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PO Box 117
221 00 Lund
+46 46-222 00 00

Does information sharing promote group foraging?

Emma Sernland^{1*}, Ola Olsson² and Noël M. A. Holmgren¹

¹Department of Natural Sciences, University of Skövde, PO Box 408, SE-541 28 Skövde, Sweden

²Department of Animal Ecology, Ecology building, Lund University, SE-223 62 Lund, Sweden

Individuals may join groups for several reasons, one of which is the possibility of sharing information about the quality of a foraging area. Sharing information in a patch-foraging scenario gives each group member an opportunity to make a more accurate estimate of the quality of the patch. In this paper we present a mathematical model in which we study the effect of group size on patch-leaving policy and *per capita* intake rate. In the model, group members share information equally in a random search for food. Food is distributed in patches according to a negative binomial distribution. A prediction from our model is that, the larger the group, the earlier each group member should leave the current patch. We also find that the benefit from enhanced exchange of information does not exceed the cost of sharing food with group members. The *per capita* intake rate decreases as the group size increases. Therefore, animals should only form groups when other factors outweigh the costs, which is easiest to achieve when the travelling time is short.

Keywords: Bayesian forager; public information; marginal value theorem; stochastic dynamic programming

1. INTRODUCTION

Why do some animals live in groups? Among the suggested reasons are that individuals in groups can avoid predators more effectively by sharing the time expended on vigilance, i.e. watching out for predators (De Ruiter 1986; Broom & Ruxton 1998). Individuals in groups can also avoid predation to a larger extent as it is harder for a predator to follow and catch one individual in a group than a lone individual (Hamilton 1971; Neill & Cullen 1974; Kenward 1978). Animals foraging in groups can increase the intake rate of food by increasing the diversity of food items, either through learning to eat new food types or through finding new foraging areas by following other group members (Giraldeau 1984). The cost of locomotion can be reduced by moving close to others (Weihs 1973; Gould & Heppner 1974) and the loss of water and warmth can be reduced by staying close together (Mertens 1969). Other individuals can also be of great help while sharing work at the nest, such as ants working in teams (Anderson & Franks 2001).

Another reason why individuals join groups is that it gives each individual the opportunity to use public information—information from other individuals in a group (for a review see Valone & Templeton (2002)). According to the information-centre hypothesis, individuals share information on where food is located (Ward & Zahavi 1973; Brown 1986; Elgar & Harvey 1987; Sonnerud *et al.* 2001). In a patch-foraging scenario (e.g. Charnov 1976), groups can find patches quicker than lone individuals (Clark & Mangel 1984). However, patches may be known to all individuals in an area, whereas the patch quality is unknown (Valone 1989). In this case, individuals can use public information to assess patch quality during ongoing foraging and decide when to leave the current patch for

the next (e.g. Valone 1989; Templeton & Giraldeau 1995a,b; Smith *et al.* 1999).

Food in nature may be distributed in patches. The empty space between patches results in a cost of time to travel between patches. Often food occurs as discrete items within a patch (e.g. Iwasa *et al.* 1981). In a given area of food patches, the number of food items in patches may follow a given distribution. A Bayesian forager (Green 1980) knows this distribution (i.e. has prior information), but the content of a specific patch is unknown. It is likely that this distribution is clumped (e.g. has a negative binomial distribution), which means that there are few patches with large numbers of prey and many patches with low numbers of prey.

On the basis of the argument that public information improves patch quality assessment (Clark & Mangel 1984; Valone 1989), we address the question if information exchange alone provides enough benefits that it would promote group foraging. Potentially, individuals may be able to exploit the positive foraging benefit of information (O. Olsson and J. S. Brown, unpublished data). We present a model for Bayesian group foragers in which individuals are assumed to be equal in all respects, possess information of equal value and share the information equally. We investigate the case in which each individual in the group shares all the information gathered by all the group members.

2. MATERIAL AND METHODS

Iwasa *et al.* (1981) showed that knowing the number of prey found and the patch searching time is sufficient information to estimate the prey content of a patch (under the given premises). The optimal Bayesian forager follows a policy of when to leave a patch that is given as a set of stopping points $\{(0, z_0), (1, z_1), \dots, (k, z_k)\}$, i.e. the forager should leave if it has spent z_n time and found n ($n = 0, \dots, k$) food items. The forager can maximize its intake rate (e.g. Green 1988), but the policy is similar

* Author for correspondence (emma.sernland@inv.his.se).

for a Bayesian forager maximizing its survival rate: it aims for the intake rate that maximizes its survival (Olsson & Holmgren 1998).

In the model we assume that the forager is searching randomly (for systematic search see Green (1980)) and is maximizing food intake rate. We solve the optimal policy for a Bayesian group forager by using stochastic dynamic programming (Houston *et al.* 1988; Houston & McNamara 1999; Clark & Mangel 2000). This is a backward iterative algorithm that finds the best state-dependent behaviour. We use two state variables—the search time (z) and the number of food items found (n). They represent the forager's state of information of the current patch. The forager has two state-dependent behavioural options: (i) to stay and continue searching for food in the current patch; or (ii) to leave for a new patch. The dynamic programming equations link gross intake of food, $G(n, z, t)$, and gross time, $T(n, z, t)$, from one step within an iteration to the next for the behavioural options:

$$\text{Search} \left\{ \begin{aligned} G(n, z, t) &= \sum_{k=0}^{k_{\max}} P(k, n, z) (G(n+k, z+1, t+1) + k) \\ T(n, z, t) &= \sum_{k=0}^{k_{\max}} P(k, n, z) (T(n+k, z+1, t+1) + 1) \end{aligned} \right\}$$

and

$$\text{Leave} \left\{ \begin{aligned} G(n, z, t) &= \sum_{k=0}^{k_{\max}} P(k, 0, 0) (G(k, 1, t+1) + k) \\ T(n, z, t) &= \tau + \sum_{k=0}^{k_{\max}} P(k, 0, 0) (T(k, 1, t+1) + 1) \end{aligned} \right\}. \quad (2.1)$$

As the iteration is backwards, the right-hand side of equations (2.1) (i.e. at $t+1$) are known. At the first iteration, G and T on the right-hand side are zero for all values of n and z (the terminal reward). As the iteration proceeds backwards, G and T increase. $G(t)$ is computed by adding k food items to the expected gross intake at $t+1$ with its state updated accordingly: $G(n+k, z+1, t+1)$ when the forager remains searching, and $G(k, 1, t+1)$ when the forager leaves for a new patch. The probability that the forager finds k food items, given n items already found during z search time, $P(k, n, z)$, is taken into account (see Olsson & Holmgren (1998) for computation of P). $T(t)$ is computed analogously, but the travelling time between patches (τ) is added when the forager leaves the patch. When the forager leaves a patch, its state variables are reset to zero. The intake rate for each behavioural option is calculated by taking the gross intake over gross time (G/T). The behavioural option that gives the highest intake rate is chosen at every iteration, and for all combinations of state variables. The process is iterated until the leaving policy is constant for 20 successive iterations. The ratio G/T approaches the long-term intake rate as t moves far away from the time horizon. The long-term intake rate that the stochastic dynamic programming algorithm yields (G/T) is influenced by the terminal reward. For an individual applying the optimal policy, we therefore calculate the long-term intake rate as

$$R = E(n) / (E(z) + \tau), \quad (2.2)$$

where the expected number of food items to be found in a patch until the forager leaves is

$$E(n) = \sum_n \sum_x n L(n, z_n | x) Q(x) \quad (2.3)$$

and the expected patch residence time is

$$E(z) = \sum_n \sum_x z_n L(n, z_n | x) Q(x). \quad (2.4)$$

$L(n, z_n | x)$ is the probability that a forager leaves at the stopping point $\{n, z_n\}$, given that there are x items in the patch from the beginning (see eqn (2-3) in Olsson & Holmgren (2000)). $Q(x)$ is the probability of the patch containing x food items, calculated from the negative binomial distribution of patch content given.

The single individual model has four parameters: the forager's search efficiency (v); travelling time; and the mean (m) and variance (var) of the negative binomial distribution of patch contents. The single individual model is modified by incorporating group size, N , into a group foraging model. The search efficiency is multiplied by N , and the resulting intake rate from the obtained policy is divided by N to get the *per capita* intake rate. All individuals are equal in this model.

We have chosen parameter values with the aim of covering a wide spectrum of foraging conditions faced by animals in the wild (table 1). Even though more extreme prey density distributions can be conceived, they become technically difficult to handle. The present range should suffice for the purpose of generating general results.

3. RESULTS

Leaving policies are convex functions of the number of prey taken over the search time (figure 1). A minimum time is always spent in the patch, indicated by the fact that each policy intersects with the abscissa. The resulting policies are arranged with respect to group size: the larger the number of individuals in the group, the shorter the residence time for each specific number of prey found (in figure 1, from left to right the policies are ordered with decreasing group size, $N = 20, 10, 5, 2, 1$). Hence, the larger the group, the less time each group member spends in the patch, as the patches are depleted faster with increasing group size. The qualitative results are common for all parameter combinations investigated.

The optimal group size for intake rate maximizers is investigated by plotting the *per capita* intake rate against group size ($n = 1, 2, 5, 10, 20$). The intake rates decrease with increasing group sizes for all parameter combinations investigated (figure 2). Hence, the forager gets the maximum intake rate when foraging alone. The effect of group size on intake rate is least when the travelling time is short (figure 2a,c), especially in combination with low search efficiency (figure 2a). In this case, the travelling time is negligible: at any time, the foraging individuals can go on to unharvested patches without paying any significant cost in terms of time. The situation approximates a systematic search in a single, unlimited patch.

4. DISCUSSION

Our results suggest that the benefit from information sharing among Bayesian foragers is insufficient to outweigh the cost due only to exploitative competition (see also Rita & Ranta 1998). There are two explanations for this result, as follows.

- (i) The time cost for travelling between patches remains constant for each individual. Within patches a group of N foragers can sample the same area (gain the

Table 1. The parameter settings used in the calculations of the optimal policies.
(All combinations of high and low values were analysed (16 cases).)

	search efficiency	travelling time	mean prey density	variance
high	1.0	2880	10	mean \cdot 50
low	0.008	0.0167	0.01	mean \cdot 1.1

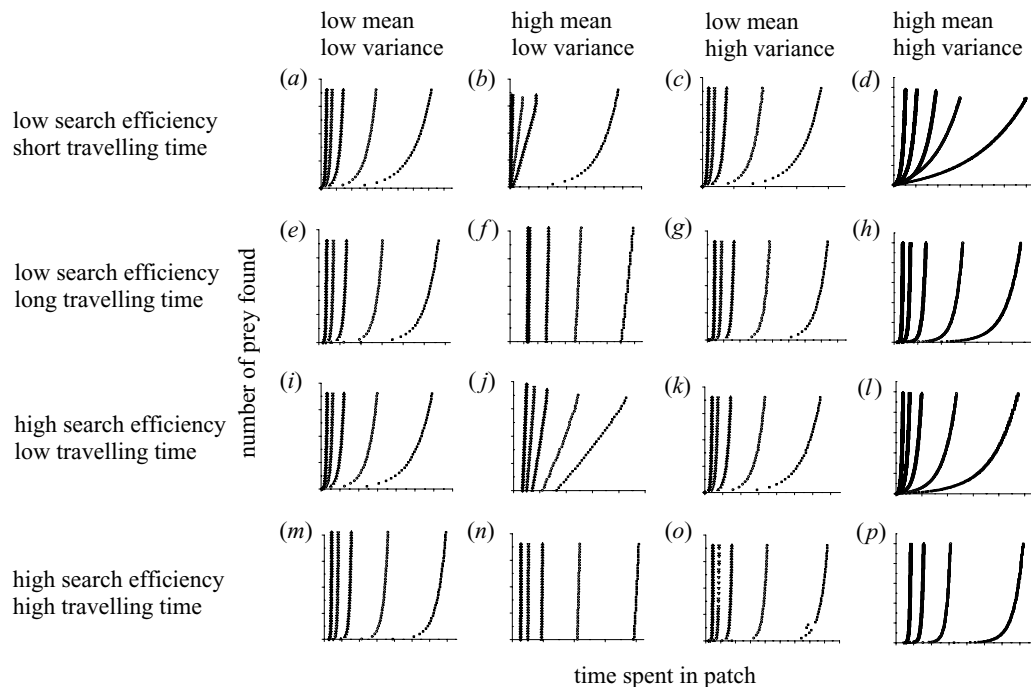


Figure 1. Leaving policies. The graphs illustrate leaving policies for groups of (from left to right) 20, 10, 5, 2 and 1 individuals, except for (p) where the case of one individual is out of the scale range. Each point is equivalent to an optimal residence time in the patch. In each case the individual leaves the patch earlier as the group size increases.

same amount of information) in $1/N$ of the time needed by a solitary forager. As a consequence, average patch residence time is reduced. The travelling time, however, remains unchanged in absolute terms—each individual has to spend the same time travelling between any two patches regardless of group size. As group size increases, the individuals will spend less time in each patch, but will visit more patches, and hence will spend more of their total time travelling. A large group of foragers will therefore in essence be caught in a perpetual skipping around the world, each gaining heaps of information but little food. Consequently, the reduction in gain rate with group size is least when the travelling time is short (figure 2*a,b*). If foragers are instead assumed to search for patches, our result with a decreasing intake rate with increasing group size may no longer apply. It has been shown that if the travelling time decreases proportionally with group size, intake rate will be independent of group size (Clark & Mangel 1986). It is worth noting, though, that from our results we cannot tell whether this also means that information is likely to be more valuable when travelling time is short. We can only conclude that even in this situation the scenario remains the same: information is insufficient to outweigh the costs owing to exploitative competition. Gain rate still

decreases with increasing group size even though the magnitude of the decrease is less than in cases with longer travelling times.

- (ii) The value of additional sampling by an extra group member decreases with group size. This effect is known from basic statistics: the reliability of the estimate of a population mean improves less for a given additional sample as the sample size increases.

There are reasons to believe that our general result is robust under the assumptions given. The limits of a large parameter space, which are likely to apply to natural situations, have been investigated, yielding qualitatively consistent results. Clumped distributions, which have been used in our analyses, are common in nature (Pielou 1977; Olsson *et al.* 1999). The other discrete statistical distributions such as Poisson and binomial distributions are more 'even' and the benefit of information is less, or even absent (O. Olsson and J. S. Brown, unpublished data). Therefore, information sharing is not likely to promote grouping within these statistical distributions either. An analytical solution to a simplified environment with only two patch types, patches with a fixed number of food items and empty patches, is presented by Clark & Mangel (1986). They also found that intake rate was decreased with group size. In a more complex environment with a distribution of patch sizes, the intake rate of group for-

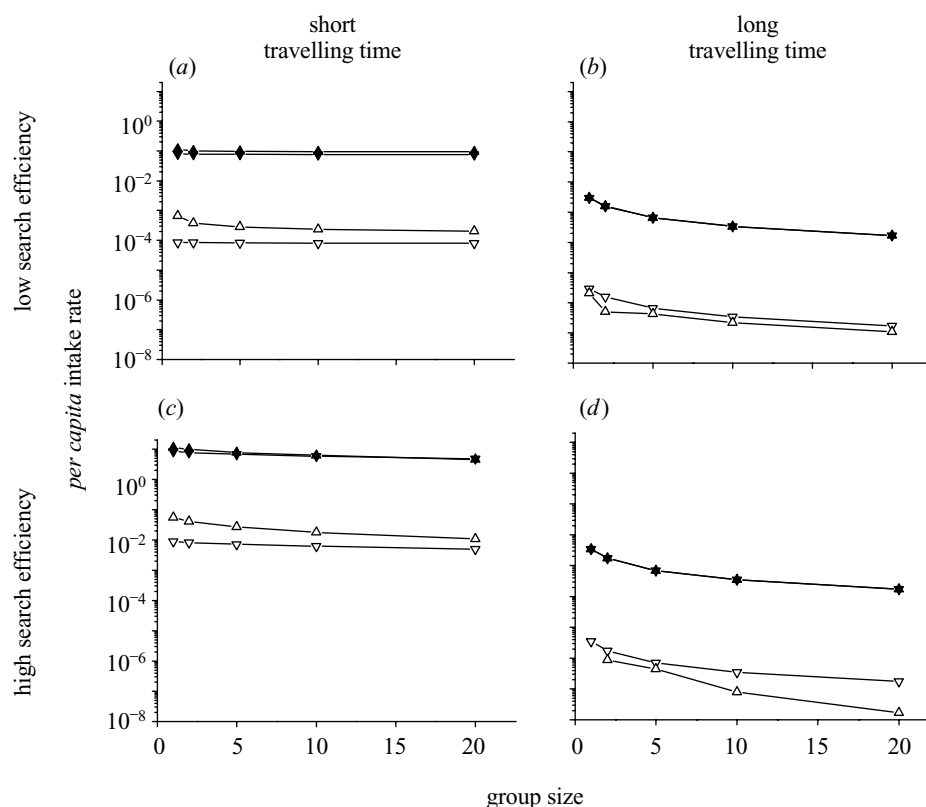


Figure 2. Intake rates. The graphs illustrate the intake rates for groups of 1, 2, 5, 10 and 20 individuals. White symbols, low mean prey density; black symbols, high mean prey density; upside-down triangles, low variance; triangles, high variance. For each case, the intake rate per individual declines as the group size increases.

agers has no analytical solution (e.g. Green 1988; Olsson & Holmgren 1998).

According to our model each individual receives a lower intake rate of food as the size of the foraging group increases (figure 2). Livoreil & Giraldeau (1997) found that spice finches (*Lonchura punctulata*) foraging in groups ate fewer seeds per unit time than birds foraging alone. Pitcher *et al.* (1982) found similar results in their studies on goldfish (*Carassius auratus*) and minnows (*Phoxinus phoxinus*), in which the intake rate of food per individual decreased as the group size increased. Livoreil & Giraldeau (1997) found results similar to ours also regarding patch-leaving decisions (figure 1). They found that spice finches foraging in groups left each patch earlier as the group size increased. When the patches are depleted the prey density declines faster as the number of foraging individuals increases.

It is generally acknowledged that there are informational benefits from grouping (Clark & Mangel 1986). Empirical studies indicate that individuals use public information and that it improves foraging. Pitcher *et al.* (1982) conducted studies on both goldfish and minnows and found that the larger the number of fish in a shoal, the shorter the time until a test individual found its first food object. This was suggested to be a result of fish observing other group members finding food and thereby themselves finding the location of food faster. Watching other individuals foraging as a way of transmitting foraging information has also been noticed in studies on birds in which a change of body posture indicates whether a foraging individual is looking for producing or scrounging opportunities

(Coolen *et al.* 2001). By observing foraging conspecifics, i.e. using public information, an individual can increase the accuracy of its estimate of current patch quality. The accuracy improves as the number of foraging individuals in the group increases. In studies on cliff swallows (*Hirundo pyrrhonota*) by Brown (1988), individual variance in foraging success decreased for birds foraging in groups compared with birds foraging alone. This may be interpreted as individuals being able to make a more accurate assessment of patch quality as the group size increased since each individual has access to more information.

We have shown consistent results in our theoretical analysis of the role of information sharing in explaining animal group formation: incompletely informed animals cannot increase their intake rate by increasing group size in a patch-foraging scenario. We also see in our results that it is when the travelling time is negligible that the negative effect of increased group size is smallest. If the travelling time becomes so short as to be insignificant, the situation approximates a systematic search in a single unlimited patch. With a systematic search, only unharvested areas are searched for food, and the cost of sharing food with group members disappears. Open land grazers live under these conditions when other factors (not included in our model) that promote group foraging outweigh the costs of increased group size. One example of such a factor is shared vigilance time by group members and the increased probability of detecting a predator (for a review see Krause & Ruxton (2002)). This may at least partly explain why many open land grazers forage in groups.

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