The effects of facilitation and competition on group foraging in patches

Marysa Laguë, Nessy Tania [1], Joel Heath, Leah Edelstein-Keshet *

Department of Mathematics, University of British Columbia, Vancouver, BC, Canada

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.

ARTICLE INFO

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.

© 2012 Elsevier Ltd. All rights reserved.

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.

* Corresponding author. Tel.: +1 604 822 5889; fax: +1 604 822 6074.
E-mail address: keshet@math.ubc.ca (L. Edelstein-Keshet).
[1] Present address: Department of Mathematics & Statistics, Smith College, Northampton, MA, USA.

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. $\hat{E}_{max}(N_c) = E_{max}\cdot(1/e) \approx 0.37E_{max}$). Similarly, when foraging with N_f other individuals, the food-finding time would drop to $0.37t_f$. It is

convenient to refer to N_c as the competition group-size and to N_f as the facilitation group-size. If N_c (or N_f) is large, it takes a large group to lead to significant competition (or facilitation).

2.2.2. Equal sharing

We also considered the case where patch resource is constant (e.g. sessile prey items) and split equally between group members. In that case, we considered rational functions of the form:

$$\tilde{E}_{max}(N) = \frac{E_{max}}{N+1}, \quad \tilde{t}_f(N) = \frac{t_f}{(N+1)^m}, \tag{8}$$

where m is a positive constant. Here we use $N+1$ (rather than just N) to maintain the $N=0$ limit as the single forager case. The expression for $\tilde{E}_{max}(N)$ is the per-individual share in a group of size $N+1$, and is intuitively clear. For example, in a group of size 2 ($N=1$) each gets an equal share of $(1/2)E_{max}$. The parameter m has the following meaning: in a group of size 2, the food-finding time changes from t_f to $[(1/2)^m t_f]$. If $m=1$, the competition and facilitation change at the same pace with increasing N. When $m>1$, there is a sharper drop in food-finding time (more facilitation), whereas when $0<m<1$, there is a sharper drop in the resource per individual as N increases (more competition).

2.3. Energy gain function for an individual foraging in a group

We first considered the interference case, adopting Eq. (7). We rescale population size by the competition group-size, defining $\overline{N} = N/N_c$. We also define the dimensionless ratio:

$$a = N_f/N_c.$$

The parameter a, which is positive, is the ratio of the facilitation and competition group sizes. Then $a \ll 1$ means $N_f \ll N_c$ which implies that $\hat{t}_f(N)$ decreases (exponentially) at a faster rate than $\hat{E}_{max}(N)$ as group size N increases; this reflects the case when facilitation outweighs competition in social foraging. The regime $a \gg 1$, conversely, means $N_f \gg N_c$, so $\hat{E}_{max}(N)$ drops faster than $\hat{t}_f(N)$ as N increases; this corresponds to the case when competition dominates over facilitation in social foraging. We refer to a as the competition-facilitation parameter for brevity, and we note that a plays a role analogous to $1/m$ in Eq. (8). We will be interested in both the high facilitation limit $a \to 0$ and high competition limit $a \to \infty$.

After scaling, we can rewrite Eq. (7) in terms of the non-dimensionalized group size,

$$\overline{E}_{max}(\overline{N}) = E_{max} \exp(\overline{N}), \quad \overline{t}_f(\overline{N}) = t_f \exp\left(\frac{-\overline{N}}{a}\right). \tag{9}$$

We denote $\overline{f}(\overline{N},t)$ as the per-individual energy gain function in the rescaled variable,

$$\overline{f}(\overline{N},t) \equiv \hat{f}(N,t) = \hat{f}(\overline{N} \cdot N_c,t) = E_{max} \frac{\exp(-\overline{N})t}{t_f \exp\left(\frac{-\overline{N}}{a}\right)+t}. \tag{10}$$

From now on, we drop the bars from $\overline{N}$ and $\overline{f}$ and simply denote the rescaled population size as N and the function of interest in (10) as f. For the purpose of optimization, the constant factor of E_{max} multiplying (10) is immaterial, and will be henceforth set to 1.

3. Results

3.1. Optimizing the rate of energy gain for group foraging

3.1.1. Interference at large group size

Using the rate of energy gain, Eq. (4) as the currency to be maximized, and the (rescaled) version of the function $f(N,t)$ given by (10) (with bars removed), we look for values t^* and N^* that maximize

$R(N,t)$ with respect to both t and N. Following rescaling, the optimal patch residence time, as given in Eq. (6), can be written as

$$t^*(N) = \sqrt{t_f \exp\left(\frac{N}{a}\right)\tau}. \tag{11}$$

Note that as $N \to 0$, this coincides with the classical result (3) for a single forager.

Solving for the optimal group size ($\partial R/\partial N = 0$) at the optimal foraging time $t^*(N)$ leads to the critical point:

$$N^* = a \ln\left(\frac{t_f}{\tau}\left(1-\frac{1}{a}\right)^2\right). \tag{12}$$

From Eq. (12) we cannot have $a=1$ as it leads to singularity. The critical points that could give an optimal time t^* for the optimal group size N^* are given by

$$t^* = \pm \frac{\tau a}{(a-1)}. \tag{13}$$

Then for feasible optimal residence time $t^* > 0$, either $a > 1$ and $t^* = \tau a/(a-1)$, or $a < 1$ and $t^* = \tau a/(1-a)$.

To check which of these cases corresponds to a local maximum we consider both a (generalized) "second derivative test" and graphical evidence. First, in Fig. 1, we show the contour plot of $R(N,t)$ for different values of the competition-facilitation parameter, a. To check if group foraging is in fact optimal compared to solitary foraging, we looked for regions where $R(N,t)$ is larger than the optimal solitary value $R(0,t^*(0))$; these are shaded in grey in Fig. 1. Within this region, any combination of patch residence time t and group size N would lead to a larger rate of energy gain than when foraging alone (at optimal condition). The maximum point of $R(N,t)$ is located within this region. We observed that when a is not too large ($a=0.3$ and 0.5 in Fig. 1), there exists a range of N and t (that is positive and biologically relevant), where $R(N,t)$ is larger that the corresponding value when foraging alone. We verified this further analytically by inspecting the Hessian matrix consisting of all the second partial derivatives:

$$H = \begin{bmatrix} R_{tt}(N,t) & R_{tN}(N,t) \\ R_{Nt}(N,t) & R_{NN}(N,t) \end{bmatrix}. \tag{14}$$

For an optimal group size and patch residence time, we need both $R_{tt}(N,t) < 0$ and $\det(H) > 0$. Second, we also plot the rate of energy gain $R(N,t)$, as in Fig. 1.

- $a > 1$ case: We found that while $R_{tt} < 0$, $\det(H) < 0$ only when $1 < a \lesssim 1.11$. Thus for a wide range of parameter value, this case will not lead to $R(N,t)$ having a local maximum at N^* and t^*. Moreover, in the narrow range $1 < a \lesssim 1.11$, we found that $N^* < 0$, as shown in Fig. 1(d). Thus, this case is not biologically relevant. We conclude that when $a > 1$, no relevant optimal group size N^* exists. This result is intuitively reasonable: when competition is stronger than facilitation, a forager does best on its own, rather than in a group.

- $a < 1$ case: This case always results in a local maximum since we found that $\det(H) > 0$ and $R_{tt} < 0$. An optimum can be seen at a positive N^* value in Fig. 1(a) and (b). Thus, we conclude that to obtain a biologically relevant optimum, we need at least $0 < a < 1$, i.e. an optimal group size exists only when $N_f < N_c$ (high facilitation case). By graphing, we also further observe that a biologically relevant value $N^* > 0$ is obtained when a is below a certain critical value that is less than one. One particular example with $a=0.8$ is shown in Fig. 1(c), where the maximum of $R(n,t)$ occurs at a negative N^* value.

We conclude that the optimal group size N^* is given by Eq. (12) provided $0 < a < 1$. The dependence of the optimal group size N^*
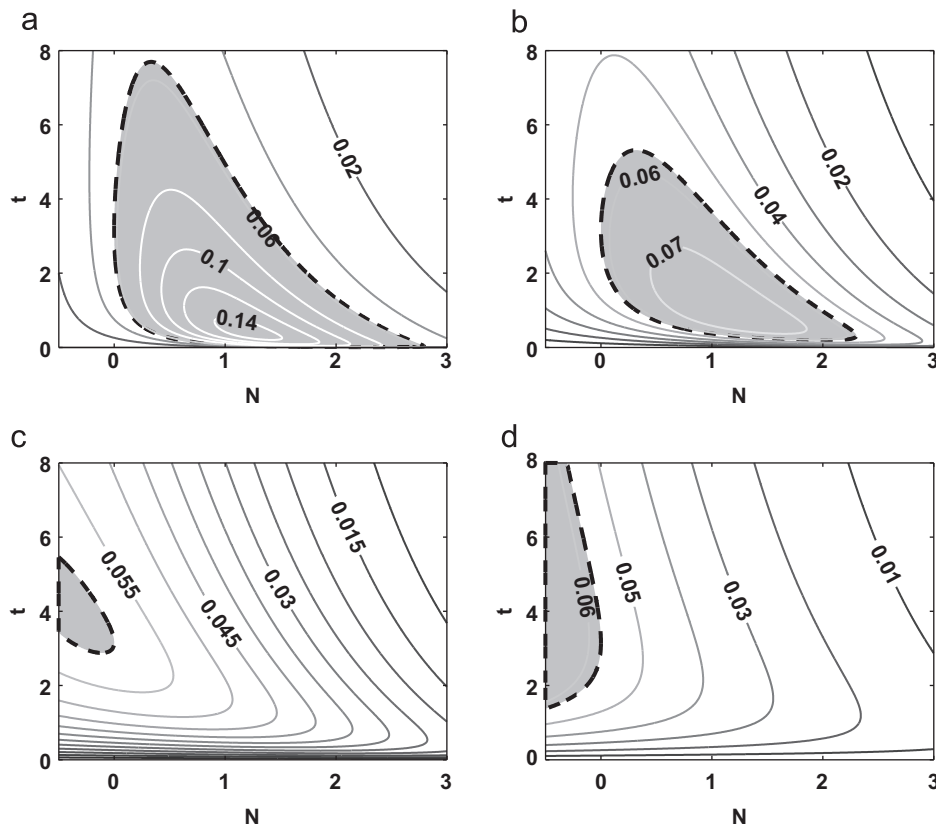
Fig. 1. Rate of energy gain optima: Contour plots of the rate of energy gain $R(N,t)$ as a function of the (scaled) social group size N and time spent foraging together in a patch t. Individual foraging time $t_f = 10$ and travel time $\tau = 1$ and values of the competition-facilitation parameter a were (a) 0.3, (b) 0.5, (c) 0.8 and (d) 1.1. Note that in (a) and (b) a maximal rate of energy gain exists for social foraging ($N > 0$), whereas for (c) and (d), individual foraging ($N=0$) is optimal. Within the grey shaded region $R(N,t)$ is larger than $R(0,t^*(0))$, the value obtained at the optimal condition when foraging alone.

on the competition-facilitation parameter a is non-monotonic as shown in Fig. 2(a). In the high facilitation regime ($a \to 0$), very small group sizes are optimal. Here, the addition of very few individuals to the group sharply reduces the time to obtain food, i.e. $\hat{t}_f(N)$ drops steeply with increasing N. In this regime, the best strategy is to maintain a small group size where the disadvantage of competition is avoided while the benefits of facilitation are already significant. As a is increased, the optimal group size also increases. In this regime it takes a larger group to reap the benefits of facilitation. The time to obtain food $\hat{t}_f(N)$ only decreases considerably when group size is increased significantly so tradeoff between facilitation and competition leads to higher optimal group size. However, when a is increased further, the disadvantage due to competition starts to outweigh facilitation so that smaller group sizes are once again optimal.

Eq. (12) also implies that N^* increases with the individual food-finding time, t_f, and decreases with travel time τ. Thus, larger τ (t_f) favors smaller (larger) groups. Specifically, N^* has an explicit dependent on t_f/τ, the ratio of the individual foraging time to the travel time. In Fig. 2(a), we plotted N^* as a function of a for several values of the ratio t_f/τ. When the ratio t_f/τ is larger, the optimal group size N^* increases. Given a value of t_f/τ, there exists a certain critical value of a above which $N^* < 0$. Here the effects of competition completely exceed any benefit from facilitation and the optimal strategy would be to forage alone. Larger value of t_f/τ leads to a higher critical value a. Thus, decreasing t_f/τ leads to a narrower range of values of a which yield $N^* > 0$.

In Fig. 3(a), we plotted the energy gain, $f(N,t)$, as a function of t for several values of N, including the optimal value $N = N^*$, and twice and half that value. For each of these, we draw Charnov's classical "rooted tangent" diagram (dashed lines emanating from

$t = -\tau$ and tangent to the curve), to indicate how the optimal time differs from case to case. (For example, t_2 is optimal for the case $N = N^*$, t_1 is optimal for $N = 2N^*$, and t_3 for $N = N^*/2$.) From this graph, it is seen that for optimal group size N^*, the rooted tangent line has the steepest slope. We found that increasing N also increases the initial slope of the function f (with respect to t) close to $t=0$, leading to smaller optimal time t^*. In Fig. 3(b) we plotted the optimal times t_1, t_2, t_3 against the respective group sizes to further emphasize the connection between optimal group size and optimal time spent in a patch.

3.1.2. Equal sharing

We asked how results change in the case of equal subdivision, with $\tilde{E}_{max}(N)$ and $\tilde{t}_f(N)$ defined in Eq. (8). As before, we set $E_{max} = 1$ and after similar calculation, we obtain the optimal group size:

$$N^* = \left[\frac{t_f}{\tau}(1-m)^2 \right]^{1/m} - 1. \tag{15}$$

Here, the parameter m plays a role analogous to the reciprocal of the facilitation-competition parameter, $1/a$, in the interference case. Eq. (15) is a local maximum when $m > 1$. Results are entirely analogous to the previous case, with the replacement $a \to 1/m$, and attest to the robustness of conclusions which are relatively independent of the choice of function to represent the effect of the group. In Fig. 2(b), we plotted the optimal group size N^* as a function of m for several values of the ratio t_f/τ. Here the high facilitation limit occurs for large m (analogous to small a) and favors small group sizes as before. Optimal foraging at a group size of $N^* > 0$ is only observed for m slightly above 1; otherwise solitary foraging is optimal. Further, larger values of N^* are
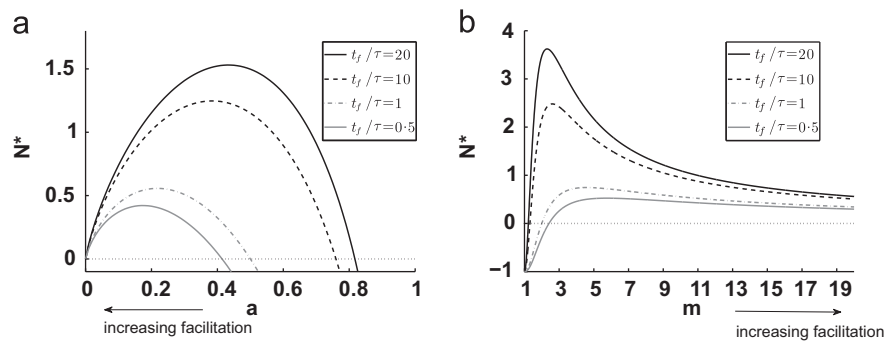
Fig. 2. The effect of facilitation on the optimal group size for the rate of energy gain currency. (a) Interference case: optimal group size N^* as a function of the competition-facilitation parameter $a = N_f/N_c$ and (b) equal sharing case: optimal group size N^* as a function of m. The ratio of individual foraging time t_f to travel time τ is varied, $t_f/\tau =$ 20, 10, 1 and 0.5.
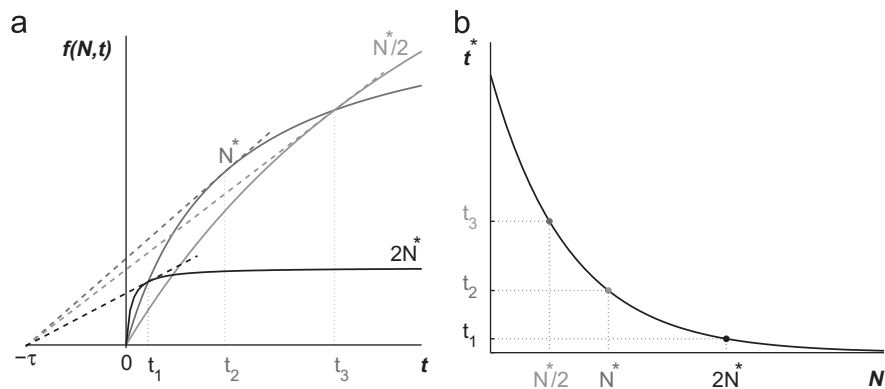

Fig. 3. Graphical solution to finding the optimal time for different group sizes. (a) shows the rooted tangent solution displaying the optimal foraging time t^* for the optimal group size N^*, and for other group sizes, $2N^*$ and $N^*/2$. As N increases, the slope of $f(N,t)$ (with respect to t) becomes steeper leading to smaller optimal time. (b) shows the optimal foraging time t^* decreases as group size N increases. Here, t_1 is the optimal foraging time for a group of size $2N^*$, t_2 is the optimal foraging time for the optimal group size N^*, and t_3 is the optimal foraging time for a group of size $N^*/2$.

observed than in the interference case (same parameter values describing solitary forager $N=0$ are used in Fig. 2(a) and (b)) since here foraging in a large group is not as unfavorable as in the interference case. Finally, we also note that N^* has the same explicit dependence on the ratio t_f/τ and changing this ratio has similar effects as before, namely increasing this ratio (either by increasing the travel time τ or decreasing the individual food-finding time t_f) leads to an increase in the optimal group size.

3.2. Deviation from optimal group size

We asked to what extent deviations in group size can affect the rate of energy gain. This question is related to the steepness of the function $\hat{R}(N,t^*)$ when N is varied about its optimal value N^*. Results for the case of interference in large groups are summarized in Fig. 4(a)–(c) for small and larger values of the parameters τ, t_f, and a. As seen in the figure, smaller values of the parameters (solid curves) produce relatively sharp optima in R, meaning that deviations in group size about the optimum N^* sharply reduce the effectiveness of the group. For larger values (dashed curves), the peak is shallower. This is particularly true of the larger a value (lowest curve in Fig. 4(c)), i.e. when $N_c \approx N_f$ so that competition and facilitation effects are more closely balanced. Thus, while deviations from the optimal group size can lead to penalty in the overall rate of energy gain, the extent to which this happens depends on a combination of factors, including the travel time, resource availability, and competition-facilitation ratio.

3.3. Alternate foraging strategies and currencies for groups

The fitness currency relevant to a forager depends on whether time or energy is limiting (Ydenberg and Hurd, 1998). We therefore considered both rate and efficiency maximization. We asked whether and how foraging strategies with other currencies would affect our conclusions, by considering three other currencies: net rate of energy gain, efficiency, and net energy gain. We applied the same analysis to each currency (calculations not shown) but limit the results to be presented for the interference case ($\bar{E}_{max}(N)$ and $\bar{t}_f(N)$ given by Eq. (9)). The per-individual energy gain $f(N,t)$ used here follows the scaled Eq. (10).

3.3.1. Rate of net energy gain

Rate maximizing is important when time is limiting (Ydenberg and Hurd, 1998; Evans, 1976; Pyke, 1980). We thus consider the net rate of energy gain, defined as

$$Q(N,t) = \frac{f(N,t) - (p_1 t + p_2 \tau)}{t + \tau}, \tag{16}$$

where p_1 and p_2 represent the energetic cost of foraging and travelling, respectively. If the costs of travelling and foraging are equal ($p = p_1 = p_2$), maximizing the rate of net energy gain (given by Eq. (16)) reduces to maximizing

$$Q(N,t) = \frac{f(N,t)}{t + \tau} - p = R(N,t) - p. \tag{17}$$
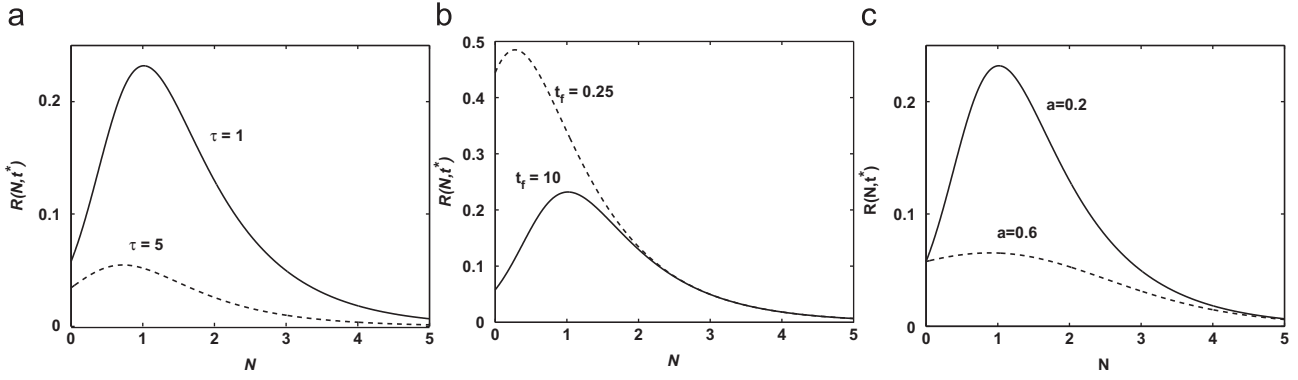
Fig. 4. Rate of energy gain $R(N,t^*(N))$ as a function of N obtained for various parameter values: effect of deviation from optimal group size. Variation in group size N can have low to drastic effects on the rate of energy gain: (a) $\tau=1$ (solid), $\tau=5$ (dashed), (b) $t_f=10$ (solid), $t_f=0.25$ (dashed) and (c) $a=0.2$ (solid), $a=0.6$ (dashed). For comparison in all cases, solid curve is obtained with the parameter values $t_f=10$, $a=0.2$ and $\tau=1$.
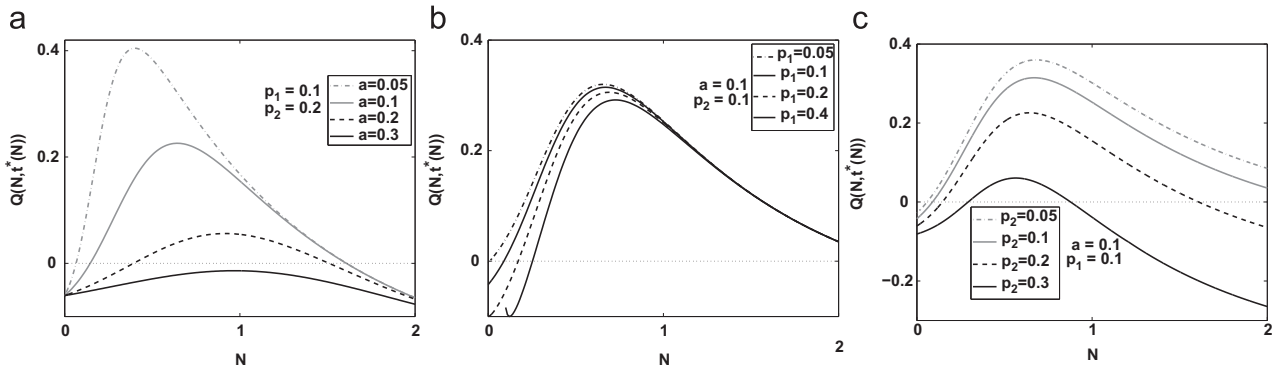

Fig. 5. Rate of net energy gain $Q(N,t^*(N))$ as a function of N obtained for various parameter values. (a) Varying the facilitation-competition parameter a while fixing the cost parameters $p_1=0.1$ and $p_2=0.2$, (b) varying the foraging cost p_1 ($a=0.1$, $p_2=0.1$) and (c) varying the traveling cost p_2 ($a=1$ and $p_1=0.1$). All other parameter values: $t_f=10$ and $\tau=1$.

Since the rate of net energy gain is simply the rate of energy gain minus some constant, the optimal foraging time and optimal group size will be unchanged from Eqs. (11) and (12).

When $p_1 \neq p_2$, the maximum point cannot be expressed explicitly as it follows a transcendental equation. In Fig. 5, we plotted the function $Q(N,t^*(N))$ using different values of a, p_1 and p_2. Similar to the result obtained while maximizing $R(N,t)$, we find that group foraging is optimal ($N^* > 0$) when the facilitation competition parameter a is small as shown in Fig. 5(a). In Fig. 5(b) and (c), we showed that increasing p_1 and p_2 reduces $Q(N,t)$ and positive optimal foraging time t^* and optimal group size N^* are only found when the foraging and traveling costs p_1 and p_2 are not too large. When the costs are too high, no maximum point exists (e.g. in Fig. 5(b) for $p_1=0.4$, $t^*(N)$ is complex for small N values) and thus it is optimal to forage alone.

3.3.2. Foraging efficiency

In some situations, foragers may maximize foraging efficiency rather than the rate of energy gain (Schmid-Hempel et al., 1985; Ydenberg and Hurd, 1998). We define the foraging efficiency as the ratio of energy gained to energy spent, i.e.

$$E(N,t) = \frac{E_{gain}}{E_{lost}} = \frac{f(N,t)}{(p_1 t + p_2 \tau)}. \tag{18}$$

In the equal cost scenario as above, ($p_1 = p_2 = p$) we have

$$E(N,t) = \frac{f(N,t)}{p(t+\tau)} = \frac{1}{p}\frac{f(N,t)}{t+\tau} = \frac{1}{p}R(N,t), \tag{19}$$

so the efficiency is simply a scalar multiple of the rate of energy gain. This means that extrema previously calculated in Eqs. (11)

and (12) are unchanged. Larger costs (higher values of p) only lead to lower efficiency value.

In the $p_1 \neq p_2$ scenario, when travel and foraging costs differ, we find that t^* and N^* depend on the ratio p_2/p_1 as follows:

$$t^* = \sqrt{\bar{t}_f(N)\tau\frac{p_2}{p_1}}, \quad N^* = a\ln\left(\frac{p_1}{p_2}\cdot\frac{t_f}{\tau}\cdot[1-(1/a)^2]\right). \tag{20}$$

In particular, if travel cost exceeds foraging cost ($p_2 > p_1$), the optimal patch residence time is larger than in previous calculations. In the opposite case ($p_2 < p_1$), a larger optimal group size is favoured. This is biologically reasonable. When it is costly to reach a patch (large p_1), it pays to stay longer in that patch. If prey is cryptic, or hard to detect in the patch, i.e. foraging is costly (large p_2), a larger group size is beneficial to facilitate prey capture.

3.3.3. Net energy gain

Yet another currency that has been considered is the net energy gain (Van Gils et al., 2003; Hainsworth and Hamill, 1993). The currency of net energy gain is the total energy gained minus the energy spent during foraging and travel, i.e.

$$G(N,t) = f(N,t) - (p_1 t + p_2 \tau). \tag{21}$$

Since p_2 and τ are constants, neither affect optima, and without loss of generality we can set $p_2\tau = 0$ for the optimization step. The optimal patch residence time is then

$$t^* = -\bar{t}_f(N) + \sqrt{\frac{E_{max}(N)\bar{t}_f(N)}{p_1}}. \tag{22}$$

For $t^* > 0$, we need $p_1 \overline{t}_f(N) < \overline{E_{max}}(N)$. That is, the total cost associated with foraging should be less than the maximum possible energy that can be obtained. Maximizing with respect to group size leads to two critical points, only one of which, is a local maximum:

$$N^* = \frac{a}{1-a} \ln\left(\frac{p_1 t_f}{a^2}\right). \qquad (23)$$

As shown in Fig. 6(a), the optimal group size increases as the ratio $a = N_f/N_c$ approaches its limiting value of 1. Using $0 < a < 1$, we see that N^* increases with t_f and p_1. If t_f is small, food is quickly found, thus there is little point in foraging in a group to further decrease the foraging time. However, if t_f is large, foraging in a group decreases the amount of time taken to find the food (facilitation) and is beneficial. Fig. 6(b) shows how N^* increases with t_f. Varying t_f has the same effect as varying p_1. As p_1 increases, it becomes more costly to forage; in order to maximize the energy gained, more individuals are needed for optimal group foraging, as shown in Fig. 6(b).

3.3.4. Currency comparisons

Overall, we find that in the scenario of equal costs ($p_1 = p_2$), optima for group foraging based on other currencies are the same as those for the rate of energy gain discussed in Section 3.1. When travel time and/or cost is high, it is beneficial for animals to stay longer in a patch, and forage in smaller groups (as travel time or cost increases, t^* increases and N^* decreases). Meanwhile, for patches with small associated travel times, larger group sizes are optimal. Distinct currencies lead to different predictions mainly in the case of unequal costs of travel and foraging, $p_1 \neq p_2$.

3.4. Patch utilization

Up to now, we have considered how group foraging affects the foraging success of individuals. We now ask a distinct but related question of how individuals versus groups affect patch depletion. One immediate question is to what extent would resources be more thoroughly depleted by a group of foragers compared to a single individual. How do facilitation and competition affect the level of depletion? We calculate resources remaining after a group of size N foragers leaves the patch at the optimal foraging time $t^*(N)$:

$$\phi(N) = E_{tot} - (N+1)f(N, t^*(N)), \qquad (24)$$

where E_{tot} is the maximum energy that can be extracted from the patch. For simplicity, here we consider the case where $E_{tot} = E_{max}$, i.e. a single forager can extract all resources available given enough time. As before, we take the total resources in a patch to be $E_{max} = 1$ (see scaling in Eq. (10)). $(N+1)f(N, t^*(N))$ gives the total resources obtained by the group after foraging for time t^* (we use the factor $N+1$ since the single forager limit is given by $N=0$).

In Fig. 7, we show the effects of facilitation and competition on patch utilization by plotting $\phi(N^*)$ as the facilitation-competition parameter is varied for both the interference case (Eq. (7)) and the equal sharing case (Eq. (8)). For the interference case, for all values of a that yield a biologically relevant optimal group size
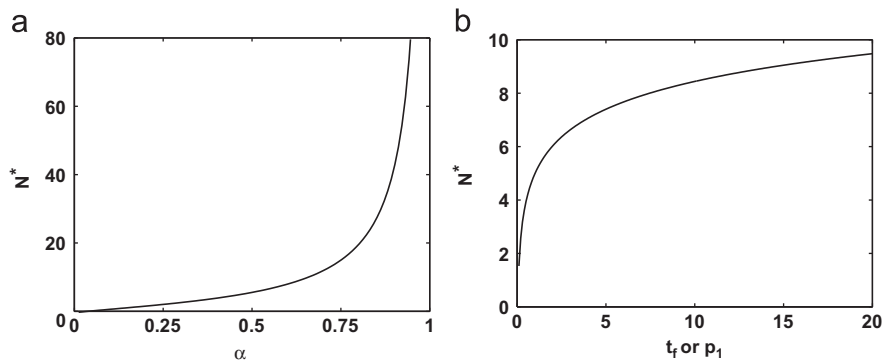

Fig. 6. Net energy gain: Dependence of the optimal group size N^* given by Eq. (23) on parameter values; (a) the competition-facilitation parameter, a; (b) the individual foraging time, t_f or p_1 (varying t_f or p_1 has the same effect). Default values: $a = 0.6$, $t_f = 10$, and $p_1 = 10$ (unless being used as the free variable). In (a), we see that N^* increases sharply as a approaches 1. In (b), we see that N^* increases sharply for small values of t_f and p_1, but increases less drastically for larger values.
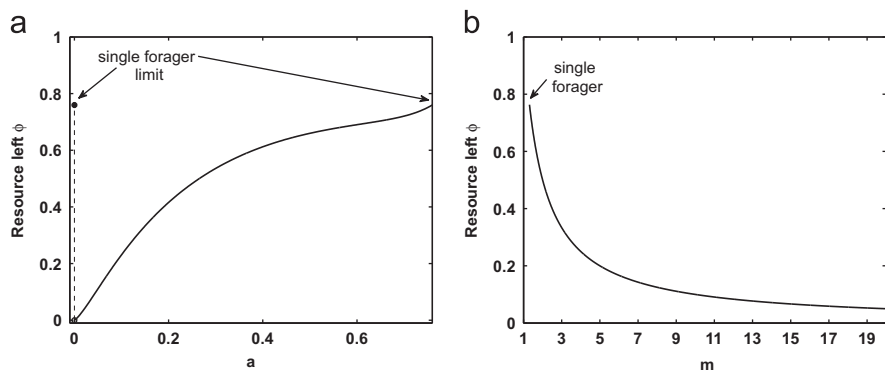

Fig. 7. The effects of facilitation on ϕ, the resources left after optimal group foraging: $\phi(N^*)$ obtained using (a) the interference assumption and (b) the equal sharing assumption ($t_f = 10$ and $\tau = 1$).
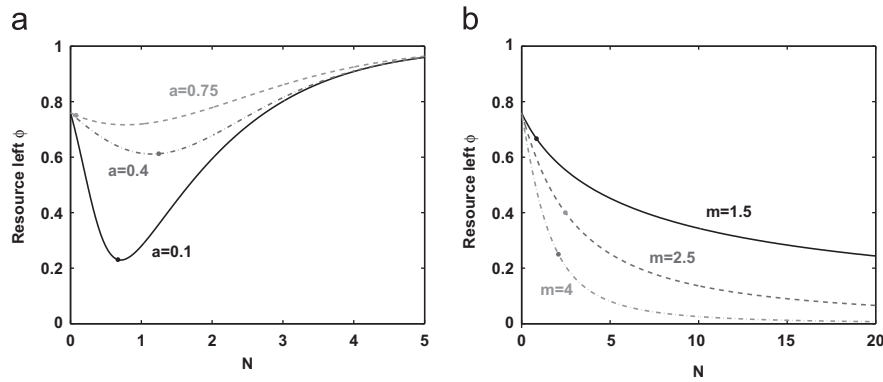
Fig. 8. Resources left after a group of size N forages at its optimal time $t^*(N)$ as defined in Eq. (24) with (a) interference assumption and (b) equal sharing assumption ($t_f=10$ and $\tau=1$ in both cases, and competition-facilitation parameters a and m are varied). ● marks the optimal group size location.

($N^* > 0$), group foraging leads to a greater patch exploitation compared to foraging alone. When a is small, facilitation is high. While the optimal group size is small, the group is able to extract resources to the fullest extent. At higher values of a however, with less facilitation, the group does not forage as effectively, leading to higher level of resources remaining (larger ϕ). For the equal sharing case, we also see a similar effect in that facilitation (high value of m) leads to more effective foraging and fewer resources remaining when the group leaves the patch. Note that for both cases, high levels of patch utilization (lower ϕ) are obtained when facilitation is highest even though the optimal group size may not be largest at the high facilitation limit.

The dependence of patch depletion on group size is shown further in Fig. 8. For the interference case, a small group can extract more resource than a solitary forager. With increasing facilitation (increasing the parameter a), the amount of resources extracted increases with group size. However, large group size leads to less efficient foraging due to interference. Far from the optimum, at high group size N, the resource extracted by the entire group is actually lower than that extracted by one solitary forager. This is not observed when group members share resources equally ("equal sharing" case). Here increasing the group size will eventually lead to a complete depletion of resources ($\phi \to 0$).

4. Discussion

Many influences contribute to collective animal behaviour, including foraging in groups (see, for example, Chapter 2 in the recent survey by Sumpter, 2010). Here we were particularly concerned with costs and benefits of group foraging. Using the classic marginal value theorem (MVT) and a simple saturating function for energy gain over time spent foraging in a patch we explored how the trade-off between facilitation and competition changes with group size, influencing the economics of foraging decisions in patches with diminishing returns. Compared to the solitary (classical) patch model, group foraging has an evolutionary advantage if the benefits of finding food more quickly through social facilitation outweighs the costs of competition, or sharing food with other group members. Our model allows this trade-off to be explicitly considered in an elementary mathematical setting.

Both the optimal patch residence time t^* and optimal group size N^* depend on the parameters such as τ, the travel time, t_f the individual foraging time, and the balance of competition and facilitation, represented by the ratio $a = N_f/N_c$ in the interference case, or parameter $m \approx 1/a$ under the equal sharing assumption. Thus, the relative strengths of competition and facilitation influence the result of this trade-off. The optimal patch residence time

increases as the travel time and the time required to find food increase. When the travel time is small, large group sizes are optimal. If t_f is large (i.e. if the time needed by an individual to find food is large), larger group sizes are optimal. The parameter a (interference case) or m (equal sharing) measures the relative competition and facilitation balance. For optimal group foraging ($N^* > 0$), we found the necessary condition of $0 < a < 1$ or $m > 1$. We found that the largest optimal group size occurs at an intermediate value of the parameter a or m, i.e. where there is a balance between competition and facilitation.

We also considered the strength of selection towards optimal group size by considering the degree to which group sizes slightly bigger or smaller than the optimal group size affect the groups foraging effectiveness. If a or τ are small, optimal group sizes produce the best rate of energy gain, while deviation from optimal group size produce considerably lower rates of energy gain. In these cases, there will be strong selection for optimal group size. In other situations however, the deviation from optimal group size will be less significant, suggesting weaker selection towards a specific optimal group size.

Our model does not include the dynamics of group formation for loose social structures where individuals can join or leave the group. This subject forms an interesting and well-studied topic of research. For example, Sibly (1983) first proposed that optimal group size is unstable as an individual can increase its fitness by joining a group of optimal size, thus increasing the group size. Further studies such as Clark and Mangel (1984, 1986), Pulliam and Caraco (1984), Giraldeau and Caraco (2000), Giraldeau and Gillis (1985), and Higashi and Yamamura (1993) deal with such issues. Here we consider that while interference and competitions influence groups size, groups arrive and depart at the same time from patches.

In their original model of patch competition, Parker and Stuart (1976) noted that patch departure rules could depend on the decisions of others (see also Goubault et al., 2005), and might therefore be best considered as a war of attrition (Maynard Smith, 1974). Sjerps and Haccou (1994) conducted a formal game theoretical analysis of this competitive scenario finding that interference can have an important influence on the evolutionarily stable patch departure rules. We assumed that the group acts as a social unit, with all individuals arriving and departing simultaneously in a patch (Giraldeau and Caraco, 2000). Future work could consider variations of this approach, incorporating the role of facilitation to understand how departure rules change when individuals do not arrive simultaneously (e.g. in producer–scrounger dynamics, Beauchamp and Giraldeau, 1997) or when they differ in their competitive abilities.

Previous versions of the social patch model, considering only competition, predict that foragers should stay for a shorter

duration and that patches should be depleted to a greater level by groups than by solitary individuals (Giraldeau and Caraco, 2000; Parker and Stuart, 1976). Our results considering the trade-off between competition and facilitation similarly indicate that groups of an optimal size will often deplete more of the patch resources than solitary foragers; however, the degree of competition vs. facilitation (parameter a in the interference case, or m in the equal sharing case) determines to what extent group vs. individual patch exploitations differ.

A major application of foraging theory has been in the context of "giving up densities" (density of resources at which individuals leave a patch) for assessing habitat quality (e.g. Brown, 1988; Valone and Brown, 1989). The difference in how extensively groups exploit a patch compared to a solitary forager can have important implications for analyzing giving up densities in the field (Livoreil and Giraldeau, 1997; Giraldeau and Caraco, 2000), highlighting the importance of empirical tests of the social patch model. The role of facilitation could further complicate these interpretations of field data. Our results indicate that facilitation will also be an important consideration in interpreting giving up densities in the field, with the details of the trade-off between competition and facilitation determining the extent of patch depletion. Empirical studies of the social patch model are surprisingly lacking (Giraldeau and Caraco, 2000) and the role of facilitation has received practically no attention in this context. Our model makes a contribution to social foraging theory by providing a starting point for understanding the trade-off between facilitation and competition (Nilsson et al., 2007). Understanding these tradeoffs during social interactions is important in shaping the functional responses of organisms and provides a mechanistic link between individual behaviour, group dynamics and community ecology.

Acknowledgments

References

Beauchamp, G., Giraldeau, L., 1997. Patch exploitation in a producer–scrounger system: test of a hypothesis using flocks of spice finches (*Lonchura punctulata*). Behav. Ecol. 8, 54–59.

Brown, C.R., Brown, M.B., 1996. Coloniality in the Cliff Swallow. The University of Chicago Press.

Brown, J., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behav. Ecol. Sociobiol. 22, 37–47.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9, 129–136.

Clark, C., Mangel, M., 1984. Foraging and flocking strategies: information in an uncertain environment. Am. Nat. 626–641.

Clark, C., Mangel, M., 1986. The evolutionary advantages of group foraging. Theor. Popul. Biol. 30, 45–75.

Evans, P., 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. Ardea 64, 117–139.

Galef, B., Giraldeau, L., 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim. Behav. 61, 3–15.

Giraldeau, L., Caraco, T., 2000. Social Foraging Theory. Princeton University Press, Princeton, NJ.

Giraldeau, L., Gillis, D., 1985. Optimal group size can be stable: a reply to sibly. Anim. Behav. 33, 666–667.

Gotmark, F., Winkler, D.W., Andersson, M., 1986. Flock-feeding on fish schools increases individual success in gulls. Nature 319, 589–591.

Goubault, M., Outreman, Y., Poinsot, D., Cortesero, A., 2005. Patch exploitation strategies of parasitic wasps under intraspecific competition. Behav. Ecol. 16, 693–701.

Hainsworth, F.R., Hamill, T., 1993. Foraging rules for nectar: food choices by painted ladies. Am. Nat. 142, 857–867.

Higashi, M., Yamamura, N., 1993. What determines animal group size? Insider-outsider conflict and its resolution. Am. Nat. 142, 553–563.

Krause, J., Ruxton, G.D., 2002. Living in Groups. Oxford University Press.

Livoreil, B., Giraldeau, L., 1997. Patch departure decisions by spice finches foraging singly or in groups. Anim. Behav. 54, 967–977.

Maynard Smith, J., 1974. The theory of games and the evolution of animal conflicts. J. Theor. Biol. 47, 209–221.

Nilsson, P., Lundberg, P., Brönmark, C., Persson, A., Turesson, H., 2007. Behavioral interference and facilitation in the foraging cycle shape the functional response. Behav. Ecol. 18, 354–357.

Parker, G., Stuart, R., 1976. Animal behavior as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. Am. Nat. 110, 1055–1076.

Perrins, C.M., Birkhead, T.R., 1983. Foraging Behaviour in Avian Ecology. Blackie and Sons Ltd, Bishopbriggs, Glasgow.

Pulliam, H., Caraco, T., 1984. Living in groups: is there an optimal group size? In: Krebs, J., Davies, N.B. (Eds.), Behavioral Ecology: An Evolutionary Approach, 2nd ed. Blackwell Scientific Publications, Oxford, UK, pp. 122–147.

Pyke, G.H., 1980. Optimal foraging in bumblebees: calculation of net rate of energy intake and optimal patch choice. Theor. Popul. Biol. 17, 232–246.

Schmid-Hempel, P., Kacelnik, A., Houston, A.I., 1985. Honeybees maximize efficiency by not filling their crop. Behav. Ecol. Sociobiol. 17, 61–66.

Sibly, R.M., 1983. Optimal group size is unstable. Anim. Behav. 31, 947–948.

Sjerps, M., Haccou, P., 1994. Effects of competition on optimal patch leaving: a war of attrition. Theor. Popul. Biol. 46, 300–318.

Stephens, D., Brown, J., Ydenberg, R., 2007. Foraging: behavior and ecology. University of Chicago Press.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press.

Sullivan, K.A., 1984. The advantages of social foraging in downy woodpeckers. Anim. Behav. 32, 16–22.

Sumpter, D., 2010. Collective Animal Behavior. Princeton University Press, Princeton, NJ.

Valone, T., Brown, J., 1989. Measuring patch assessment abilities of desert granivores. Ecology 70, 1800–1810.

Van Gils, J., Schenk, I., Bos, O., Piersma, T., 2003. Incompletely informed shorebirds that face a digestive constraint maximize net energy gain when exploiting patches. Am. Nat. 161, 777–793.

Yamamura, N., Tsuji, N., 1987. Optimal patch time under exploitative competition. Am. Nat. 553–567.

Ydenberg, R., Hurd, P., 1998. Simple models of feeding with time and energy constraints. Behav. Ecol. 9, 49–53.