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The effects of facilitation and competition on group foraging in patches

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HIGHLIGHTS

- ▸ We study the effects of facilitation and competition on group foraging in patches.
- ▸ Using the marginal value theorem, we find the optimal group size and residence time.
- ▸ Trade-offs between facilitation and competition influence the optimal group size.
- ▸ Groups are predicted to exploit patches differently than individual foragers.

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ABSTRACT

Significant progress has been made towards understanding the social behaviour of animal groups, but the patch model, a foundation of foraging theory, has received little attention in a social context. The effect of competition on the optimal time to leave a foraging patch was considered as early as the original formulation of the marginal value theorem, but surprisingly, the role of facilitation (where foraging in groups decreases the time to find food in patches), has not been incorporated. Here we adapt the classic patch model to consider how the trade-off between facilitation and competition influences optimal group size. Using simple assumptions about the effect of group size on the food-finding time and the sharing of resources, we find conditions for existence of optima in patch residence time and in group size. When patches are close together (low travel times), larger group sizes are optimal. Groups are predicted to exploit patches differently than individual foragers and the degree of patch depletion at departure depends on the details of the trade-off between competition and facilitation. A variety of currencies and group-size effects are also considered and compared. Using our simple formulation, we also study the effects of social foraging on patch exploitation which to date have received little empirical study.

1. Introduction

Understanding the economic basis of how animals should allocate time spent foraging in a patch before departing to search for new patches has been a cornerstone of foraging theory. Although the patch model has been applied to a wide variety of contexts for solitary foragers (Stephens and Krebs, 1986; Stephens et al., 2007), the role of group foraging or the social patch model has received considerably less attention (Giraldeau and Caraco, 2000). In parallel to Charnov's (1976) Marginal Value Theorem (MVT), Parker and Stuart (1976) independently published a similar framework adapting a mating system model to a foraging system. Through this formulation, they considered competition for resources among a group of foragers in a patch. They acknowledged that in addition to this type of competition, group foraging may facilitate finding food and affect prey intake rates (e.g. producing an Allee effect). This facilitation was not, however, included in their model or other models (Yamamura and Tsuji, 1987) to date. Here we adapt the MVT idea to consider both competition and facilitation in patches by groups of foragers.

Foraging in groups brings both costs and benefits (Perrins and Birkhead, 1983; Clark and Mangel, 1986; Giraldeau and Caraco, 2000; Galef and Giraldeau, 2001; Krause and Ruxton, 2002). For a variety of species, being part of a group can increase foraging success through increased searching capacity, information exchange, and capture efficiency (Sullivan, 1984; Gotmark et al., 1986; Brown and Brown, 1996; Perrins and Birkhead, 1983). This effect, however, can depend strongly on group size, and the costs of increased competition or interference may outweigh the benefits of facilitation in larger groups. The social patch model with competition indicates that foragers should leave a patch earlier (and more thoroughly depleted) when foraging in groups than when foraging alone (Parker and Stuart, 1976; Giraldeau and Caraco, 2000). However, the effects of facilitation could influence this result.

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Here we adapt the MVT to consider costs and benefits of both competition and facilitation. We ask whether and how a trade-off between these factors influences the optimal number of individuals in a group and their patch residence-time. We restrict attention to social animals that travel and forage together, arriving and departing from a patch simultaneously. We also focus on the situation that the timescale of resource renewal is much longer than the timescale of patch exploitation. Given that time and/or energy may be the limiting factor in different circumstances (Ydenberg and Hurd, 1998), we consider strategies that optimize either rate or efficiency currencies. We incorporate an additional factor, namely facilitation, to the theory of social foraging in patches, allowing us to consider how the trade-off between competition and facilitation influences decisions about how long to stay in a patch.

2. Mathematical models

2.1. Optimal foraging time for a single forager

Here we briefly summarize the classical Marginal Value Theorem (Charnov, 1976) before extending it to group foraging. The time required to travel between food patches is denoted τ. The time spent foraging in a patch is t, and $f(t)$ is the total energy gained by foraging in a patch for time t. We consider the rate of energy gain function as the currency of interest, defined as

$$R(t) = \frac{f(t)}{t+\tau}. \tag{1}$$

Elementary calculus leads to the well-known result that optimal patch residence time t^* satisfies $f'(t^*) = f(t^*)/(t^*+\tau)$, provided that $f(t)$ is concave down. A well-known graphical solution (the rooted tangent) is often used to locate the optimal value t^* on the time axis. This will be discussed further on.

While a wide variety of energy gain functions are theoretically possible (Stephens and Krebs, 1986), we consider a classic case of diminishing returns. We model diminishing returns using the following saturating function:

$$f(t) = \frac{E_{max} t}{t_f + t}. \tag{2}$$

Eq. (2) describes the energy gain of an individual. This function levels off to a constant, E_{max}, the maximal energy level that can be extracted from a patch by an individual foraging for a long time. (Alternately, this parameter represents the maximal attainable per-forager resource quantity in some other currency, such as number of prey items.) The parameter t_f is a typical time scale for a single forager to find resources. In fact, for the specific choice of (2), t_f is the time at which the forager finds half of the resources they could maximally attain ($t = t_f$ implies $f = E_{max}/2$). Small t_f implies rapid success finding food in the patch, and a correspondingly steep initial increase of the function f.

For a single individual, with energy gain $f(t)$ given by Eq. (2), it can be shown by optimizing R with respect to t that the optimal patch residence time t^* is

$$t^* = \sqrt{t_f \tau}. \tag{3}$$

Thus, the optimal time is independent of E_{max}. Moreover, it increases with t_f and with τ.

2.2. Effect of group size

We now generalize the model to account for group foraging. First note that the social version of Eq. (1) would take the form:

$$\hat{R}(N,t) = \frac{\hat{f}(N,t)}{t+\tau}, \tag{4}$$

where, to avoid confusion, we use "hats" here and later to indicate functions analogous to $R(t)$ and $f(t)$ that depend on both foraging time and group size. $\hat{f}(N,t)$ is the total energy gain by *each* individual when foraging in a group with N additional members (group size $N+1$) for time t. Optimizing the behaviour now corresponds to maximizing $\hat{R}$ with respect to both N and t, which requires finding t^* and N^* satisfying both

$$\left.\frac{\partial \hat{R}}{\partial t}\right|_{N=\text{constant}} = 0, \quad \text{and} \quad \left.\frac{\partial \hat{R}}{\partial N}\right|_{t=\text{constant}} = 0.$$

As both $\hat{R}$ and $\hat{f}$ are taken to be smooth functions of N and t, the order of differentiation to identify the t and/or N coordinate of the critical point is immaterial. For example, we may first consider N constant and compute the optimal time $\hat{t}^*(N)$ (which leads to an expression analogous to Eq. (3) that depends on N) and then solve for N^* by setting $\partial\hat{R}/\partial N(N,\hat{t}^*) = 0$. We carry out this procedure for different assumptions about the N dependence, below. In addition, we also verified that we obtain local maxima, rather than other types of critical points analytically (by computing second derivatives) and/or graphically.

We now define $\hat{E}_{max}(N)$ and $\hat{t}_f(N)$ as, respectively, the per-individual resource available, and the food-finding time when an individual forages in a group with N additional members (group size of $N+1$). Then

$$\hat{f}(N,t) = \frac{\hat{E}_{max}(N) t}{\hat{t}_f(N) + t}. \tag{5}$$

For a fixed group size (N is constant), the optimal time is obtainable simply by carrying out the previous single-variable procedure, leading to

$$t^*(N) = \sqrt{\hat{t}_f(N)\tau}, \tag{6}$$

which is, as before, independent of $\hat{E}_{max}(N)$.

In order to consider the effects of group size, we take the following considerations in choosing appropriate functions for $\hat{E}_{max}(N)$ and $\hat{t}_f(N)$. As N increases, competition between group members should lower per-individual resource availability, and facilitation should lower the time to find the food. Hence, both $\hat{E}_{max}(N)$ and $\hat{t}_f(N)$ should be functions that decrease with N. Here we study two variants of the model, one in which group members interfere (preventing each other from obtaining the available resources effectively), and another in which they always share the resources equally.

2.2.1. Interference at large group size

We first considered a case where competition and interference in large groups cause additional depletion and division of resources, making less and less energy available per individual. If prey sense a larger group of predators more easily than a smaller group, they may escape from the patch with higher probability. This could lead to a depletion/interference effect that increases with group size. We thus assume that $\hat{E}_{max}(N)$ and $\hat{t}_f(N)$ depend exponentially on N, i.e.

$$\hat{E}_{max}(N) = E_{max} \exp\left(\frac{-N}{N_c}\right), \quad \hat{t}_f(N) = t_f \exp\left(\frac{-N}{N_f}\right). \tag{7}$$

The variable N represents the number of additional individuals in a foraging group, so the limit $N=0$ is the single forager case. As N gets large, both $\hat{E}_{max}(N)$ and $\hat{t}_f(N)$ tend to zero faster than $1/N$. There is less energy available than would be the case with equal subdivision (considered in the next case). The parameters N_c and N_f correspond to group sizes. If an individual forages in a group with an additional N_c members, the resource available to it drops to 37% of what it can gain in solitary foraging, because it has to compete with group members (i.e. $\hat{E}_{max}(N_c) = E_{max} \cdot (1/e) \approx 0.37 E_{max}$). Similarly, when foraging with N_f other individuals, the food-finding time would drop to $0.37 t_f$. It is