



Assessing the risk for an obligate scavenger to be dependent on predictable feeding sources



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ABSTRACT

For scavenging species that evolved to search for ephemeral and unpredictable resources, supplementary feeding may act as an ecological trap. Increasing food predictability may lead to the emergence of foraging routines liable to make individuals too dependent on human-mediated feeding. Using recent methodologies (Fourier, Wavelet and conditional entropy-based analyses), we investigated the degree of routine movement behaviour in a population of Eurasian Griffon vultures (*Gyps fulvus*) that mostly feed on livestock carrion provided at Supplementary Feeding Stations (SFS). Overall, the levels of routine behaviour were low. Only 10% of the SFS included within an individual's home range were periodically visited for some time, with a period ranging from 1 to 6 days. The closer a SFS to the nest and the higher the frequency of food supply, the more likely was a vulture to visit this SFS periodically. Vultures also tended to repeatedly visit some series of SFS more often than expected if they would forage at random, but the levels of routine remained relatively low. Our results suggest that the management of supplementary food through a network of numerous small SFS does not substantially disrupt the natural foraging behaviour of vultures, whereas large, frequently replenished SFS tend to artificially increase their level of routine. We thus recommend managers to preferentially rely on a system of dilution of carcasses across the environment to protect the opportunistic behaviour typical of wild vultures.

1. Introduction

By modifying the availability and attractiveness of resources (e.g. habitat, mate, food), ecological restoration projects and other management practices may lead animals into an evolutionary trap (Schlaepfer et al., 2002), likely to induce population declines (Fletcher et al., 2012). In particular, evolutionary traps can occur when humans modify the distribution or the predictability of food resources, resulting in resources that are more attractive than other despite they entail a reduced fitness (Robertson et al., 2013). A good example is provided by the habit of feeding passerine birds in cities (Robb et al., 2008). However, supplementary feeding is widely used as a conservation tool for many species of birds (Fasciolo et al., 2016; González et al., 2006; Robb et al., 2008) and mammals (López-Bao et al., 2010) whose productivities or individuals' survival is limited by food scarcity or quality (toxicity). Human-mediated feeding has been shown to bring benefits, such as an increase in survival and in the probability of settlement, but also drawbacks, such as the unnatural concentration of individuals likely to increase their vulnerability to risk of predation or spreading

infectious diseases (Anderson and Anthony, 2005; Piper, 2006; Robb et al., 2008; Thompson et al., 2008). The impacts of the artificial modification of the dynamics of food availability on wildlife remain poorly understood.

Carcass provisioning at supplementary feeding stations (SFS) is one of the most widespread but controversial practice in the conservation of avian obligate scavengers (Cortés-Avizanda et al., 2016; Piper, 2014), which are considered the most threatened functional guild among birds (Buechley and Şekercioğlu, 2016). It has been demonstrated that SFS can have negative effects at the individual level (e.g. attraction of individuals in poor body condition in Egyptian vulture *Neophron percnopterus*; García-Heras et al., 2013), at the population level (e.g. decrease in adult survival rate and productivity in bearded vulture *Gypaetus barbatus*; Oro et al., 2008) and at the community level (e.g. higher level of predation on ground-nesting birds near SFS (Cortés-Avizanda et al., 2009)). SFS may promote intra- and inter-specific competition to the detriment of immature individuals (Duriez et al., 2012) and shy species (Cortés-Avizanda et al., 2013). Moreover, the interruption of supplementary feeding could have disastrous

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consequences like massive mortality due to starvation or change in diet if wildlife became dependent on it (Donazar et al., 2009).

Recent studies raised concerns about vultures altering their natural foraging behaviour in response to supplementary feeding, up to becoming dependent on it (Kane et al., 2016; Phipps et al., 2013). While scavengers have supposedly evolved to search for unpredictable resources in natural systems characterized by stochastic variations (Houston, 1974; Ruxton and Houston, 2004), SFS provide food in a spatially and possibly temporally predictable way. In a natural context, vultures are expected to rely mainly on public information provided by the behaviour of other individuals (Buckley, 1997; Harel et al., 2017; Prior and Weatherhead, 1991). However, in the presence of SFS, vultures may be led to rely more on personal, memory-based information to find food. Two theoretical studies (Deygout et al., 2009, 2010) showed that vultures might be more efficient to find carcasses by behaving routinely (visiting SFS in a specific and repeatable order) rather than by interacting with conspecifics to gain information about food location when the density of SFS across the landscape is low and/or the proportion of spatially predictable resources is high. These results lead to re-framing the question of the uncontrolled side effects of SFS on individual behaviour, of great concern from the conservation point of view as they may directly influence demographic parameters such as dispersal, reproduction and survival, and hence the viability of populations (Fielding et al., 2014; García-Heras et al., 2013; Robb et al., 2008). Thus, the level of dependence on SFS may be estimated through the behavioural routines they may induce, but this approach has received little attention from conservation biologists so far.

Routine movement behaviour involves movement repeatability, which can occur at the temporal or spatial levels, as a response to the predictability of resource renewal after a local depletion. Such predictability may be used by individuals for adjusting the timing of movement recursions, which are classically observed in animals performing home range behaviour (Bar-David et al., 2009; Benhamou and Riotte-Lambert, 2012), to the most profitable food patches. At the temporal level, routine behaviour implies that a given site is visited at regular intervals, i.e. periodically, as a response to periodic drivers (Bar-David et al., 2009; Riotte-Lambert et al., 2013). At the spatial level, routine behaviour implies that movement recursions take the form of repeated ordered sequences of visits to several sites (Riotte-Lambert et al., 2017).

The population of Eurasian griffon vultures (*Gyps fulvus*) in the Grands Causses (Southern France) is mostly supported by the management of livestock carcasses through a network of SFS, composed of 3–5 (depending on years) collective SFS (CFS) where food supply is highly predictable in time and space, and c. 100 individual SFS (IFS), managed directly by farmers, where food supply is more irregular in time. This context provides the opportunity for addressing whether routine foraging behaviour may be induced by such a carcass-supply management scheme in a wild scavenger. A previous study, based on a within-home range compositional analysis of habitat selection by GPS-tracked vultures, showed that CFS were preferentially selected compared to IFS in most seasons (Monsarrat et al., 2013). Here we used high resolution GPS tracks to estimate (1) to what extent a given SFS tends to be visited periodically by a given bird, using a method based upon Fourier and wavelet analyses of binary time series (Riotte-Lambert et al., 2013), and (2) the degree of routine movement in the sequences of visits to SFS, using a method based upon the computation of conditional entropy (Riotte-Lambert et al., 2017). We predicted that (1) CFS, where food is predictable both in space and time, should mainly structure the foraging behaviour of vultures; (2) the higher the frequency of food supply, inherent to the type of a SFS (CFS vs IFS), the higher its probability to be periodically visited by a vulture; (3) in accordance with the central-place foraging theory, vultures should prefer nearby feeding sites, hence not visiting the farthest SFS routinely, except if the net energy gain (e.g. at CFS) was higher than at nearest sites; (4) with a few CFS and numerous IFS, the overall carcass-supply

management scheme in the Grands Causses should prevent vultures to be highly routine-prone despite the existence of supplementary feeding.

2. Methods

2.1. Study area and GPS tracking

The study area, the “Grands Causses” region, southern France, is a semi-steppic landscape where sheep husbandry remains preponderant and where > 300 pairs of griffon vultures breed (Appendix A). Through the management of SFS, livestock mortality provides food resources for vultures (details in Monsarrat et al., 2013).

In the current study, we focused on 15 breeding individuals (8 males and 6 females, sexed by genetic analyses, and 1 undetermined), which were tracked using solar-powered UvA-BITS GPS loggers (<http://www.uvabits.nl>; Bouten et al., 2012), attached with a non-abrasive Teflon harness. The data used here are a sub-sample of the GPS tracks used in Monsarrat et al. (2013). We focused on locations recorded with high-resolution (i.e. one GPS fix every minute) for two summer months (July–August 2011) to study the daily movements of vultures and their visits to SFS in detail.

2.2. Visits of vultures to feeding stations

In 2011, carcasses could be legally supplied at two CFS (≈ 3.5 tons of carcasses monthly supplied in summer) and 71 IFS (≈ 4.4 tons of carcasses monthly supplied in summer) (Appendix A). Hence, food availability greatly varied between both types of SFS. In summer, 2.9 ± 1.8 (mean \pm SD) carcasses were provided every 1.0 ± 0.8 days at a CFS, making resources spatially and temporally predictable, whereas at an IFS, 1.0 ± 0.9 carcasses were provided every 29.4 ± 19.1 days, making food predictable in space but not so in time. This constituted a quasi-experimental framework to test our hypothesis that vultures' foraging behaviour should be influenced by the predictability of resources in space and time.

We considered that a vulture visited a SFS when it came within 1 km (in the horizontal plane) of this site, a distance at which a vulture should be able to identify a livestock carcass (based on Fischer, 1969's estimate of visual resolution of 120 cycles per degree). We pooled the SFS whose 1-km radius buffers overlapped. All the birds we tracked behaved as central-place foragers, as they were feeding offspring that remained at nests in the canyons harbouring the main colonies (Appendix A). Canyons furthermore generate good thermal and orographic updrafts that are used preferentially by soaring birds (Treep et al., 2015). We therefore excluded 16 SFS (one CFS and 15 IFS) located within a 1-km buffer along the canyons that harbour the colonies, as vultures were likely to fly back and forth to their nests along these canyons for reasons of aerology, irrespective of the potential presence of food.

2.3. Analyses of periodicity of visits

We looked for a possible periodic use of SFS by vultures (Fig. A.1) using a method involving Fourier and wavelet analyses of binary time series (Riotte-Lambert et al., 2013; Appendix B). For each individual and each SFS visited at least three times, we built up a 62-day binary time series by attributing a ‘1’ if the vulture visited the SFS and ‘0’ otherwise for each day of July and August, and computed its Fourier spectrum (example in Appendix B.1.). Statistically significant periodicities in Fourier spectrums were then detected using permutation tests, irrespective of the duration of the time for which this periodicity was expressed. To consider only periodicities that are biologically significant, series showing a statistically significant (at $p = 0.05$) periodicity on the Fourier spectrum were not considered as really periodic when the periodicity was expressed for less than twice the detected period, as revealed by the wavelet spectrum (example in Appendix

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