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Public information and patch estimation for group foragers: a re-evaluation of patch-quitting strategies in a patchy environment

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Classical foraging theory states that animals feeding in a patchy environment can maximise their long term prey capture rates by quitting food patches when they have depleted prey to a certain threshold level. Theory suggests that social foragers may be better able to do this if all individuals in a group have access to the prey capture information of all other group members. This will allow all foragers to make a more accurate estimation of the patch quality over time and hence enable them to quit patches closer to the optimal prey threshold level. We develop a model to examine the foraging efficiency of three strategies that could be used by a cohesive foraging group to initiate quitting a patch, where foragers do not use such information, and compare these with a fourth strategy in which foragers use public information of all prey capture events made by the group. We carried out simulations in six different prey environments, in which we varied the mean number of prey per patch and the variance of prey number between patches. Groups sharing public information were able to consistently quit patches close to the optimal prey threshold level, and obtained constant prey capture rates, in groups of all sizes. In contrast all groups not sharing public information quit patches progressively earlier than the optimal prey threshold value, and experienced decreasing prey capture rates, as group size increased. This is more apparent as the variance in prey number between patches increases. Thus in a patchy environment, where uncertainty is high, although public information use does not increase the foraging efficiency of groups over that of a lone forager, it certainly offers benefits over groups which do not, and particularly where group size is large.

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Optimal foraging theory, mostly centred around Charnov's marginal value theorem (Charnov 1976), predicts how long an individual forager should remain feeding in isolated and depleting food patches, before quitting to move to the next patch, with the aim of maximising long term capture rates and thus fitness. Much work has been carried out in this field, and several models have been developed to explain foraging behaviour based upon this theorem. However, many animal species are known to live and feed in groups (Krause and Ruxton 2002) and although there are many theories which suggest benefits to aggregation (Krause and Ruxton 2002) few offer any direct benefits in terms of foraging. One theory which does so, suggests that animals feeding in groups may prevent a reduction in their prey capture rates by utilising prey capture information supplied by other group members (Clark and Mangel 1984, 1986, Valone 1989, 1993). This is generally termed public information use. Foraging groups deplete prey resources at a rate faster than for a lone forager. However, this means that

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information about the quality of a patch is also being obtained faster by the group. If all individuals are able to recognise when each other forager makes a prey capture, they should be able to make an accurate estimate of this decreasing patch quality, allowing them to quit patches close to the optimal threshold level.

Valone (1993) examined the effect of public information use in cohesive, socially foraging groups, in an environment in which food is distributed unevenly between a series of discrete patches. In such an environment, the distribution of prey between patches may be known to a forager, but since the number of prey in each patch may be quite variable, the exact number of prey in any patch is unknown. Foragers must therefore estimate the quality of each patch through sampling as they search for food, in order to decide when they should quit the patch and move to another. Iwasa et al. (1981) developed a formula which generates a good estimate of patch quality in such an environment for a lone forager, where only the distribution of prey between patches, the number of prey items caught in a patch, and the time spent searching in a patch, are known to the forager. Valone (1993) presented a group foraging model based on Iwasa et al.'s (1981) estimator equation. Groups remained tightly cohesive at all times, with all individuals forced to enter and leave patches simultaneously. However, within a patch foragers search randomly and independently of each other and often maintained different estimates of patch quality, according to their own individual prey capture success. Thus some conflict must occur between individuals in a group as to when they should leave a patch. Valone examined three different patch quitting strategies to dictate how such groups decide when to leave a patch. He compared the foraging efficiency of these with that of groups using public information of all prey capture events made by the group. Since all foragers acquire the same patch information in these groups, they will all share the same estimate of patch quality and so will want to leave the patch at the same time.

Valone showed that sharing public information does indeed benefit group foragers, in comparison to those groups which do not. Groups using public information were able to quit patches closer to the threshold quitting value, and experienced higher capture rates, than those using the other three patch quitting strategies, although they were never as successful as lone foragers. However, we believe that Valone's implementation of Iwasa et al.'s (1981) estimator is not entirely correct, causing inconsistencies in his model and thus making proper evaluation of his results more difficult. Here, we present an revised version of Valone's model and re-evaluate the assumptions made by public information theory.

Model description

The marginal value theorem (Charnov 1976) states that foragers should remain in a food patch until their instantaneous capture rate has fallen to the average capture rate they would expect to obtain over the environment as a whole – this is the marginal capture rate and should be equalised over all patches visited (Charnov 1976, Brown 1988). In groups, foragers using public information of all prey capture events should be better able to do this, since each forager will have more information of the patch quality at any time, so enabling them to generate a more accurate estimate of the true patch quality, and thus allowing them to quit patches closer to the marginal capture rate.

A deterministic model such as Charnov's (1976) is limited here in two ways, because it assumes that food is obtained by foragers continuously and that a forager automatically knows, at any point in time, the exact rate at which food is being found (Oaten 1977). Unfortunately, prey is rarely acquired at a continuous level by a forager, but is more often found stochastically, in discrete packages (i.e. a food item-a bird, a seed, or berry). So more realistically, a forager will need to know how many prey items it should leave in the patch when it quits, rather than a specific rate of capture. Foragers should therefore try to quit a patch when they have depleted it to a threshold number of remaining prey items-we call this the optimal value of C – which should be equalised over all patches visited, as would the marginal capture rate. This is the LOC, or left-over constant described by Green (1988). But in order to do this, foragers must know how many prey items remain in a patch at any time (Green 1988). Again, this seems an unrealistic assumption to make for most natural ecological situations. It seems far more likely that foragers will only have some idea or expectation of how prey is distributed throughout the environment, rather than absolute knowledge of the quality of food patches, and they will form an estimate based upon this prior expectation and their experience foraging in a patch. In this case the model suggested by Charnov (1976) does not always hold true (Green 1980, 1988, Olsson and Holmgren 1998). When there is uncertainty about patch quality it may be more valuable for a forager to spend a longer time searching in order to obtain more information about its true quality. However, providing a forager has prior knowledge of how the prey is distributed in its environment (i.e. it feeds there frequently, so has an expectation of the distribution of prey likely to be found in a patch), and compares its continued foraging success against this expectation, it can still produce a pretty good estimate of the true quality of a patch and hence when to leave it (Iwasa et al. 1981).

Prey distribution

Valone (1993) models a scenario where prey items are distributed between patches according to a negative binomial distribution in an attempt to mimic a patchy environment, with distribution parameters λ and α. A property of the negative binomial distribution is that the variance is higher than its mean, so that the actual number of prey in each patch may be highly variable and while many patches contain very few (or zero) prey items, a few patches will contain many prey. Valone defines the distribution parameters as $\lambda = 500$, and $\alpha = 0.3$, so the number of prey items in any patch before the foragers arrive on it (X) has a negative binomial distribution with a mean $\lambda\alpha = 150$ and variance $\lambda\alpha(1+\alpha) = 195$. However, attempting to use patch sampling to discriminate between patches is effective "if and only if the between-patch variance of prey abundance is sufficiently large" (Iwasa et al. 1981), and so here we expand on Valone's (1993) work by simulating several prey environments, to examine the effects of public information use under different levels of patch variation. Fig. 1 shows an example plot of a negative binomial distribution, for parameter values $\lambda = 6$, alpha $= 25$, in comparison to one using Valone's (1993) parameter values.

In our model the number of prey in each patch is found using the random number rejection technique (Evans et al. 1993), where α defines the probability of finding prey, and λ defines the number of attempts in which prey is not found until the xth success. We simulate foraging activity in six different prey environments, where we vary both the mean number of prey per patch, and the variance of prey between patches. We model two main prey environments, with a mean number of prey items per patch = 150 (small) and 250 (large). For each of these environments we model patches with three types of variance: small, medium and large (mean = 150: variance = 1650, 2400, 3900; mean = 250: variance = 2750, 5250, 8062.5).

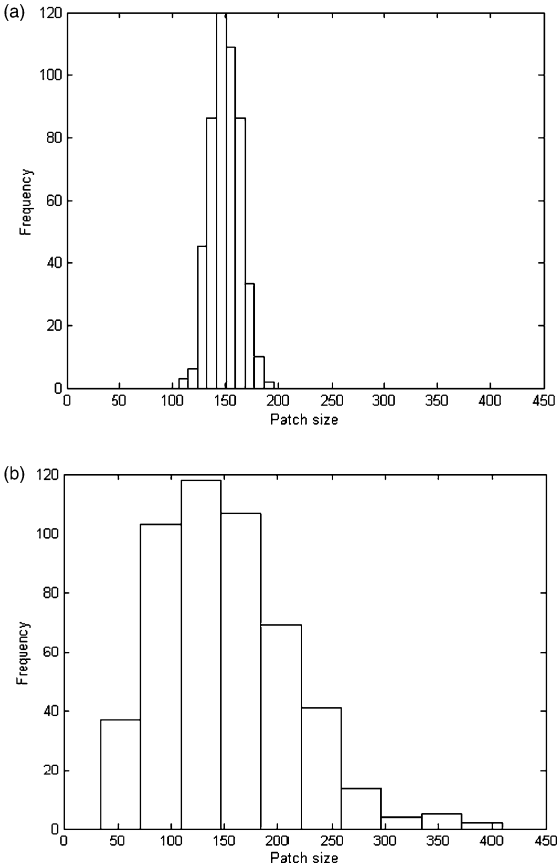

Fig. 1. Example plots showing the initial number of prey (X) occurring in a series of 500 patches, according to a negative binomial distribution, with the mean number of prey per patch = 150. (a) parameter values: $\lambda = 500$, $\alpha = 0.3$, variance = 195 (as suggested by Valone 1993). (b) parameter values $\lambda = 6$, $\alpha = 25$.

Inter-patch travel time

Since foragers can only feed within patches, they must travel between patches in order to feed, and thus incur a travel-time cost as they do so. This ultimately affects the length of stay in each patch. We assume inter-patch travel time (T) to be a function of the size of the group (N), so that as group size increases the time spent travelling between patches decreases proportionally:

$$T(N) = \left(\frac{T_1}{N}\right) \quad (1)$$

where T_1 = the inter-patch travel time for a lone individual. We follow Valone (1993) and Ruxton (1995b) and assume a value of $T_1 = 400$. A single forager thus takes 400 time units to travel between patches. Using this function, a group of two individuals takes half this time to find a new patch, so $T = 200$. A group of 3 individuals incurs only a third of this T_1, so $T = 133$. This is an ideal situation, and is probably unlikely to be true in nature. In a wild situation animals are likely to become less efficient at searching an area as group size increases, because the chance of two or more animals searching in the same place at one time increases, and search-overlap occurs (Ruxton 1995a, Ruxton and Glasbey 1995). However, this function between group size and search rate is a simple one to model, and is a suitable and convenient simplification for the simulations we are running here.

Searching for food

We assume that foragers have knowledge of the prey environment they are feeding in and have a prior expectation of the mean number of prey items ($\lambda\alpha$) when they enter a patch, and the variance between patches, but do not know the actual number of prey items existing on any one patch (X). Prey are hidden so foragers do not know whether they will find prey on each search attempt or not. Each food item has equal energetic value and can only be found whole, so a forager either finds and consumes a prey item or doesn't, and so scores either 1 or 0, respectively. Prey is not replaced once found and since foragers search randomly and independently of other foragers, prey decreases as it is exploited and the probability of finding a prey item decreases linearly with the number previously found.

Each forager searches a patch at a rate S_1; i.e. they make S_1 search attempts per unit time. Since patches initially contain X prey items, the probability of finding prey on each search attempt is X/patch size. Like Valone (1993), for convenience and simplicity we assume here that patches contain a maximum of 500 prey items. Although by definition patches described by a negative binomial distribution do not have a theoretical upper limit to their size, we cannot accurately calculate searching rates without ascribing such limits. Using the values of λ and α we have chosen, we can be confident that fewer than 1% of patches will contain more prey than this arbitrary limit. In trial simulations, replacing this value of 500 with 5000 did not lead to any differences in our results, but dramatically slowed simulation time.

All foragers in a group search the patch at the same rate, and thus a group of N foragers find prey items at a rate R(X), which is given by:

$$R(X) = \frac{XNS_1}{500} \tag{2}$$

Since finding prey is a Poisson process, the time taken to find a prey item can be found stochastically using the exponential distribution with a mean 1/R(X). All foragers are assumed to be equal in foraging ability, and so each prey item is found and is allocated to a random forager. Prey resources then decrease by one and the time taken to find the next prey item thus becomes: (R(X-1)). This departs from the models of Valone (1993) and Ruxton (1995b) because it effectively means that time is continuous in our model, rather than being counted in arbitrary time steps.

Patch estimation and patch quitting strategies

Iwasa et al. (1981) suggests that for a lone forager feeding in a patchy environment the best estimate (E) it can make of the remaining number of prey is a function of the time spent foraging on the patch (t), and the number of prey items taken in that time (n), and is described by the estimator equation:

$$E\,(n,t) = \frac{\lambda + n}{e^{At}\left(\frac{\alpha+1}{\alpha}\right) - 1} \tag{3}$$

where A = the searching rate (the fraction of the patch searched per unit time).

With public information use

In a situation where all foragers have access to public information of all prey capture events, each will have exactly the same knowledge as each other individual in the group. We can re-phrase the above estimator function to incorporate our definition of group patch searching rate:

$$A = \frac{NS_1}{500} \tag{4}$$

(where the N = the number of foragers in the group, S_1 = the search rate of one individual, and 500 = the assumed size of the patch). Equation 3 thus becomes

$$E_N(n,t) = \frac{\lambda + n}{\exp\frac{NS_1 t}{500}\left(\frac{\alpha+1}{\alpha}\right) - 1} \tag{5}$$

We call this strategy the totalinfo strategy.

Without public information use

In groups which do not have access to public information each individual does not know the true value of n. A specific individual, i, knows only how many prey items it has found itself (n_i), and so must use its own foraging success to produce an estimate of patch quality. It can do this by multiplying this number, n_i, by the number of individuals in the group, and so the estimator function in Eq. 3 becomes:

$$E_{i,N}(n,t) = \frac{\lambda + Nn_i}{\exp\left(\frac{NS_1 t}{500}\right)\left(\frac{\alpha+1}{\alpha}\right) - 1} \tag{6}$$

But since foraging is an inherently stochastic process, each individual's estimate is likely to be different from that of other individuals in the group, and there will be some disagreement over when to quit a patch. In order to maintain group cohesiveness, the group must employ rules to govern exactly when to leave the patch. We use two of the patch quitting strategies suggested by Valone (1993) which may be used by non information sharing groups to achieve this:

1) first – the group leave with the first individual whose estimate, E, falls below the threshold prey value, C.

2) leader – the group leave when the E of one particular individual, for example the most dominant member of the group, falls below the prey threshold, C.

We also use a third strategy suggested in a similar study by Ruxton (1995b):

3) paired – the group leave when the estimate of any two individuals falls below the prey threshold, C.

However, despite the convincing results obtained by Valone (1993), we believe that this model contains an inconsistency in the use of Iwasa et al.'s (1981) estimator function. Within patches, each forager estimates the number of prey items that remain using this estimator, but the method Valone (1993) uses to calculate the rate at which foragers find prey (R(X)) conflicts with an important assumption of this function. The estimator remains true only if prey resources in a patch decrease in proportion with the number taken by foragers: $R(X) = NS_1(X/P)$, where $N =$ the number of individuals in a group, $S_1 =$ the search rate of one individual, $X =$ the number of prey remaining in a patch and $P =$ the size of the patch (the maximum number of prey a patch can contain). Valone (1993) breaks this assumption by describing the rate at which foragers find prey, R(X), with a sigmoid curve (see his Fig. 1). This implies that the probability of finding the next prey item does not decrease linearly with the number of prey already found (n), and thus the estimator equation cannot be used correctly as the two statements contradict with each other. No explanation is given in his paper as to how he obtained this function.

The aim of this paper is to re-examine the foraging efficiency of groups using the above three non information sharing strategies (first, leader and paired) in comparison with groups which use public information of prey capture events occurring in a patch (totalinfo). We expand on the work of Valone's (1993), and Ruxton (1995b), by increasing the range of prey environments examined. We also consider a larger range of group sizes.

Optimal values of C

Here, we assume that foragers have evolved to use the optimal value of C in the environment in which they feed. Since this value is dependant upon the average travel time between patches, it also seems likely that this value will vary depending upon the size of the group, and the efficiency with which foragers utilise their search time in a patch. Other models, (Valone 1993, Ruxton 1995b) adopt patch quitting thresholds which seem arbitrary and may not necessarily be optimal. We simulate foraging behaviour over a series of patches, quitting at each possible value of C. We repeated this for a range of group sizes (1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 20, 50, 100, 500, 1000) using each of the patch-quitting strategies (first, leader, paired and totalinfo) described above, in each of the six prey environments described above. Mean prey capture rates were recorded for foragers quitting patches at each of these C values.

Each simulation was repeated 500 times and the mean capture rate for groups quitting at each value of C was calculated in each trial. When plotted, the resulting curves show the success of foragers leaving patches at each quitting value of C. The optimal value C was the value which produced the highest capture rate in each simulation (i.e. the peak of the curve). Figure 2 shows the optimal values of C obtained.

Results

Finding the optimal value of C – with public information use

In all simulations the optimal value of C for groups using public information remained constant over all group sizes (Fig. 2, only results for patch mean $=250$ are shown). As group size increases there is no effect on the optimal point at which foragers should quit a patch. Groups sharing public information effectively act as one super-individual: they deplete a patch (on average) at a rate directly proportional to the size of the group, but since inter-patch travel time is inversely proportional to the size of the group these two factors cancel each other out. Considering this, we should not expect the optimal value of C to change with increasing group size.

In patches with a prey mean of 250 the optimal value of C is higher than those with a prey mean of 150. In patches containing a mean of 150 prey items foragers should quit when approximately 50 prey remain (results not shown), while in patches containing a mean number of 250 prey, they should quit patches when approximately 90 prey remain. This finding agrees with classical optimal foraging theory since foragers should harvest fewer prey from patches when feeding in a richer environment.

In the same way, foragers should harvest patches to a lower level when the travel time between patches is longer, since increasing inter-patch travel time decreases the richness of the environment by decreasing prey density. Similarly, larger groups should have to harvest patches to a lower level, because this has the same effect on each individual as decreasing prey density, although indirectly. However, in these simulations we are not merely increasing the size of the group but also simultaneously decreasing the value of travel time per individual. So, although a group of N individuals receive only 1/Nth of the available prey resources, they also only incur 1/Nth of the travel cost. As explained above, the two cancel each other out and so we should not expect to

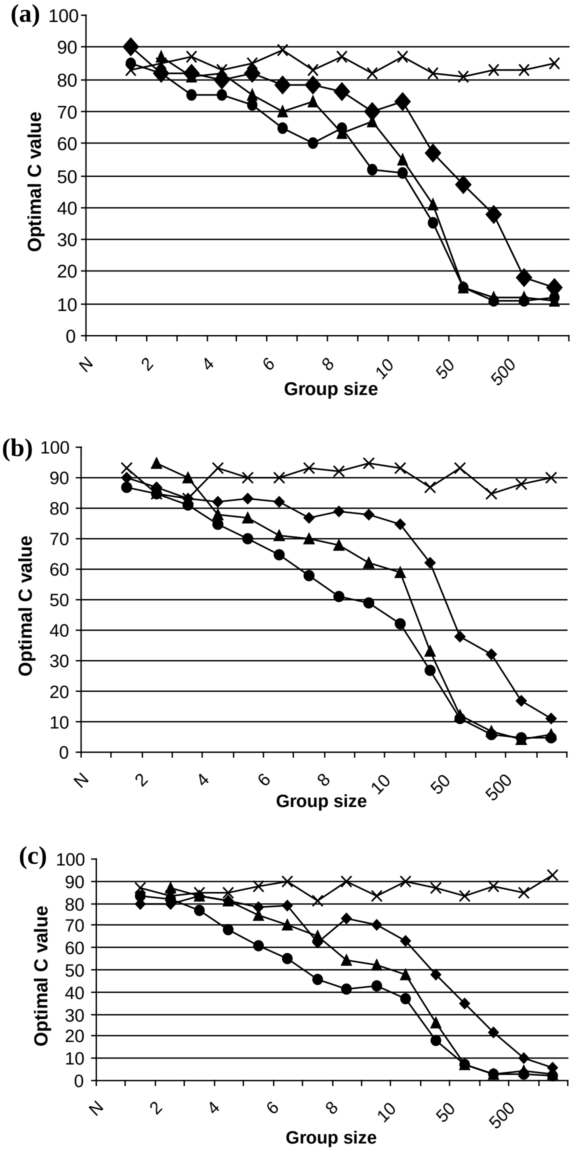

Fig. 2. Optimal values of C obtained for prey distribution environments with a mean = 250 prey items per patch (a) variance = 2750; (b) variance = 5250; (c) variance = 8062.5. Legend: -x–x- = totalinfo; -●–●- = first; -◆–◆- = leader; -▲–▲- = paired.

see any change in optimal C values with changing group size, since the relative prey density remains constant.

Finding the optimal value of C – without public information use

In all three non information sharing strategies (first, leader, paired) the optimal value of C decreases with increasing group size (Fig. 2, only results for patch mean = 250 are shown). Thus, in order to behave optimally, larger groups using these strategies must harvest all patches to a lower level of prey before quitting. This is important because it immediately suggests that groups using these strategies are not as efficient as groups which share public information, and are incurring some cost as a result. Classical foraging theory states that foragers should deplete patches to a lower level when the travel cost between patches is higher, but since travel time does not differ here between strategies, this cost must be originating elsewhere. The only difference between each group in these simulations is the strategy employed to quit patches, and so this cost is likely to be arising because of the constraints placed on groups by the particular patch quitting strategy being used. For example, in the first strategy the group will leave patches with the first individual who estimates the patch to be below the threshold level. Since the first individual will by definition be the one experiencing the worst foraging success, it seems likely that the group will probably leave most patches too early, thus not using them to their full potential. Groups using this strategy must therefore harvest each patch to a lower level in order to make up this cost, just as they should if travelling further between patches. So, the extent to which a forager acts optimally in non public information sharing groups will depend upon the constraints placed upon them by the patch quitting strategy employed by the group.

This explanation is demonstrated further in Fig. 3. We ran an extra simulation using the first strategy, but made them quit patches at the optimal C values obtained for the totalinfo strategy, which are higher and remain constant. We assume that these optimal C values are perfectly optimal, i.e. the'best' values that could possibly be used for a given prey distribution (it is intuitive that the values obtained by totalinfo groups would be the best

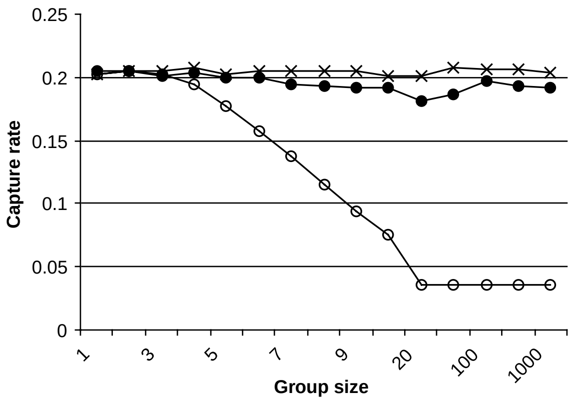

Fig. 3. Prey capture rates of first strategy using optimal C values obtained by groups using the first strategy (–●–), and'perfect optimal' C values obtained for totalinfo strategy (–○–), and also totalinfo groups using'perfect' optimal C values obtained by total info strategy (–x–). Mean = 250, variance = 8062.5.

possible, because of the nature of the strategy). Figure 3 shows that when the groups using the first strategy aim to quit patches at the'perfect' optimal value of C, they actually do far worse than if they use the optimal C values obtained for the first strategy. Forcing them to quit patches at this value does not allow them to make up the cost incurred as a consequence of being inefficient. The cost that non public information sharing groups incur because of the constraints placed on them by the patch quitting strategy cannot possibly be made up if they try to behave'perfectly'. The best they can do is try to make up the cost as best they can, i.e. by adjusting their threshold value of C and depleting patches to a lower level before quitting.

Ruxton (1995b) suggested that groups quitting patches when two individuals want to leave (paired strategy) will fare better than those using the first strategy because the likelihood of quitting due to random bad luck will be reduced – two individuals must both be experiencing bad luck at the same time. The patch is more likely to genuinely be poor. Optimal values of C were also consistently higher for groups using the paired strategy (Fig. 2) than those using the first strategy, in all expect the highest group sizes, thus supporting Ruxton's (1995b) hypothesis. In groups containing 100, 500, 1000 individuals, as for the first strategy, the optimal value of C was close to zero, indicating that the foragers should try to remain until the patch is almost exhausted of prey before quitting. Thus in both the first and paired strategies, foraging in large groups is very inefficient, incurring a heavy cost and therefore requiring that they harvest each patch to a lower prey level before quitting.

Results for the leader strategy show that optimal C values are higher than those of both first and paired strategies, for all group sizes. Hence, groups using the leader strategy are more efficient foragers than both first and paired groups, and suffer a lower cost as a result. The leader strategy relies on the estimate of one specific individual to decide when to quit patches, and thus these groups will not always leave patches too early. Sometimes the leader individual will be the first to want to leave a patch, but it will also sometimes be the last, and all other ranks in between. On average then, the leader individual will neither want to quit patches too early, nor too late, but when it is best to do so.

Foraging efficiency – patch quitting in cohesive groups

We used the optimal values of C obtained in the above simulations as threshold prey patch quitting values to assess the foraging efficiency of the four strategies described above. We simulated foraging activity, in which groups using each of the above strategies visited a series of 500 patches with the aim of quitting at the corresponding optimal C value, in order to maximise foraging efficiency. Each simulation was repeated 2000 times. It has been shown previously (Green 1988, Olsson and Holmgren 1998) that for a negative binomial prey distribution a forager should not strictly quit patches when its estimate of patch quality has fallen to a constant threshold level, in order to maximise its long term prey capture rate. During early stages in a patch the forager should ignore low patch estimates, since there is a chance that this estimate will increase again after further searching. However, we do not expect that our simplification of using a constant patch quitting threshold of prey (optimal C) will qualitatively effect our results, and this simplification greatly reduces our already considerable computational requirements.

Patch estimation and quitting strategies

There are several ways in which foraging efficiency can be analysed. Prey capture rate is perhaps the most important here, since this is a direct measure of the amount of food eaten by a forager in a given time. Foragers with the highest capture rate are thus maximising the amount of food they consume. We calculate the total number of prey items which have been consumed by the group, divided by the total time spent foraging (including inter-patch travel time), and divide this by the number of individuals in the group, for each simulation. This gives us the feeding rate of each individual forager.

In order to maximise prey capture rates, foragers should try to quit patches when they have depleted the number of prey items remaining to the optimal value of C. We assess the ability of foragers to do this by subtracting optimal value of C from the value of C at which they actually quit a patch. The closer this difference is to 0, the better the foragers are able to quit patches at the optimal value of C. We calculate the mean difference between actual and optimal C over all patches in each simulation. However, considering this mean value on its own can be misleading, since foragers may be over- and under-utilising the patch by a great many number of prey items, while the mean would still indicate that they're quitting patches close to the optimal value of C. To counter this, we also look at the coefficient of variation of the quitting values of C over all patches visited in each simulation. This gives us the level of variation between the quitting values of C obtained by each group. A low coefficient of variation suggests that the group is consistently quitting patches close to a given value. Using both of these tools in combination offers a good measure of the ability of a group to quit patches at a value close to the optimal C, and how consistently they do this.

With public information use

Prey capture rates
In all simulations the capture rates of groups sharing public information remains constant for groups of all sizes (Fig. 4, only results for patch mean = 250 are shown). Increasing the variance in prey number between patches does not affect capture rates by group foragers sharing public information. However, by altering the patch mean capture rates do change. Where the mean prey number is 250 the prey capture rates are approximately 0.2, while for a mean of 150 the capture rates are 0.12, so decreasing as the patch mean decreases.

Quitting patches at optimal C
In all simulations the difference between the actual quitting value of C and the optimal value of C remains close to 0 for Totalinfo groups of all sizes (Fig. 5). Similarly, the coefficient of variation remained constant for all group sizes, in each simulation (Fig. 6). Thus, group foragers sharing public information are able to quit patches not only almost perfectly close to the optimal value of C, but they to do so consistently, despite any increase in the prey variance between patches and regardless of group size.

Without public information use

Prey capture rates
In both of the prey environments used here (patch mean = 150, 250) where the variance in prey number is low (variance = 1650, 2750 respectively), groups using the first strategy obtain capture rates similar to lone foragers, but this decreases slightly with increasing group sizes (Fig. 4). As variance between patches increases, however, capture rates decrease more markedly with increasing group size, suggesting that larger groups suffer lower foraging efficiency in comparison to smaller groups, and also groups sharing public information.

Interestingly, the lowest capture rates are not seen by the largest groups in any of these simulations. In groups of 100 individuals and over, these suddenly increase again. This is likely to be because in extremely large groups the number of prey taken in a given time increases in comparison to smaller groups, so the number of prey remaining is closer to the optimal value of C when groups leave. In this model an individual makes its estimate of patch quality by multiplying its own foraging success by the number of individuals in a group. As group size increases this becomes a more and more unrealistic assumption, but it is actually beneficial when the patch is being harvested so quickly because it acts as a kind of early warning system in large groups. Looking at the first strategy, in small groups this method of estimation often means that the groups quit patches too early. But in larger groups the patch becomes depleted much more quickly and the number of remaining prey is genuinely lower, so these groups no longer quit so early.

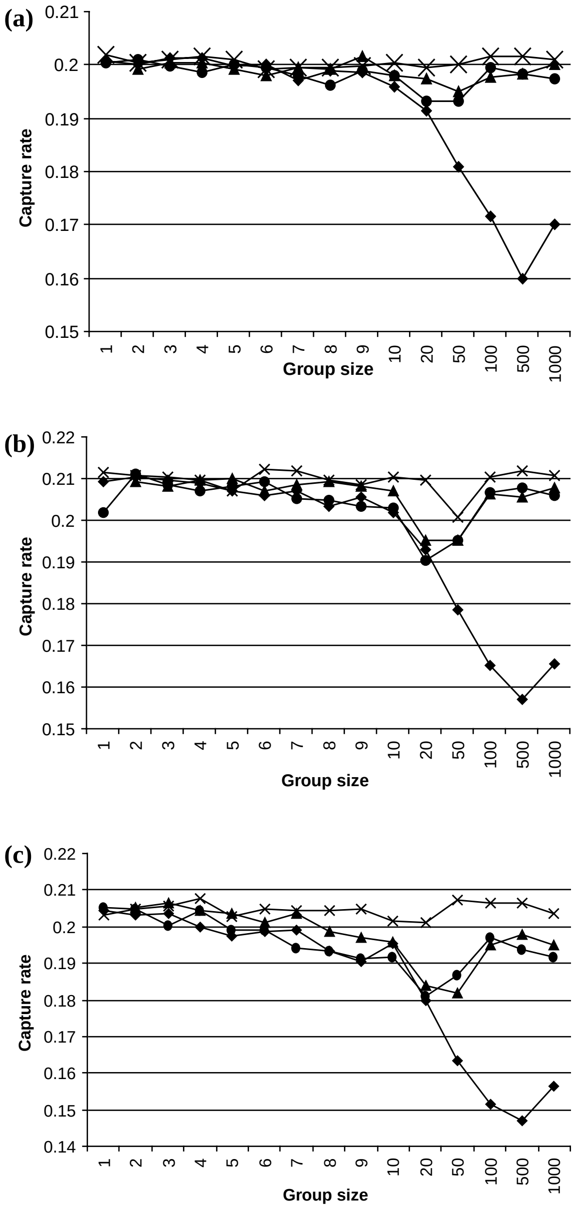

Fig. 4. Prey capture rates obtained by foraging groups using three patch quitting strategies and for groups sharing public information, in prey distribution environments with a mean = 250 prey items per patch: (a) variance = 2750; (b) variance = 5250; (c) variance = 8062.5. Legend: -x–x- = total info; -●–●- = first; -◆–◆- = leader; -▲–▲- = paired.

This trend is repeated almost exactly in groups using the paired strategy. In smaller groups there is some evidence supporting Ruxton's (1995b) theory that relying on the estimate of two individuals, will reduce the likelihood of quitting patches due to the bad luck of one individual, as the paired strategy shows slightly

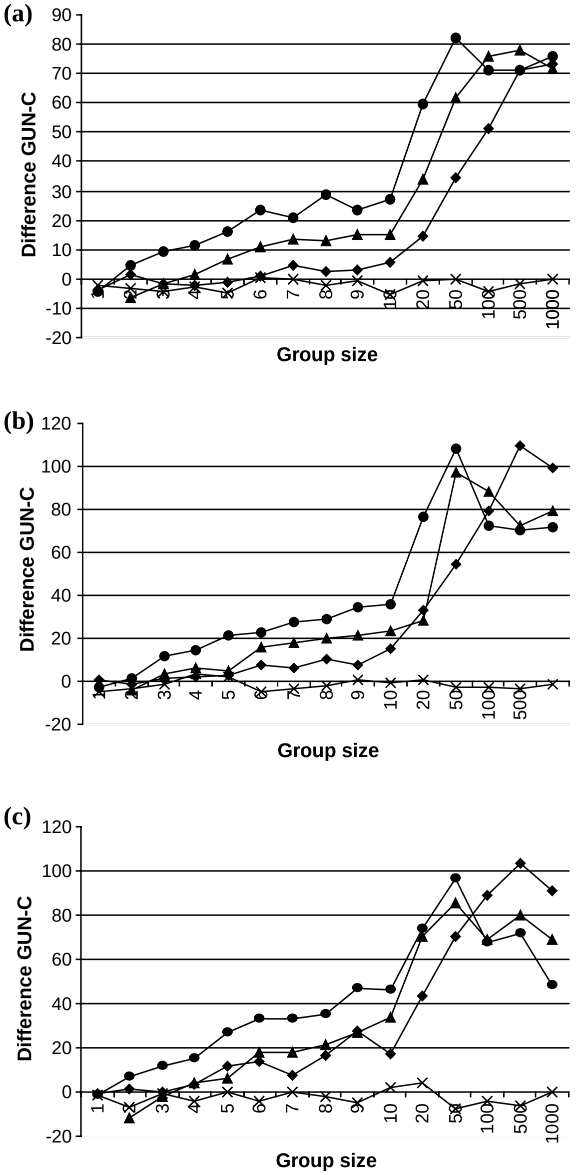

Fig. 5. Difference obtained by subtracting the optimal value of C from the actual quitting value of C, by foraging groups using three patch quitting strategies and for groups sharing public information, in prey distribution environment with a mean = 250 prey items per patch: (a) variance = 2750; (b) variance = 5250; (c) variance = 8062.5. Legend: -x–x- = total info; -●–●- = first; -◆–◆- = leader; -▲–▲- = paired.

higher prey capture rates than the first strategy (Fig. 4). But in larger groups again this advantage is lost because it prevents foragers quitting patches, when in fact it would be beneficial to do so.

For groups using the leader strategy, capture rates are not independent of group size, as theorised by Ruxton (1995b) but decline at a similar rate to those of first and paired strategy. But in contrast to these two, this decline continues as group size increases. Because the leader strategy relies on the estimate of one specific individual to initiate quitting a patch, rather than just any individual, there will be a tendency to remain feeding in patches which are poor if the leader is still successful, but also to quit patches too early if the leader is not so successful. In large groups, even a small amount of time can mean a big difference in the number of prey actually found in each patch, so the number found between patches will be very variable, thus having a profound effect on capture rates.

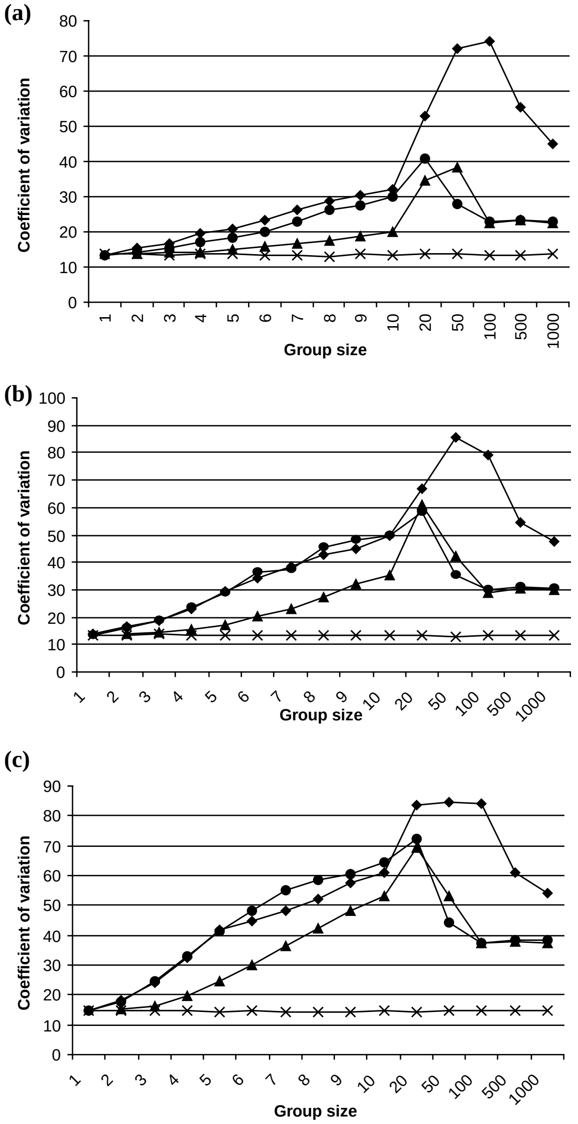

Fig. 6. Coefficient of variation of the quitting value of C obtained by foraging groups using three patch quitting strategies and for groups sharing public information, in prey distribution environments with a mean = 250 prey items per patch: (a) variance = 2750; (b) variance = 5250; (c) variance = 8062.5. Legend: -x–x- = total info; -●–●- = first; -◆–◆- = leader; -▲–▲- = paired.

Quitting patches at optimal C

For lone foragers, the difference between the quitting and optimal value of C was 0, or close to it, in all simulations (Fig. 5). For the first strategy, as group size increases this difference also increases, so foragers are leaving patches increasingly earlier in larger groups. This supports the hypothesis that foragers using this strategy may be vulnerable to'runs of bad luck' (Valone 1993, Ruxton 1995b). This loss becomes quite substantial, since groups quit patches as many as 100 prey items too early. However, in the largest groups, this difference decreases again, supporting the explanation above, that larger groups deplete patches more quickly and so when first groups quit patches it is genuinely becoming poor-the number of remaining prey being closer and closer to the optimal value of C on quitting as group size increases.

The coefficient of variation in quitting C also increases with increasing group size, indicating that first groups quit patches less consistently at a given value of C as group size increases (Fig. 6). Large groups sample more of a patch than small groups, so there is a potential for greater variance in the estimates between individuals over time. Since the first strategy draws from only one extreme of this sample (i.e. the lowest) there is a greater chance of this deviating from the average. However, in the largest groups the variation in the number of prey on departing a patch decreases again and levels off at a constant value. In very large groups, foragers will tend to quit patches immediately, because a forager finding prey assumes that each other forager has also done so, and the patch must therefore be empty. For example, in a group of 500 individuals, a forager finding prey will immediately assume that all other 499 members of the group have also found prey. Since the patch is expected to only contain a mean of 250 prey items the forager therefore assumes it is empty and will want to quit straight away. In such a short time spent in each patch the variability in the number of prey taken by the group will be smaller and so the actual quitting value of C remains relatively constant between patches.

A similar pattern to this is seen in groups using the paired strategy, with the difference between quitting C and optimal C, and the coefficient of variation in quitting C, both increasing with increasing group size, and then dropping and levelling off in the largest groups (Fig. 5, 6). However, for the paired strategy the difference between quitting C and optimal C is smaller than for the first strategy – these groups quit patches closer to the optimal value of C than groups using the first strategy. This supports Ruxton's (1995b) theory, that groups relying on the agreement of two individuals to quit a patch will be less susceptible to the bad luck of one individual. However, coefficient of variation in the quitting value of C is higher for this strategy (Fig. 6). This is likely to be because the group remain in the patch for a longer time, thus allowing greater variation to build up in the number of prey taken between patches.

Where group size is small, the leader strategy was able to quit patches at a C value close to the optimal, similar to groups using public information (Fig. 5). But as group size increases above 10 individuals, leader groups quit patches progressively earlier. In all but the largest groups, the leader strategy quits patches closer to optimal C than first or paired groups, but when group size is very large this benefit is lost because of the improvement in patch quitting ability seen by the first and paired strategies.

The coefficient of variation in quitting C for the leader strategy increases with group size, and falls again at the higher group sizes (Fig. 6). When group size is fairly small, this variation is similar to that of the first group. However, when groups contain more than 10 individuals, this continues to rise and so this becomes worst of all the strategies. Again this can be explained by the rate at which a patch is depleted in larger groups. Both the paired and the leader strategy reduce the vulnerability of foraging groups to quitting patches because of the bad luck of one individual. This relies on the assumption that patches are good in quality (i.e. they contain a number of prey higher than the optimal C). As group size increases prey are depleted considerably more quickly than in small groups, and the patch is much more likely to actually be poor. It should be no surprise then that the best strategy at avoiding premature patch-quitting when group size is low, is actually the most detrimental when group size is large, because it inhibits patch-quitting.

Discussion

The results presented here show fairly conclusively that sharing public information does give an advantage, in terms of foraging efficiency, to animals feeding in cohesive groups in an uncertain environment. In groups which do not share public information each forager samples only a fraction of the patch, and its estimate of patch quality is totally dependent upon it's own foraging success. By assuming that each other forager experiences the same foraging success as itself, the variability in patch estimate between individuals may be very high, particularly in large groups. It follows that each forager is quite likely to have a very different estimate and so will want to leave the patch at a different time to other individuals in the group (Valone 1993). Where groups are tightly cohesive this is impossible and certain rules must be employed to determine when the group can actually quit the patch. Thus foragers may suffer because they cannot necessarily quit patches when they want to, and will be forced to quit when they do not want to.

Groups using public information overcome this, because every individual knows exactly how many prey have been found in a patch at any one time. Since all foragers share this estimate of patch quality they therefore agree over when to quit a patch (Clark and Mangel 1984, 1986, Valone 1993).

These simulations show that sharing public information enables groups to quit patches close to the optimal prey threshold level, regardless of group size. This supports the conclusions Valone (1993) and Ruxton (1995b), despite the differences between these models and the one presented here. This is emphasised in environments which are highly variable, in which the quality of each food patch is unpredictable (Clark and Mangel 1984, 1986).

Our results also show that public information use does not offer benefits to groups over lone foragers. Each individual in a group may generate a more accurate estimate of patch quality because it is acquiring information from a greater number of sources, but this does not enable them to quit patches closer to the optimal value of C, nor does it offer higher capture rates. This is also in agreement with previous work (Clark and Mangel 1984, 1986, Valone 1993).

The benefit of public information use is highlighted here by the examination of optimal C values between strategies. Previous studies have adopted arbitrary patch quitting values (Valone 1993, Ruxton 1995b), which may not necessarily be optimal, and in fact may be detrimental to foragers. We show that the point at which foragers quit patches is heavily dependent upon their efficiency as foragers and also as patch quitters. Foragers which are not efficient, for example because they are poor at searching for or handling prey, or because, like here, they are restricted in their freedom to quit patches, will suffer some cost which ultimately affects the extent to which they must harvest a patch in order to maximise feeding rates – this is akin to increasing travel time between patches. It is particularly interesting to note that even when using the optimal values of C obtained for each non public information sharing strategy, these groups suffer in comparison to those using public information. This emphasises further the advantage groups can gain by using public information.

In summary, although sharing public information does not offer an advantage to groups over lone foragers, it does offer several benefits over foragers in cohesive groups. Such groups face restrictions in their freedom of movement and use foraging time less efficiently. Sharing public information prevents this by ensuring that each forager has the same estimate of patch quality, thus removing any conflict over when the group should quit each patch. The work presented here suggests that the use of public information is not likely to promote group foraging by itself, which is in agreement with Sernland et al. (2003). However, for individuals which already forage in groups, for example because of a high predation risk, sharing public information may offer yet another advantage to being in such a group.

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