Impact of food predictability on social facilitation by foraging scavengers

Chloé Deygout,a,b Agnès Gault,c Olivier Duriez,c François Sarrazin, and Carmen Bessa-Gomesa,b
aUnité Mixte de Recherche 7625 Ecologie et évolution, Université Pierre et Marie Curie, Centre National de la Recherche Scientifique, École Normale Supérieure, 7 quai Saint Bernard, Bâtiment A, 7ème étage, Case 237, 75005 Paris, France, bAgroParisTech, Institut National de Recherche Agronomique, Unité Sous Contrat 2031 Ecologie des populations et communautés, 16 rue Claude Bernard, 75005 Paris, France, and cUnité Mixte de Recherche 7204 Conservation des Espèces, Restauration et Suivi des Populations, Université Pierre et Marie Curie, Muséum National d’Histoire Naturelle, Centre National de la Recherche Scientifique, 61 rue Buffon, 75005 Paris, France

Foraging individuals may use either personal information derived from their own previous experience or social information obtained vicariously. When resources are unpredictable, personal information may be of little use, as illustrated by Gyps vultures that historically rely on unpredictable carrion and social foraging strategies. But human activities may increase resource predictability, for example, the implementation of feeding stations makes food patches more spatially predictable for scavengers. We explored the impact that different levels of resource predictability might have on the use of personal or social information in foraging strategies. We developed an individual-based spatially explicit model of foraging Gyps vultures in the presence of feeding stations to explore different search strategies as well as different management scenarios. Changes in food predictability may affect social foragers, and their adaptation to new conditions is likely to depend on their ability to use different types of information. In our work, when resources were predictable, individuals using previously acquired personal information (“Trapliners”) were more successful than those relying on social information (“Networkers”). The situation was reversed when there were few predictable resources. Local enhancement, a social cue from feeding conspecifics that was available to all strategies, did not benefit Trapliners who were more aggregated than Networkers and suffered more strongly from competition on the food resources. In large populations, even when some resources were predictable, Trapliners were not more successful than other strategies. Key words: feeding stations, Gyps, individual-based model, social information. [Behav Ecol 21:1131–1139 (2010)]

Foraging behavior largely depends on the nature of the exploited resources, as characterized by their location, size, and quality. This behavior includes both the acquisition of resources and the acquisition of information on these resources (Clark and Mangel 1984). The importance of information in shaping foraging strategies is today well established, and it is generally acknowledged that individuals may acquire information from different sources. In particular, it may be personal information, derived from one’s previous experience, or it may be social information, acquired from interacting with conspecifics (Danchin et al. 2004; Dall et al. 2005).

Using social information is beneficial in that it may reduce the cost of individual searching, particularly when resources are unpredictable (Rafacz and Templeton 2003). If resources become predictable in time and space, for example, because of human activities, selective pressures on foraging behavior may change. Social foraging may thus become less beneficial because individuals adapted to these predictable sites may no longer need to interact with conspecifics to gain information on resource location and instead chose to visit these sites regularly based on their personal knowledge.

Such changes in foraging behavior are likely to be observed in vulture species, such as griffons (Gyps sp.). They are obligate scavengers, and the costs and benefits associated with carrion use have affected the evolution of their foraging behavior (Wilbur and Jackson 1983). They are specialized in the consumption of large mammal carcasses, which are rare and unpredictable at the landscape scale but also divisible between many individuals. The attraction of searching individuals to feeding conspecifics, a phenomenon called local enhancement (Buckley 1996), increases the search efficiency of vultures. It reduces the time necessary to find resources although not necessarily entailing an important cost in terms of competition for resources (Beauchamp 1998).

Because the patchy and unpredictable nature of the resources exploited by vultures is central aspects to understand the evolution of their foraging ecology (Ruxton and Houston 2004), any modification to the distribution of resources either in space or in time is likely to affect their foraging behavior. The reduction in range and abundance of many wild mammals has seriously constrained carrion availability for vultures. Moreover, in most developed countries, intensive husbandry practices and sanitary measures have limited the access to livestock carrion. To restore vulture populations, the establishment of feeding stations has often been promoted (Houston 2006; Oro et al. 2008).

We present theoretical work aimed at investigating the potential effects of resource predictability on the foraging behavior of scavengers using either personal or social information. An individual-based modeling approach was used to explore how foraging efficiency can be affected by changes in resource predictability. This approach has proved valuable in the past to model foraging behavior (e.g., Dumont and Hill 2001; Goss-Custard and Stillman 2008) and animal movements (e.g., Ahearn et al. 2001; Duriez et al. 2009). Two main questions...
were explored using this theoretical model, namely 1) whether making resources predictable (through feeding stations) can affect the ability of individuals to find resources and favor those that use personal information on resource location and 2) to what extent these predictable resources affect the use of social information.

In order to compare the use of different kinds of information, we investigated 3 hypothetical search strategies. Local enhancement is used by all strategies as social information concerning resource detection (e.g., Houston 1974; Buckley 1996), but the importance of this information largely depends on the search strategy. In the case of a random search strategy, local enhancement has an important impact on the foraging success, and this success largely depends on the existence of a sufficiently large number of conspecifics from whom information can be acquired (Jackson et al. 2008). Indeed, local enhancement is only effective for such a strategy when density is high enough so that, by chance alone, individuals may have a successful conspecific within their detection range. This strategy does not consider the existence of previous personal information and was used in our study as a control strategy that nevertheless has been observed in wild animals, for example, caribou during the winter months (Bergman et al. 2000). Second, we also studied the case where vultures could use previously acquired personal information concerning resource location, so that they might repeatedly visit the various feeding stations, a strategy similar to that of “traplining” hummingbirds that have regular foraging routes linking resource patches (Temeles et al. 2006). Finally, we considered the case where foraging vultures were able to form groups with other individuals, maintaining visual contact in order to maximize the acquisition of social information on conspecific success (Buckley 1996). This strategy is built upon the hypothesis that social information may be so important for foraging success that it constrains individuals in their movements in order to ensure that they will be in a position to benefit from the foraging success of others. Their own success may nevertheless be negatively affected by this strategy if it results in higher aggregation on carrion and thus in increased competition.

Our modeling work was based on the situation encountered in the Causses, southern France, which is characterized by extensive sheep rearing and where griffon vultures have been reintroduced in the 1980s (Terrasse et al. 1994). In that area, feeding stations provide a large amount of livestock carrion, but vultures can also find some carcasses in natural areas, for example, from animals that have recently died but have not yet been retrieved by farmers.

**MATERIALS AND METHODS**

We build an individual-based spatially explicit model of the daily foraging process of scavengers. It includes different search strategies, which vary in their sources of information. Individuals can use either personal information such as knowledge of feeding station location or social information on conspecific movements, leading to the formation of search networks that maximize the use of social information. We determine the foraging efficiency of these strategies under various management scenarios, including some alternative management practices that cannot be easily investigated empirically. A preliminary version of this model is described in Deygout et al. (2009). In this new version, we improve the method to consider different sources of information and add resource exploitation features. The model is written in the object-oriented programming language Java and uses the RePast agent-based simulation toolkit (North et al. 2006). The program is available upon request to the corresponding author. A list of the parameters, their notation, and definition is available in Table 1.

The model is based on a grid made of 100 square cells of 2 × 2 km, which can contain a food patch and/or foraging individuals (see Supplementary Material A for details about the grid). Each model run simulates a 10-h foraging day, divided in 200 time steps of 3 min. Feeding stations are cells randomly selected for each simulation, and they do not necessarily contain food. At the start of each simulation, N_r resources are randomly and independently located in the habitat: a proportion p_MB of “managed” resources in feeding stations and the rest in the remaining cells (which correspond to natural areas such as pastures). Once created, these resources will remain in the same cell until they are completely exploited, keeping social information on their location valid for a certain amount of time. Moreover, Gyps vultures roost and breed in colonies, which are located at the center of the home range. Thus, the N_cenl individuals in the model are located in the central cell at the beginning of the simulation. At every time step, we modeled 4 different processes: search, resource detection, food ingestion, and energy expenditure.

**The search and detection processes**

At the start of every time step, each individual may acquire social information on nearby conspecific success. If a conspecific within a certain radius d_k (local enhancement distance, expressed in number of cells) has found a food patch, then the searching individual also detects that patch and ends its “search” process to join its conspecific there, attracted by local enhancement. Otherwise, the search continues, and the individual moves to another cell, choosing its direction according to its search strategy (see below). Once the individual has moved, it checks its new location for resources. If resources are present, the individual stays in this cell and now plays the role of attractor to conspecifics by local enhancement. At the next time step, individuals that have not yet found resources go on searching.

When deciding where to go, individuals are able to use the 2 sources of information (personal and social), defined as 2 vectors of weights for each possible direction:

- w_P: a vector of personal information that takes larger values in the direction of the nearest feeding station. Biologically, we assume that vultures acquired this information previously by repeatedly finding resources at the same place. Thus, in the model, individuals know the position of each feeding station before the start of the simulation;
- w_S: a vector of social information that takes a larger value in a direction already adopted by a nearby conspecific. We emphasize that the focal individual does not move toward its nearby conspecific but that they move in parallel directions. Biologically, we assume that vultures acquired this information by maintaining eye contact with nearby foraging birds. Thus, the only social information taken into account by this vector w_S is conspecific direction. Nevertheless, by doing so, individuals also increase their chance of acquiring social information on resource location.

Moreover, an additional constraint on home range, preventing individuals from venturing too far from the colony, is expressed as a vector of spatial information for each possible direction d_cy. The value of the weight for the direction to the colony in vector d_cy increases, whereas the individual moves away from the colony and remains negligible for all other directions (see Supplementary Material A for details on d_cy). In addition to personal or social information, many environmental factors can influence vulture movements while foraging, for example, landscape configuration or meteorological conditions. A certain degree of stochasticity in individual movements is allowed to account for these unquantified external constraints.
A linear combination of all these vectors, presented in Equation 1, gives the weight $w_k$. The probability of going in direction $k$ is the value of $w_k$ after the vector $w$ has been normalized to a unit vector.

$$w_k = a_0 + a_{PI} \times w_{PI,k} + a_{SI} \times w_{SI,k} + z_{HR,k}$$

(1)

The coefficients of this linear combination are as follows:

- $a_{PI}$, the relative importance of personal information,
- $a_{SI}$, the relative importance of social information, and
- $a_0$, the relative importance of random search (without information) to allow for sampling and environmental stochasticity.

Hence, individuals can integrate the different sources of information, given the constraint of Equation 2 and that each coefficient has a value between 0 and 1.

$$a_0 + a_{PI} + a_{SI} = 1$$

(2)

In any given run, all individuals use the same combination of values for $a_0$, $a_{PI}$ and $a_{SI}$, that is, the same strategy. We defined the following foraging strategies (illustrated in Figure 1):

- the “Random” strategy where every direction has the same probability to be chosen and individuals forage at random (when $a_0 = 1$ and $a_{PI} = a_{SI} = 0$);
- the “Network” strategy where individuals take into account the direction chosen by a nearby conspecific and are thus inclined to form social networks that result in foraging parties (when $a_0 = a_{SI} = 0$ and $a_{PI} = 1$);
- the “Traplining” strategy where individuals know the locations of the feeding stations and are thus inclined to go from one feeding station to another, in a way that recalls traplining (when $a_0 = a_{SI} = 0$ and $a_{PI} = 1$ for strong...
Trapping or when \( a_0 = a_{pt} = 0.5 \) and \( a_{sl} = 0 \) for mild trapping.

**Feeding behavior**

Field observations of feeding events have shown that only a few dozens of vultures gain access to the carrion at a given time (Bosé and Sarrazin 2007). In our model, only a limited number \( N_{init,max} \) of individuals can really access resources at one time because strong competition occurs during feeding events. Additional individuals join a queue and gain access in a random order once a spot is made available by the departure of a sated individual. Instantaneous intake rate \( IR \) for those that do access the resource is defined following Equation 3, according to a theoretical maximum intake rate \( IR_{max} \) and 3 constraint coefficients: positive density dependence at low densities (cooperation for vigilance or carrion opening, e.g., via \( f_e \) Jacobs 1984; Equation 4), competition by interference at higher densities (via \( f_i \) Equation 5), and competition by exploitation (or depletion, via \( f_p \) Equation 6) (see Goss-Custard 1980).

\[
IR = IR_{max} \times f_p \times f_i \times f_e, \quad \text{(3)}
\]

\[
f_p = \frac{N_i^{k_p}}{N_i^{k_p} + m_p} \quad \text{(4)}
\]

\[
f_i = \frac{1}{1 + (N_i/m_i)^{k_i}} \quad \text{(5)}
\]

\[
f_e = \left( \frac{R}{R + m_e} \right)^{k_e} \quad \text{(6)}
\]

Where \( k_p, m_p, k_i, m_i, k_e, m_e \) are parameters in the model (see Table 1 and Supplementary Material B), \( N_i \) is the number of individuals accessing the food, and \( R \) is the remaining amount of resources (in grams) in this cell.

This instantaneous intake rate is determined for all \( N_i \) individuals feeding simultaneously on a given resource, and each of them obtains the same amount of resources. Once an individual is sated, that is, its energy budget \( E \) reaches the maximum value \( E_{max} \), it leaves this cell and moves toward the colony. Also, if its instantaneous intake rate is lower than 1 g or if there is no food left in the cell, then that individual resumes its search for resources.

Aspects related to energy expenditure were purposefully kept simple. Parameters are expressed in grams, as a quantity of resources, considering an energy density of meat of 5.2 kJ g\(^{-1}\) (Ruxton and Houston 2002), in order to keep a common currency between the quantity of resources available and that of resources ingested. With a basal metabolic rate of 24 W (Ruxton and Houston 2002), the basal energy expenditure corresponds to 4.32 kJ per time step of 3 min. We approximately converted this to a basal metabolism \( E_B \) of 1 g of resource per time step. Regarding flight, we considered the movement metabolism \( E_M \) to be related to the basal metabolism by \( E_M = 0.5 E_B \), a relationship similar to that of another large soaring bird for which flight costs have been measured precisely, the wandering albatross, Diomedea exulans (Weimerskirch et al. 2000). No other additional metabolic costs are considered in this model (see DISCUSSION).

**Simulation experiments**

Considerations regarding detection range, cell size or time step length can be found in Deygout et al. (2009) as well as in the Supplementary Material A. The parameter values are based on current knowledge of vulture ecology (Pennycuick 1972; Houston 1974; Mundy et al. 1992; Cannatá 2004; Carrete and Donazar 2005; Gauld 2006; Bosé and Sarrazin 2007; Jackson et al. 2008) and are summarized in Table 1.

The results presented below are based on means of 300 Monte Carlo simulations. We mostly studied the impact of 2 main parameters: the proportion of managed resources (i.e., placed on feeding stations) \( p_{mr} \) for management aspects and population size \( N_{init} \) for social aspects. An individual is defined as “successful” if its energy budget is balanced at the end of the simulation, that is, when its daily energy gain is higher than its expenses. We measured the proportion of successful individuals in the population \( p_{success} \) the proportion of individuals that landed on a resource during the simulation \( p_{Landed} \) (which represents the search efficiency, regardless of exploitation possibilities), the proportion of landings due to local enhancement (as opposed to direct detection) \( p_{LE} \), and the average density of individuals on detected resources \( d_{Landed} \).

In order to understand how the model parameters could affect our results, we made a sensitivity analysis by exploring multiple model parameterizations (sets of parameter values) defined by assigning a random value to each parameter, independently of the others, chosen in an interval around the default value (Table 1). In any given run, all individuals used the same parameter values. We analyzed the results of these simulations by means of random forest analyses (Breiman 2001). This technique is a machine-learning algorithm based on classification and regression tree analyses (De’ath and Fabricius 2000) that combines a large number of trees for prediction. Regression trees consist of a series of binary splits on the explanatory variables that finally lead to a predicted value for the response variable. They are constructed by recursively partitioning the data set into 2 subsets based on the optimal split among all possible splits in all explanatory variables. The optimal split is the one that most reduces the mean squared error. The partitioning is continued until a partition (i.e., node of the tree) consists of only one observation. In the random forest procedure, many of these trees are built, and variation in the collection of trees is controlled by combining the use of a bootstrap sample of the data and the random selection of explanatory variables, which are used to build each tree. This nonparametric procedure is known to accommodate large numbers of explanatory variables and to model complex interactions between them (Cutler et al. 2007). Our goal was to screen parameters and summarize our large data set. Random forests were calculated using \( R \) (version 2.7.1; Ihaka and Gentleman 1996) and the randomForest package (Liaw and Wiener 2002). We constructed 2000 regression trees and used a random subset of 3 quarters of the parameters as explanatory variables at each node. The statistical model obtained could then be validated by applying its output to data not used to build this model. The “importance” of an explanatory variable is determined with a permutation procedure. The values for a given explanatory variable are randomly permuted over the test data set, and the resulting reduction in model accuracy is assessed. The larger is the reduction, the more important is the explanatory variable. We used an importance threshold of a 10% increase of the mean standard error.

**RESULTS**

**Sensitivity analysis**

Sensitivity analysis using random forests indicates that the number of resources \( N_{mr} \) the population size \( N_{init} \), and the
distance of local enhancement $d_{LE}$ were parameters of primary importance (Figure 2). Moreover, the maximum energy level $E_{\text{max}}$ and the basal metabolism $E_B$ also appeared as relatively important parameters to explain the proportion of successful individuals $p_{\text{success}}$. The search strategy also comes out as being a main determinant of foraging success as indicated by the importance of personal information use $a_{PI}$ and that of social information use $a_{SI}$. Regarding resource management, the proportion of managed resources $p_{\text{MR}}$ was relevant, whereas the number of feeding stations $N_S$ was not. Interestingly all feeding parameters, that is, that determine how much an individual could eat during one time step ($k_p$, $m_p$, $k_p$, $k_m$, $m_p$, $E_{\text{max}}$, and $N_{\text{ind,max}}$), were not selected by this method.

**Impact of resource spatial predictability**

For a population living in an area with only a few feeding sites, resource spatial predictability depended mainly on $p_{\text{MR}}$, the proportion of resources allocated to feeding stations of known location. For the Traplining strategy, both the proportion of successful individuals $p_{\text{success}}$ and the proportion of individuals that landed on a resource $p_{\text{landed}}$ increased with the proportion of managed resources (Figure 3). In contrast, for strategies that made no use of personal information, such as the Random and the Network strategies, this parameter had no impact on either $p_{\text{success}}$ or $p_{\text{landed}}$ (Figure 3). When considering the relative success of the 4 strategies examined here, we observed that the Network strategy always performed better than the Random strategy and had a higher proportion of successful individuals than both Traplining strategies when resources predictability was low. Nevertheless, as soon as resource predictability became higher than 20% (meaning there is one chance in 5 to find resources in a feeding station), the proportion of successful individuals for the Traplining strategies increased and could become greater than that of the Network strategy (Figure 3b).

Resource spatial predictability was also studied by varying the number of feeding stations while keeping the amount of resources available constant (Figure 4). Indeed, increasing only the number of feeding stations, which mimicked individual herdiers managing their own feeding station, decreased the probability of a feeding station containing resources from 1 for 5 stations to 0.025 for 200 stations. This reduced predictability did not affect the Random and Network strategies (Figure 4a) whereas, for the Traplining strategy, the proportion of successful individuals decreased. As before, when predictability became too low, the Network strategy outperformed the Traplining one.

**Sensitivity of strategies to facilitation**

If strategies were sensitive to social facilitation, then an increased number of conspecifics would have a positive impact on foraging success. When considering the impact of the number of conspecifics, for small populations ($N_{\text{ind}} < 100$), the proportion of individuals that landed (Figure 5a) as well as the proportion of successful individuals (Figure 6a) both increased with population size for the Random, Network, and mild Traplining strategies. Also for small populations, the success of the strong Traplining strategy was constantly maximum, independently of population size, and thus did not increase (Figure 6a). In spite of this, when looking at the proportion of landings that is due to local enhancement (Figure 5b), the strong Traplining strategy used local enhancement even more intensely than the alternative strategies. Hence, important levels of local enhancement were present for all strategies.

**Sensitivity of strategies to competition**

For large populations ($N_{\text{ind}} > 100$), all strategies were affected by competition and the proportion of successful individuals decreased in consequence, but this effect was most important for the Traplining strategy (Figure 6a). The general trend for Traplining individuals was to independently follow similar paths, which consequently led to a much higher aggregation on resources than the other strategies, even when compared with the Networking strategy (Figure 6b). Thus, the Traplining strategy appeared to be the strategy that would be the most vulnerable to competition, as also shown by the steep decline in success when population size increased (Figure 6a).

Indeed, when looking at the proportion of individuals that landed on resources (showing efficiency to find a resource patch, independently of its exploitation), the strong Traplining strategy seemed to be the most efficient, whatever the proportion of predictable resources (Figure 3a) or the number of individuals (Figure 5a). However, the costs of competition were the highest for this strategy. When considering the proportion of successful individuals (including exploitation and thus competition over resources), more than 20% of resources had to be predictable for the Traplining strategy to be the most efficient strategy (Figure 3b). Increasing the number of

---

**Figure 2**

Sensitivity analysis based on a random forest for the proportion of successful individuals $p_{\text{success}}$. Parameters are grouped by category, and "pop." is short for "population" (see Table 1 for parameter notations). The horizontal dashed line represents the importance threshold at 10% increase in mean standard error.
feeding stations decreased the Traplining individuals’ aggregation on resources (Figure 4b) but not sufficiently to compensate the decrease in search success due to the lower predictability (Figure 4a).

Concerning the Random, Network, and mild Traplining strategies, they were less affected by competition, namely due to their lower levels of aggregation (Figure 6b). Nevertheless, they still experienced a decreased search success at high densities (Figure 5a). This was due to the fact that resource patches were quickly fully exploited at higher population sizes. Hence, individuals that did not find food early on would then experience fewer resources. This phenomenon did not seem to impair their use of local enhancement (Figure 5b). Hence, the time needed to fully exploit carrion at each site is sufficiently long for social cues to remain valid.

**DISCUSSION**

In an environment with spatially predictable resources, the value of personal information is expected to be high when foraging (Hewitson et al. 2005). We have shown that indeed using personal information leads to higher search efficiency even when as little as 20% of the resources are spatially predictable. Nevertheless, in large populations, the benefits of using personal information in terms of search efficiency can be outbalanced by increased aggregation at a few predictable resource sites, resulting in strong competition and in an overall reduction of the foraging efficiency. Individuals using social information also had a reduced foraging efficiency in large populations, but this reduction was much less dramatic than for individuals using personal information. Indeed, in the model, aggregation on resources was lower when using social information compared with personal information. The higher aggregation we observe when individuals use personal information is relatively counterintuitive and in contradiction with the conceptual theory of social foraging (Giraldeau and Caraco 2000). Indeed, using social information usually results in higher aggregation than using personal information, whether when foraging (Skogland 1985; Shrader et al. 2007) or choosing breeding habitat (Doligez et al. 2003). However, in our study, predictable resources were aggregated in a few patches such that individuals using personal information and thus sharing the same knowledge of predictable patch location tended to independently follow similar paths to the same resource patches and therefore aggregated on those. As they follow similar paths, they have access to information on conspecific success and often join them on feeding sites, but this phenomenon contributes little to their foraging
success because they would have landed on the feeding sites even in the absence of conspecifics.

When the number of predictable resource patches (i.e., feeding stations) increased, the aggregation of individuals using personal information on resources decreased. However, if the overall amount of resources remained unchanged, increasing the number of spatially predictable resource patches was coupled with a lower probability of finding resources on these patches, and the gain obtained by reduced competition could not compensate the loss in search efficiency. Hence, a decrease in aggregation was accompanied by a decrease in the chances of being successful for these individuals. Interestingly, an intermediate foraging strategy that used both personal information and random sampling of the environment (the mild Traplining strategy in our study) proved to be much more resilient than a strategy using only personal information. This mixed strategy led to levels of aggregation on resources similar to those of strategies using social information or random sampling of the environment and was less sensitive to variations in resource predictability than the strategy using only personal information. Nevertheless, this mixed strategy often remained less efficient than any “pure” search strategy using only social or only personal information.

Conspecifics could also limit foraging success by their absence. Indeed, so far, we have considered how aggregation and ensuing competition affect foraging success of contrasting search strategies at large population sizes. But when population size is small, strategies based on social information may become ineffective (Jackson et al. 2008). Because all strategies allowed individuals to acquire information through local enhancement, we would expect foraging success to depend on conspecific success and to increase with population size. However the importance of this social cue varied among strategies. Not surprisingly, the success of the Network strategy was the most positively affected by the increasing numbers of conspecifics at small population sizes. For the strong Traplining strategy based on personal information, local enhancement did not contribute to foraging success. Because using personal information was so efficient even when only a small proportion of the resources was predictable, this strategy would always allow a proportion of the population to exploit successfully predictable resource patches, whereas a number of other resources were not exploited (Deygout et al. 2009). In contrast, the constraint on movements imposed by the Network strategy did not affect the ability to fully exploit the available resources (Deygout et al.
2009). Hence, the proportion of the population that could not gain access to the predictable resources because of competition might resort to an alternative foraging strategy, allowing both strategies to coexist. Our work was not focused on evolutionary or plastic processes: we studied an established system where the population as a whole used a given strategy. However, integrating a dominance hierarchy in the model, with different foraging strategies for the different dominance classes, might bring new insights about the consequences of resource availability changes. Field observations showed that adult griffon vultures tend to use feeding stations that are more spatially predictable than younger birds (Gault 2006).

It might be argued that energetic costs, considering only basal and movement metabolic rates, were too simple. Other activities such as feeding or interfering with conspecifics are also energetically costly: metabolic rate can be up to 4 times higher during agonistic interactions in guilis and geese (Kanwisher et al. 1978; Wascher et al. 2008). However, these costs (about 40 g in the model, corresponding to about 4 E3 over a 30-min meal) would still be quite low compared with the maximum daily expenditure considered with basal and movement metabolism only (about 300 g) and the potential reward of gorging on food (about 1000 g).

In conservation planning, attractive feeding stations may play an important role by favoring the use of personal information in the populations at stake. For small populations, using personal information led to better chances of success than using other kinds of information. In the case of vultures, Jackson et al. (2008) illustrated that the use of conspecifics as a source of information made social foraging vulnerable to Allee effects, that is, a positive density dependence at low population densities (Stephens et al. 1999). The more a strategy relies on conspecifics, the more sensitive it should be to an Allee effect. Because the Network strategy enables individuals to stay closer to each other than the Random strategy, the intensity of the Allee effect on individuals using the Network strategy could be lower than predicted by Jackson et al. (2008) who considered a kind of Random strategy. However, the strong reliance of the Network strategy on conspecifics means that this effect would still be present. Hence, if vultures use personal information, implementing feeding stations can help boosting small populations, as demonstrated by their important role in reintroduction programs during the first phases of population establishment (Terrasse et al. 2004).

With large population sizes, feeding station management should be carefully considered in order to balance the potential benefits for conservation with the possible negative impacts on foraging behavior. When scavenger access to resources is limited by sanitary regulations, such as in Europe nowadays (Tella et al. 2004), the Parc National des Cévennes, the UMR 7204, and the UMR 7625.

### SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

### FUNDING

Agence Nationale de la Recherche (ANR-07-BLAN-0201) and the Ministère de l’Écologie, de l’Énergie, du Développement durable et de l’Aménagement du territoire (MEEDDAT, Program DIVA). Fellowship from the Ministère de l’Enseignement supérieur et de la Recherche to C.D.

We would like to thank 2 anonymous reviewers for their comments and suggestions. This study was conducted within a collaborative framework that involved the Ligue pour la Protection des Oiseaux (LPO), the Parc National des Cévennes, the UMR 7204, and the UMR 7625.

### REFERENCES


