, respectively, and 156 (±18) individuals for the *Pragmatic* scenario (Fig. 1). The population did not persist with either the *Company* scenario or the *Certain* scenario. Finally, for both *FastI* and *FastES* scenarios, the carrying capacities were intermediate, with 309 (±25) and 435 (±43) individuals, respectively.

EFFICIENCY OF CARCASS DISPOSAL

The lowest efficiency occurred for the *Feeding station* scenario: 86·15% efficiency with 740 (±99) carcasses remaining per year. Intermediate efficiencies of carcass disposal were obtained for the *Compromise* scenario (91·19% efficiency and 470 (±52) carcasses remaining per year) and the *Pragmatic* scenario (92·64% efficiency and 393 (±45) carcasses remaining per year) (Fig. 2). The average number of carcasses remaining per vulture was 1·31 under the *Feeding station* scenario, 0·83 under the *Compromise* scenario and 2·48 under the *Pragmatic* scenario.

The efficiency of carcass disposal was total for the *Company* scenario, as well as for the *Certain* scenario. As for the *FastI* and *FastES* scenarios, because the farmers know which service providers will eliminate the carcasses, there were no carcasses remaining. Thus, there is a 100% efficiency as well as persistence of the vulture population.

DELAY BEFORE CARCASS DISPOSAL

Despite the fact that *FastI* and *FastES* optimized delays (respectively, 1·4 ± 0·4 and 1·3 ± 0·7 days), the delays were very similar to those from the other strategies (from 1·6 ± 0·7 days for *Compromise* scenario to 1·8 ± 0·8 days for *Certain* scenario) (Fig. 2).

CARBON EMISSIONS

The *Feeding station* scenario produced no carbon emission at all, while the lowest annual emissions occurred for the *Compromise* scenario (8·42 ± 0·66 tons per year) (Fig. 2). Carbon

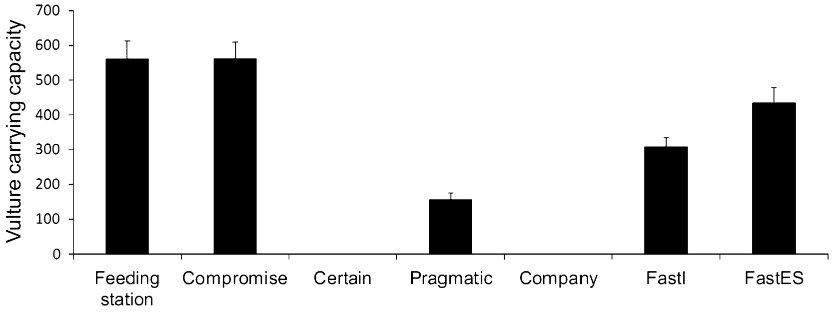

Fig. 1. Vulture population carrying capacity according to the various scenarios.

emissions from the *Pragmatic* scenario reached 28·45 (±1·36) tons per year. For the *Company* and *Certain* scenarios, emissions were 33·11 (±1·18) and 32·89 (±1·43) tons per year, respectively, almost four times higher than the *Compromise* scenario.

The lowest amount of carbon emitted per carcass per year was 0·16 kg from the *Compromise* scenario. For the other scenarios, emissions were between 0·54 (*Pragmatic* scenario) and 0·63 kg of CO_2 (*Company* scenario).

In the *FastI* and *FastES* scenarios, 27·10 (±1·15) and 19·85 (±1·04) tons of carbon, respectively, were emitted per year, as well as 0·51 and 0·37 kg of carbon per eliminated carcass.

COSTS OF CARCASS COLLECTION

As defined in the model, there were no costs for the *Feeding station* scenario. The lowest costs were for the *Compromise* scenario at €10 678 (±1 171) per year, while the costs for the *Pragmatic* scenario reached €94 296 (±8 589). The highest costs were for the *Company* and *Certain* scenarios, almost twelve times higher than the costs of the *Compromise* scenario, increasing to €131 465 (±10 364) and €127 587 (±10 940), respectively (Fig. 2).

In the *FastES* scenario, the collection costs were €43 913 (±4445) per year, and about twice that amount in the *FastI* scenario (€81 508 ± 6564 per year). These optimal strategies thus lead to intermediate costs compared to the other strategies.

Discussion

RESPONSES OF THE ECOLOGICAL SERVICE TO THE CARCASS DISPOSAL STRATEGIES

The *Pragmatic* strategy uses the vulture-mediated service opportunistically, when livestock mortality occurs on days that the Company is unavailable. This strategy leads to higher carbon emissions and collection costs, as well as more carcasses remaining per vulture when compared to the *Compromise* scenario. Basically, the number of carcasses that can be consumed by the scavengers depends on their food requirements, which is linked to the realized carrying capacity of the vulture population. In the *Pragmatic* scenario, carcass disposal practices limit the size of the vulture population, vulture food requirements stay low and the ecosystem service remains of poor efficiency. The *Pragmatic* scenario corresponds to an 'under exploitation' of vulture-mediated service that does not enhance the benefits provided by vultures neither does it reduce sanitary risk.

Nevertheless, the impact of carcass disposal practices on the vulture carrying capacity is limited: although the *Compromise* and *Feeding station* scenarios entail two different carcass disposal strategies, they yield similar vulture carrying capacities. In addition, when all farmers use the *Feeding station* scenario, the number of carcasses remaining is higher, suggesting a low efficiency of the ecosystem service. In the Grands Causses, the temporal mismatch between seasonal livestock mortality and the food requirements of the vulture population actually reduces its ability to respond to the demand for carcass removal through all year (Dupont *et al.* 2011). In Spain, empirical study showed that before the Bovine Spongiform Encephalopathy crisis, some feeding stations were not used by vultures from November to April, resulting in many unconsumed carcasses (Camiña 2006). The efficiency of this ecosystem service is compromised by a lack of understanding of vulture population dynamics. The *Compromise* strategy allows the benefits provided by the vultures' ecosystem service to be optimized while reducing sanitary risks. This strategy is indeed based on effective carcass disposal: farmers put carcasses on a feeding station only if previous carcasses have been successfully removed by vultures. So, farmers' practices strongly depend on vulture population food requirements.

The comparisons between these three scenarios illustrate that beyond a simple numerical relationship with the number of feeding stations, the way they are utilized can greatly affect the benefits provided by vultures and the sanitary consequences. The *Compromise* strategy maximizes the match between the 'demand' (i.e. carcass disposal through vulture-mediated service) and the 'offer' (i.e. the vulture food requirements) of the ecological service.

Interestingly, if minimizing time to removal is used as a criterion to select the carcass disposal system by all farmers, the vulture population always persists even if farmers have a preference towards the Company's service (*FastI*). Mechanistically, the more vulture feeding stations are used by farmers, the greater the size of the vulture population and the lower the time to disposal over a wider area. This strengthens the case that vultures can offer a very efficient alternative for carcass disposal irrespective of whether farmers are interested in feeding

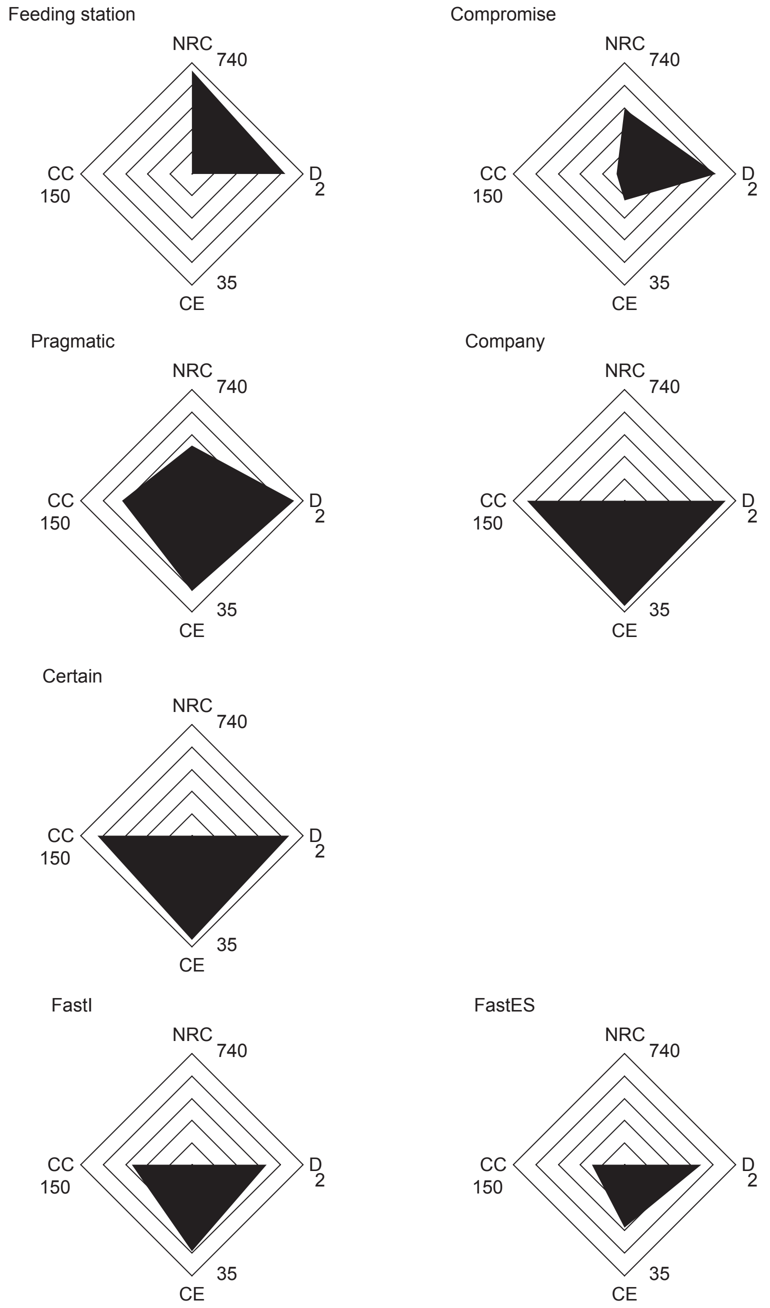

Fig. 2. Consequences of carcass disposal according to the various scenarios. The centre of each square is the origin for the four axes. All variables are means of the measure over a year. NRC, number of remaining carcasses; D, delay before carcass disposal (in days); CC, cost of collecting by the company (in Euros); CE, carbon emissions (in tons).

them. In the Grands Causses region, the time for carcasses to be detected by vultures has been estimated to be around 30 min (Gault 2006; Deygout *et al.* 2009); this is frequently cited by farmers as a decisive criterion for choosing the vulture-mediated service rather than the industrial service.

If all farmers adopted the criterion of certain carcass disposal (*Certain* strategy), the vulture population would go extinct. The seasonality in livestock mortality means that fewer farmers use the vulture-mediated service in winter (Dupont *et al.* 2011), the amount of food available for vultures declines, their numbers thereby reducing the carrying capacity for the rest of the year. As a consequence, the vulture population size is lower the next winter, more farmers stop using their feeding station because there are fewer vultures to dispose of the carcasses, and so on until feeding stations are no longer provisioned at all and the vulture population goes extinct.

These scenarios illustrate that decision criteria based on the rapidity and efficiency of carcass disposal can have effects on the dynamics of the whole system. Reducing the time taken for carcass disposal may be the most appropriate criterion, favouring the ecological service as well as decreasing sanitary risk and farmers' inconvenience.

LONG-TERM BENEFITS OF THE ECOLOGICAL SERVICE PROVIDED BY VULTURES

Reconciliation ecology is based on socially inclusive conservation strategies (Rosenzweig 2003). The relationship between farmers and vultures depends on reciprocal benefits (Sarrazin *et al.* 2006). However, preserving a win–win situation is not straightforward partly due to mismatches between the 'offer' and the 'demand' for ecological service provided by scavengers. First, the 'demand' for carcass disposal could be higher than the 'offer' by vultures. When there is an overexpectation of the efficiency of the ecological service, sanitary risks can increase and farmers may stop considering vultures to be an efficient carcass disposal system until, finally, they stop provisioning feeding stations and the vulture population goes extinct.

Secondly, the 'offer' could be higher than the 'demand'. For instance, European regulations concerning bovine spongiform encephalopathy surveillance in Spain forced farmers to use a private company for carcass disposal rather than traditional feeding stations (muladares), impacting scavenger populations such as griffon vultures (Tella 2001; Camiña 2004). The sudden lack of food led to a change in vulture feeding behaviour patterns (e.g. direct attacks on livestock), an increase in admissions of juvenile vultures to rescue centres, lower productivity (Azmanis 2009), and a decrease in the number of breeding pairs (A. Camiña, personal communication). In addition, the lack of food possibly induced human–wildlife or human–human conflicts (i.e. between vultures and farmers as well as between farmers and conservationists when vultures became aggressive towards livestock).

It is therefore important to avoid a mismatch between the offer and demand related to the ecological service provided by scavengers. The management of carcass disposal should involve all the different stakeholders (i.e. farmers, wildlife managers, sanitary authorities, industrial companies or governmental institutions) and should explicitly consider the ability of vultures to remove carcasses. Policy-makers should be encouraged to integrate the ecological service provided by vultures when drafting legislation that affects scavengers in order to prevent dramatic ecological and environmental consequences. The economic and environmental benefits of conserving vultures so that they can perform a carcass disposal service may represent a convincing argument.

Comparisons of the consequences of different management or legislation options through agent-based modelling are powerful and interesting way to identify optimal management strategies and to foster coordination and cooperation among stakeholders. Working meetings involving all the different stakeholders to discuss the economic, environmental and ecological outputs of different modelling scenarios would allow the consequences of alternative actions to be demonstrated to help optimize carcass disposal. This has been done in this study via meetings involving governmental and non-governmental institutions, farmers and local councillors. This first step could be improved to support the collective decision-making process. For instance, the two approaches 'companion modelling' (Barreteau *et al.* 2003; Collectif ComMod 2005) and 'agent-based participatory simulations' (Guyot & Honiden 2006) directly involve stakeholders in the design of the agent-based model and simulation. Such participatory approaches allow stakeholders to test their management scenario and facilitate their appropriation of the simulation results.

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