

A common assumption of optimal foraging theory is that natural selection has favoured animals that forage in an optimal way, as such an ability increases the individual's probability of survival [4, 5]. This argument is used to support optimality principles in biology, and is at the base of optimal foraging theory [6].

Efficient foraging is clearly beneficial when food is in short supply, but even when food is plentiful, efficient foraging is advantageous as it leaves more time for other activities such as territory defence, predator avoidance, or mating [4]. We focus on the idea that foraging in groups may increase effectiveness while foraging [7]. Moreover, when food is hidden, or requires a significant initial investment of effort to attain, the cost to the individual can be reduced through "team work" arising from group foraging. The cost and benefits of grouping are discussed extensively by Krause & Ruxton [3].

We consider (1) what conditions benefit group foraging, and (2) whether there is an optimal group size. If such an optimal group size exists, (3) how would that size depend on the availability of food and associated costs such as distance to the food, and (4) how does variation in group size affect the group's effectiveness when foraging?

The foraging model we consider utilizes "central place foraging," where individuals must return to a central site (i.e. a nest), while food is localized in identical "patches" away from the central site (see Charnov's Marginal Value Theorem [1]). We focus on finding the optimal time to remain in a patch and the optimal group size with which to forage in order to maximize an individual's rate of energy gain.

It should be noted that not all animals forage in a way which optimizes the rate of energy gain. Alternate foraging "currencies" include efficiency [8], net rate of energy gain, and net energy gain [2]. We consider the classical Marginal Value Theorem (optimizing the rate of energy gain), modified by group size - this is a simplification of natural behaviour that leads to very tractable analysis.

We define the rate of energy gain in a group of size N as the total energy gained over the time taken to gain that energy,

$$R(N, t) = \frac{f(N, t)}{t + \tau}, \quad (1)$$

where t is the patch residence time, $f(N, t)$ is the energy gained by a forager during time t spent in a patch, and τ is the amount of time a single individual spends travelling to/from the patch.

We consider a simple saturating energy gain function $f(N, t)$,

$$f(N, t) = \frac{K_{max}(N)t}{k(N) + t}. \quad (2)$$

Here, K_{max} is the saturation level (the total amount of food a single individual is able to extract from a patch), while k corresponds to the time at which half of the maximum energy gain occurs:

$f(k) = K_{max}/2$. It is then easy to solve for the optimal foraging time, to get $t^* = \sqrt{k(N)\tau}$. We can verify through elementary calculus that such a t^* is in fact a maximum.

We assume that both the individual's share of the resource and the time taken to find food decrease with group size N , leading us to consider $K_{max}(N) = B \exp\left(\frac{-N}{b}\right)$ and $k(N) = C \exp\left(\frac{-N}{c}\right)$. We eliminate some constants through rescaling, setting $a = b/c$ and $A = C$ for convenience of notation. These equations can then be substituted back into Eqn. (2). The constant A corresponds to how quickly animals can initially find food when foraging alone, as $k(0) = A =$ time to find half the available food. When A is very small, an optimum occurs at negative, i.e. nonbiological values of N^* ; this corresponds to the case where foraging alone is more beneficial than foraging in a group.

We can now solve for the optimal group size ($R_N(N, t^*) = 0$) at the optimal foraging time t^* , to find that $N^* = -a \ln\left(\frac{a^2\tau}{A(a-1)^2}\right)$. This is only a biologically relevant maximum if $0 < a < 1$.

This same analysis can be applied to various currencies which a forager may seek to maximize. Notably, the currencies net rate of energy gain and efficiency result in nearly identical optimal patch residence times t^* and optimal group sizes N^* .

We asked whether specific functional forms of $K_{max}(N)$ and $k(N)$ affected our conclusions. To check this, we considered a variant of the model with power functions in place of exponentials, and came to the same general conclusions.

In response to the first question we posed, we found that group foraging is beneficial if the benefit associated with finding food more quickly in a group outweighs the cost of sharing food with other group members. We found an expression describing the optimal group size N^* , as we set out to do in our second question. Regarding question (3), we found that the optimal patch residence time and optimal group size depend on the parameters τ , the travel time, $A = k(0)$, the time required for a single individual to consume half the available energy in the patch, and a , the ratio of the two group sizes b and c . 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 A is large (i.e. if food is hard to attain), larger group sizes are optimal. We also found that $0 < a < 1$ in order to support group foraging. As $a = b/c$, this means that group foraging only has the possibility to be beneficial if $b < c$: b , the group size required to decrease K_{max} (the total food available per individual) by a factor of $1/e$ must be less than c , the group size required to decrease k (the time required for a single individual to find half the available food) by a factor of $1/e$. The largest optimal group sizes occur when a is neither very close to 0 nor 1. Lastly, we asked how group sizes slightly bigger or smaller than the optimal group size affect the groups foraging effectiveness, as in Fig 1. If a or τ are small, optimal group sizes produce a high rate of energy gain, but slight variation in group size results in considerably lower rates of energy gain. In some situations however, small differences in group size don't change the rate of energy gain by very much, such as when a and τ are large. As such, it is of less importance that animals forage with the exact optimal number of individuals in order to attain a high rate of energy gain. However, we conclude that, depending on the environment, foraging in a group of optimal size can drastically increase an individual's rate of energy gain in comparison to foraging alone or even in groups of non-optimal size.

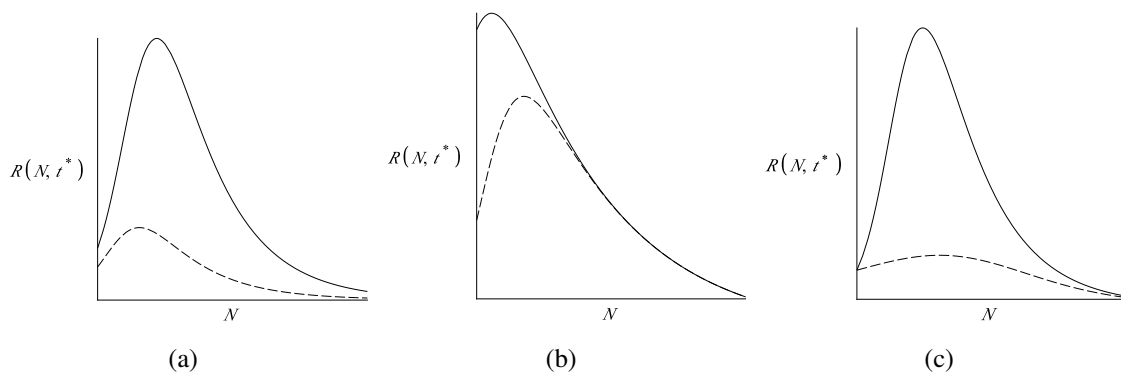


Figure 1: Rate of energy gain $R(N, t^*)$ plotted with respect to group size with different values of τ , A , and a . Variance in group size N can have little to drastic effects on energy gain, depending on these parameters. (a) $\tau = 1$ (solid), $\tau = 5$ (dashed). (b) $A = 1/4$ (solid), $A = 5$ (dashed). (c) $a = 0.2$ (solid), $a = 0.6$ (dashed).

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