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Population ecology

The effect of social facilitation on foraging success in vultures: a modelling study

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The status of many *Gyps* vulture populations are of acute conservation concern as several show marked and rapid decline. Vultures rely heavily on cues from conspecifics to locate carcasses via local enhancement. A simulation model is developed to explore the roles vulture and carcass densities play in this system, where information transfer plays a key role in locating food. We find a sigmoid relationship describing the probability of vultures finding food as a function of vulture density in the habitat. This relationship suggests a threshold density below which the foraging efficiency of the vulture population will drop rapidly towards zero. Management strategies should closely study this foraging system in order to maintain effective foraging densities.

Keywords: local enhancement; Allee effect; food finding; scavenging; scrounging; social facilitation

1. INTRODUCTION

Searching for food is a major preoccupation of many taxa. Local enhancement or social facilitation, where conspecifics provide information about the position of food, is widespread in animals (Krause & Ruxton 2002). It has been particularly studied in birds (Fernández-Juricic & Kacelnik 2004), where it is thought to be one of the selection pressures leading to colonial breeding and communal roosting strategies (Hiraldo *et al.* 1993; Sonerud *et al.* 2001; Wright *et al.* 2003).

The impact of the behaviour of conspecifics on foraging success is difficult to measure in field studies, but lends itself to a modelling approach. Griffon vultures (genus *Gyps*) are highly specialized scavengers that rely on finding carcasses of large ungulates. Although highly dispersed and temporally ephemeral, each food source contains sufficient food for many individuals. When foraging, griffon vultures soar at up to 800 m above ground (Pennycuick 1972) affording them a large field of view over their habitat. Although some fresh carcasses are located directly by searching birds, the majority of individuals find food by following other vultures. A chain reaction of information transfer extends from the carcass as descending birds are followed by other birds, which themselves cannot directly see the carcass, ultimately drawing birds from an extensive area over a short period of time (Houston 1974). The detection distance for a carcass on the ground is considerably less than that of a descending bird for a variety of reasons. A flying bird is often physically larger than the food source (*Gyps* vultures have wingspans up to 2.5 m), which is moving at high speed (the vertebrate eye is particularly sensitive to movement), and there are none of the physical barriers, such as trees and vegetation, which impede detection of objects on the ground.

We use an individual-based spatially explicit simulation model to relate foraging success to the densities of both food sources (carcasses) and searching birds. This question has applied relevance, because within the past 10 years, due to environmental contamination, populations of *Gyps* vultures (most markedly the three Indian species: *Gyps bengalensis, Gyps indicus* and *Gyps tenuirostris*) have crashed from being among the most abundant birds of prey in the world to critically endangered (Oaks *et al.* 2004). Most *Gyps* vulture populations are currently receiving active conservation management, and an understanding of the consequences of reduced vulture numbers on the foraging success of the remaining population may help to determine their future conservation management.

We have taken, whenever possible, parameters from published field studies. But for many variables, such as detection distances, there are little data. Hence, we do not imply that our model predictions are accurate quantitative predictors of actual foraging success, but the implications of the predicted relationship between foraging success and bird and carcass density will apply regardless of the exact values used, and demonstrate the impact of socially derived information to nearby conspecifics on food intake.

2. MODEL DESCRIPTION

Parameters on carcass density were derived from the Serengeti ecosystem in Northern Tanzania, using estimates of carcass density derived in Houston (1979). The Serengeti is one of the few ecosystems where large mammalian biomass has not been severely disrupted by human action. Elsewhere, large carcass biomass is often higher, where domestic stock are kept at higher densities than the ecosystem can support, or lower, where wild ungulate numbers have been depleted by hunting. We investigated a wide range of values of carcass density above and below those estimated for the Serengeti. Flight parameters have been taken from the literature but detection distances are uncertain. Popular literature confers on vultures' visual acuity far greater than our own, although we know of little scientific justification for this. Fischer (1969) trained a captive European griffon vulture (*Gyps fulvus*) in a test chamber and concluded that visual acuity was about twice that of humans. Pennycuick (1972), while following vultures in a sailplane, observed that one bird detects a feeding party of vultures from a distance of 4 km, so we used this value, although it is probably conservative. We took detection distance for carcasses without any vultures to be 300 m, although it is likely to be more than that in short grassland and less in densely vegetated land.

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The habitat is a 50×50 km square with periodic boundary conditions (i.e. a bird flying off one edge reappears on the opposite edge and distances are adjusted accordingly). Each individual simulation lasts for one foraging day, which assumes that vultures actively forage for 3 hours each day (Boshoff *et al.* 1983). At the start of each simulation, M carcasses and N vultures are randomly, and independently, located in the habitat. Vultures are initially given a random direction along which they proceed at a speed of $v=33\ \mathrm{km\ h^{-1}}$ (Pennycuick 1972) and change their direction by 45° every 60 min on average (determined randomly with fixed probability per unit time). The model is updated every 1 s of real time so that each vulture flies 9 m per iteration. The vultures continue this searching flight until they visually locate a carcass, which occurs at 0.3 km for carcasses unoccupied by other vultures and at 4 km for carcasses occupied by other vultures (see above), at which point they change direction and proceed directly towards the carcass at a speed of $v=33\ \mathrm{km\ h^{-1}}$. Vultures are assumed to have 360° vision. They then remain stationary at the carcass for the duration of the simulated foraging day.

We allow vultures to detect other vultures descending towards a carcass at a distance of 4 or 10 km. By these means, a vulture can locate a carcass without initially actually seeing the carcass itself. Furthermore, we allow chains of vultures to form, so that a vulture flying towards a visible carcass may be followed by another vulture that cannot directly see the carcass, which in turn is followed by a more distant vulture. The detector flies directly towards the detected descending bird until such time as it detects the carcass for itself, or detects another bird that is nearer to the carcass (as determined by it having descended for longer and thus to a lower height).

At the end of the foraging day, we record the proportion of vultures that successfully reached a carcass. Each simulation was replicated 200 times and an average proportion of birds locating a carcass was calculated, which (since all our simulated vultures are identical) represents the probability that a vulture will find food in a day. Simulations were run across a range of combinations of carcass and vulture densities (figure 1*a*,*b*).

(a) *Notes on parameter values*

The probability that a solitary foraging vulture in our model finds food is directly related to the area it sweeps in a foraging day. Assuming no overlap of flight path, this is given by a rectangle with two semicircles at each end

$$P_{\mathrm{locate}}=\frac{M((2r\times v\times t)+(\pi\times r^2))}{A},$$

where r is the distance at which an undiscovered carcass is visible; v is the flight speed in $\mathrm{km\ h^{-1}}$; t is the time spent foraging in hours; A is the area of the habitat in $\mathrm{km^2}$; and M is the number of carcasses in the habitat.

Although the situation is complicated and requires simulation for multiple vultures where overlap of flight path and interactions occur, this equation shows that any increase in the numerator parameters will increase the probability of finding carcasses. Furthermore, overlap in flight path will reduce the probability of finding carcasses.

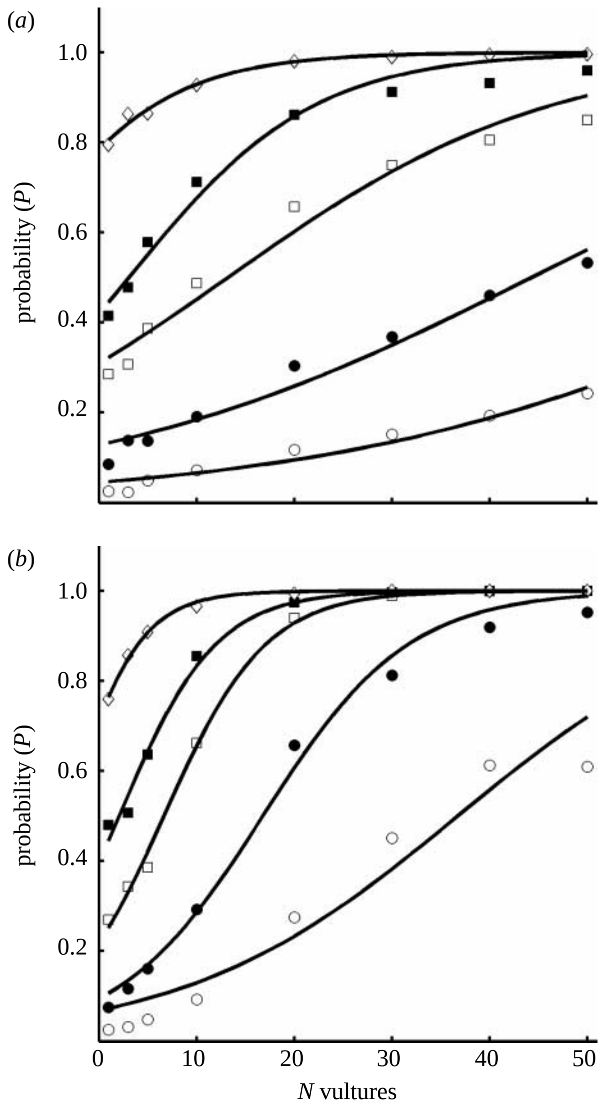

Figure 1. Model predictions for the probability of a vulture reaching a carcass on any given day (3 hours foraging), as a function of vulture and carcass numbers in a fixed area of $2500\ \mathrm{km^2}$. Undiscovered carcasses can be detected at a maximum distance of 300 m, those with vultures already feeding on them at 4 km. Vultures descending towards a discovered carcass can be detected at a range of either (*a*) 4 or (*b*) 10 km. Carcasses: diamonds, 50; filled squares, 20; open squares, 10; filled circles, 3; and open circles, 1.

3. RESULTS

Figure 1 shows the probability that a vulture finds food as a function of foraging vulture population size for a range of carcass densities. The simulations are subject to stochastic events, and the raw data for a given carcass density showed strong nonlinearity, hence a sigmoid function, $P_{\mathrm{find\_food}}=1/(1+\exp(-b_1-b_2\times N))$ was fitted using logistic regression for ease of visual interpretation.

As the number of foragers increases so too does the probability of finding a carcass in a foraging session. This relationship is well described by a sigmoid curve, the horizontal shift and shape of which changes with carcass number. For low carcass numbers, the probability of a single vulture finding food approaches zero. As the number of vultures in the system increases, so the probability of finding food initially increases exponentially for all vultures and then slows as the number of vultures saturates the system. Increasing carcass numbers means that even a solitary vulture is more likely to find food in a foraging session. The addition of vultures to the system now leads to a higher increase in the initial probability of finding food than in the lower carcass density simulations. The system quickly saturates both as carcass and vulture numbers increase such that even a solitary vulture can locate a carcass approximately 80% of the time when there are 50 carcasses in the 2500 km^2 habitat.

4. DISCUSSION

Griffon vultures detect food sources in two ways: either by directly locating a carcass on the ground or by following conspecifics that are drawn towards a carcass already discovered by other birds. The second detection method is extremely efficient, which can result in several hundred birds reaching a dead animal within hours of its death, and is largely responsible for vultures being the dominant secondary consumers within African savannah ecosystems (Houston 1974, 1979). The importance of using conspecifics as cues to food location in this system ensures that foraging success is nonlinear with respect to vulture density and is in fact found to be sigmoid. Efficient foraging can only be achieved when foragers are searching at such a density that all individuals are always within visual contact of a number of other individuals. Below this density, the information chain becomes increasingly broken and individual foraging success declines disproportionately rapidly. This strong nonlinearity was a persistent feature of our model, occurred in many other simulations (not shown) with alternative plausible parameter values, is the key prediction of our model, and has important consequences for conservation management.

Once vulture populations fall below a critical level, the feeding efficiency of each remaining individual falls dramatically, which will further accentuate population collapse leading to a spiral towards extinction. Some vulture populations are already so critically endangered over most of their range that they are effectively extinct in the wild, and are dependent on captive breeding programmes aiming for eventual reintroduction back into the wild (Pain *et al.* in press). Reintroduction is most likely to succeed if large numbers of individuals are released simultaneously at the same site to ensure that individuals will benefit from social facilitation and will probably need to be supported initially by supplementary feeding, concentrated in high densities, to compensate for the reduced foraging efficiency of birds during the early stages of reintroduction.

Our model suggests that some decline in vulture numbers can occur with little obvious effect on the foraging success of those remaining. However, below a certain critical density, further population declines lead to large and potentially catastrophic declines in the foraging performance of those remaining. If this foraging decline leads to additional mortality, then the situation will self-reinforce and rapidly worsen. On the positive side, if management interventions can raise both vulture and carcass densities sufficiently high, then there can be spectacular improvements in the performance of the local community of vultures through local enhancement effects. However, management must focus on high local populations rather than aiming to induce recovery over a wide geographical range. Detailed field studies focusing on the searching and chain-forming behaviour of wild vultures would provide the data required to build more quantitative models.

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