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An evolutionarily stable joining policy for group foragers

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An evolutionarily stable joining policy for group foragers

Abstract

For foragers that exploit patchily distributed resources that are challenging to locate, detecting discoveries made by others with a view to joining them and sharing the patch may often be an attractive tactic, and such behaviour has been observed across many taxa. If, as will commonly be true, the time taken to join another individual on a patch increases with the distance to that patch, then we would expect foragers to be selective in accepting joining opportunities: preferentially joining nearby discoveries. If competition occurs on patches, then the profitability of joining (and of not joining) will be influenced by the strategies adopted by others. Here we present a series of models designed to illuminate the evolutionarily stable joining strategy (ESS). We confirm rigorously the previous suggestion that there should be a critical joining distance, with all joining opportunities within that distance being accepted and all others being declined. Further, we predict that this distance should be unaffected by the total availability of food in the environment, but increase with decreasing density of other foragers, increasing speed of movement towards joining opportunities, increased difficulty in finding undiscovered food patches and decreasing speed with which discovered patches can be harvested. We are further able to make predictions as to how fully discovered patches should be exploited before being abandoned as unprofitable, with discovered patches being more heavily exploited when patches are hard to find, patches can be searched for remaining food more quickly, forager density is low and foragers are relatively slow in travelling to discovered patches.

Introduction

If food is patchily distributed and patches are challenging to locate, then detecting the discoveries of others with a view to joining them and sharing the discovered resource may be an attractive strategy. Such behaviour is common among, for example, human fishermen and has been reported in a wide range of non-human species (see Giraldeau and Beauchamp 1999 and references therein). This scenario has also been subject to extensive theoretical development (well summarised in Giraldeau & Caraco 2000). Models of joining behaviour are commonly categorised as either information-sharing or producer-scrounger models: in the first type foragers are assumed to be able to search for joining opportunities and for undiscovered food patches concurrently, whereas in the second type these activities are mutually exclusive. Attention has tended to focus on producer-scrounger models, because the benefits of the “producer” and “scrounger” tactics are dependant on the frequency with which they are played in the local population. In contrast, Girardeau and Beauchamp (1999) argue that in its simplest form the information sharing model has rather less interesting behaviour, where the only stable strategy is to join at every opportunity because nothing is gained by refraining from joining when others join. That is, if the sensory properties of a social foraging situation are such that searching for joining opportunities does not detract from an individual’s ability to search for undiscovered food patches, then current non-spatial models suggest that we should see simple inflexible behaviour where all individuals take advantage of all opportunities to join.

It has been noted several times (e.g. Ruxton 1995; Ruxton et al. 1995) that the predictions of an information-sharing model should become more interesting if space is considered explicitly. This introduces a cost ignored by previous models: the time invested in travelling to a patch discovered by another. During this time, the original discoverer of the patch, and any other individuals that have less far to travel to the patch, will deplete the food on the patch (making it less valuable to the new arrival than a patch that it discovers for itself). Hence, both Ruxton (1995) & Ruxton et al. (1995) suggest that we should in fact expect flexible behaviour from individuals in an information-sharing situation. Specifically, they suggest that individuals should have a policy of responding to joining opportunities that occur close to them and ignoring those that occur further away. The aim of this paper is to formalise this idea in a spatially-explicit analytic model that can be used to generate the first quantitative predictions of a flexible joining policy within an information-sharing

scenario, and make predictions of how we should expect joining behaviour to be influenced by qualities of the foragers and their environment. We do this by building three models. In the first, we summarise the optimal behaviour of a single individual in an environment with food patches that are challenging to find and exhaustible. We then introduce a model where there are few individuals and joining opportunities are rare, such that a focal individual is presented with a single opportunity to join another at a food patch. The primary function of this second model is to help develop insights and methodology that are then used in the more-complex final model that relaxes the simplifying assumption of the previous model that foragers are rare, and produces predictions regarding an evolutionarily stable flexible joining policy.

Model 1: A single forager

The first scenario we examine is that of a lone forager searching its environment for food patches. Each patch takes an average time E to locate. Upon discovery, the patch has food of value V_{max} hidden within it. The forager is able to search the patch at a fixed intensity α , such that if at time t since discovery of the patch, an amount of food $F(t)$ remains, then the instantaneous rate of food discovery is $\alpha F(t)$. Food is not replaced as it is discovered and consumed by the predator, so that we can describe the change in food density over time (since discovery of the patch) by a simple negative exponential

$$F(t) = V \exp(-\alpha t). \tag{1}$$

Since, the gain rate on a patch declines over time, there is an optimal point at which the forager should quit a food patch, and begin to search for another. This optimal point maximises long-term gain rate (Charnov, 1976; Iwasa et al 1981; Valone, 1993). Suppose that the forager chooses to leave the patch when its value has fallen to some level v . From (1), this occurs after a time (τ) on the patch given by

$$\tau = \frac{1}{\alpha} \ln\left(\frac{V}{v}\right). \tag{2}$$

The reward rate (R) to a forager adopting this strategy is given by

$$R = \frac{V - v}{\tau + E} = \frac{V - v}{\frac{1}{\alpha} \ln\left(\frac{V}{v}\right) + E} \quad (3)$$

We want to find the value of v (denoted v^*) that maximises R . This can be found by setting the differential of R with respect to v equal to zero. After some manipulation this gives

$$\ln\left(\frac{V}{v^*}\right) = \frac{V}{v^*} - 1 - \alpha E \quad (4)$$

If we then substitute (4), back into (3), then much simplification occurs and we find that under the optimum quitting strategy, the gain rate (R^*) is given by

$$R^* = \alpha v^*. \quad (5)$$

This is logical as it indicates that an individual will leave a patch at precisely the time when its rate of food gain from the patch falls to the level of its long-term food acquisition rate.

Figure 1 demonstrates that there is always one and only one solution to (4). It is also easy to see from Figure 1 that V/v^* increases as either α or E increases, and hence v^* decreases (and the forager remains longer on a patch) as either α (the searching intensity) or E (the time taken to find a patch) increases. Both these results can be explained intuitively: an increasing intensity of searching increases the instantaneous gain rate for a given level of food remaining and so makes the patch profitable for longer, and if more time is invested in finding each patch, then discoveries must be exploited more fully to compensate. It is clear from this argument and from the form of (5) that the gain rate when adopting the optimal quitting strategy (R^*) decreases with increasing time to find patches (E). We can see from the arguments of Figure 1 that V/v^* increases slower than linearly with increasing α , and hence the gain rate R^* increases with increasing α , as we would intuitively expect. From (4), we can see that v^* is a fixed fraction of V for given values of α and E , and so multiplying V by a factor k simply changes causes v^* (and hence R^*) to change by the multiplicative factor k also. This accords with our intuition that, say, doubling the amount of food in the system should lead to a doubling in average food uptake rates.

Model 2: One joining opportunity

We imagine that the forager of the last model is faced with a choice. Another forager has just discovered a food patch a distance x from the focal forager. If the predator wants, it can travel at speed S to the already-discovered patch, and share the patch with the other forager, or it can ignore this opportunity and continue foraging in exactly the same way as before. We wish to understand how the best choice is influenced by the value of x . To simplify our calculations, we assume that no subsequent joining opportunities will arise, and that only the focal forager can share the newly found patch with its discoverer.

If the focal forager decides to reject this foraging opportunity, then its strategy, in terms of how long to remain on a patch is unchanged from (4), and its gain rate will be given by (5).

We now consider the situation where the focal forager joins the other forager. Firstly, it takes the focal individual a finite time (x/S) to reach the discovered patch, such that at the time of its arrival (which we label as time $t=0$), the food value of the patch has decreased from V to V_x given by

$$V_x = V \exp\left(\frac{-\alpha x}{S}\right). \quad (6)$$

The two foragers then share the patch, such that its food value declines so that at time t , with $F(t)$ remaining then the instantaneous depletion rate is $2\alpha F(t)$, and each forager gains half of this food reward. It is assumed that both foragers have the same long term uptake rate, and will thus choose to leave the patch at the same moment (the departure of one does not alter the instantaneous uptake rate of the other if it stays, although it would slow down the rate of its decline), so this is reasonable. If the focal forager leaves the patch and begins to search for a new one, when the food value of the patch declines to value v_x , then it is easy to show that the time spent on the patch τ_x is given by

$$\tau_x = \frac{1}{2\alpha} \ln\left(\frac{V_x}{v_x}\right) \quad (7)$$

and so the rate of gain associated with that patch visit (R_x) is given by

$$R_x = \frac{0.5(V_x - v_x)}{\frac{x}{S} + \tau_x}. \quad (8)$$

We need to find the value of v_x (termed v_x^*) that maximises R_x . By analogy with the equivalent calculation in Model 1, it is easy to show that this is given by

$$\ln\left(\frac{V}{v_x^*}\right) = \left(\frac{V \exp\left(-\frac{\alpha x}{S}\right)}{v_x^*}\right) - 1 - \frac{\alpha x}{S}, \quad (9)$$

with the associated gain rate (R_x^*) being simply αv_x^* .

It is advantageous for the focal forager to take the foraging opportunity providing that the rate of gain from doing so (R_x^*) is greater than its long term average otherwise (R^*); this condition simplifies to $v_x^* > v^*$.

The closer the patch that the focal individual can share (the smaller x), the more attractive joining becomes, since the patch will have been depleted less before the focal individual arrives and less time will have been spent travelling to it. If a certain x makes a patch unattractive to join, then the same is true for all greater values of x . Similarly, if a value of x makes a patch attractive to join, then the same is true for all smaller values of x . Thus there is a critical value of x (x_c), for all distances lower than this the patch should be joined and for all greater distances it should not. At the critical distance, the gain rate from joining ($R_{x_c}^*$) is equal to the long term gain rate (R_x) and so $v_{x_c}^* = v^*$. Combining (4) and (9), we can obtain an expression in x_c and v^* :

$$\left(\frac{\alpha v^*}{V}\right) \left(E - \frac{x_c}{S}\right) = 1 - \exp\left(-\frac{\alpha x_c}{S}\right) \quad (10)$$

Since, v^* can be found from (4) providing the values of V , E and α are specified, this allows x_c to be found, provided the value of S is also specified. The left-hand term in (10) must be non-negative since the right-hand term is. Thus, for joining to be attractive, it is clear that the maximum time taken to travel to the patch that can be joined (x_c/S) must be less than the time taken to find an undepleted patch by normal searching (E). We can see that letting x_c

vary from zero to ES , the left-hand term decreases linearly from a positive value to 0, whereas the right-hand term increases from 0 to a positive value. This guarantees that there is always one (and only one) solution for x_c , where $0 < x_c < ES$.

In order to explore the effect of the values of the parameters V , E , α and S on x_c , let us consider the special case where $\alpha x_c \ll S$: this allows the approximation

$$1 - \exp\left(\frac{-\alpha x_c}{S}\right) \approx \frac{\alpha x_c}{S}. \quad (11)$$

Substituting this into (10) gives

$$x_c = \frac{ESv^*}{V + v^*}. \quad (12)$$

Speed of movement towards a patch that can be joined (S) has no effect on v^* , and so we see (from (12)) that x_c increases with increasing S (in fact x_c is simply proportional to S irrespective of our assumption). This is as we would expect, since increasing S will reduce the amount of depletion that has occurred before the focal individual reaches the patch. We see from (4) that v^* is a fixed proportion of V (the exact proportion being defined by the values of α and E), so changing the value of V (and keeping other parameter values the same) has no effect at all on x_c . Again, this makes intuitive sense; since all patches start with the same value of V , changing the value of V does not make one patch (the one that can be joined) any more or less attractive relative to other patches that the focal forager will find itself. Increasing the intensity of searching within a patch (increasing α) acts to decrease the value of v^* and so decreases the value of x_c . This occurs because increasing α increases the amount of depletion that occurs before the focal individual arrives to join the other forager. Although it also increases the instantaneous feeding rate after joining, this is also true of patches that the focal forager finds itself (and for which there is no prior-depletion cost). Hence, the overall effect of increasing within-patch foraging intensity (α) is to make joining less attractive (decreasing x_c). To explore the effect of varying the value of E (the time taken for the forager to find a patch on its own) we first note that (12) can be re-written as

$$x_c = \frac{ES}{1 + \frac{V}{v^*}}. \quad (13)$$

From Figure (1) we see that V/v^* increases with increasing E , although the gradient of the relation is less than 1. This being so, (13) suggests that x_c will always increase with increasing E . Again, this makes intuitive sense, if patches are hard to find by other means, then joining the discoveries of others should become more attractive. Because of the intuitive nature of these explanations, and because none of the intuitive explanations required the assumption that $\alpha x_c \ll S$, we would expect these qualitative relations to hold even outside this limiting case.

3. Multiple foragers

We now relax the assumption of Model 2 that there is a single joining opportunity. We now assume that there are a number of foragers, spread at uniform density λ throughout the two dimensional surface on which patches are distributed. We assume that all of these foragers are identical, and each has the same critical distance (x_c) below which they respond to the discoveries of others. Let us assume again that at time equal to zero, a forager discovers a food patch. All prey within a radius of x_c will respond by travelling towards the patch at speed S . For the convenience of this derivation, we focus on an individual that is exactly at distance x_c from that discovered patch. The number of individuals on the patch at any time t , we define as $Y(t)$. We can see that between times t and $t + \delta t$, the number of individuals arriving at the patch (δY) is the number in the circle of radius $(St + S\delta t)$ minus the number in the circle of radius St :

$$\delta Y = \pi\lambda((St + S\delta t)^2 - (St)^2) = \pi\lambda(2S^2t\delta t + S^2(\delta t)^2). \quad (14)$$

In the limit $\delta t \rightarrow 0$, we form the differential equation

$$\frac{dY}{dt} = 2\pi\lambda t S^2. \quad (15)$$

Using $Y(0) = 1$, this can be solved to give

$$Y(t) = 1 + \pi\lambda S^2 t^2. \quad (16)$$

If we substitute x_c/S for t , then the average number of individuals per patch is $1 + \pi\lambda x_c^2$. To decide on the optimal value of x_c , we consider an individual at a distance x_c which must

decide whether to join the patch or not. If it chooses go to the patch, it will expect on average $1+\pi\lambda x_c^2$ individuals to be already on the patch when it arrives, and so it will take this number to $2+\pi\lambda x_c^2$ when it arrives. Of course, the actual number of individuals will be an integer that will vary between instances of patch discovery depending on the exact positioning of individuals at the moment when the patch was discovered. Hence, we assume that foragers do not base individual joining decisions on the fine detail of such exact positioning of others, but rather based their decision making in all cases on the average positioning and behaviour of other individuals.

Next we must calculate the value (V_{xc}) of the patch at the point when the focal individual arrives. We know that $F(0) = V$ and that the rate of change in food value on the patch is given by

$$\frac{dF}{dt} = -\alpha Y(t)F(t). \quad (17)$$

Solving (16) & (17) gives

$$F(t) = V \exp\left(-\alpha\left(t + \left(\frac{\pi\lambda S^2 t^3}{3}\right)\right)\right). \quad (18)$$

This gives

$$V_{xc} = V\left(\frac{x_c}{S}\right) = V \exp\left(\left(\frac{-\alpha x_c}{S}\right)\left(1 + \frac{\pi\lambda x_c^2}{3}\right)\right). \quad (19)$$

We continue to follow the logic of the last two models, first calculating the time (τ_x) that the focal individual spends on the patch that it has joined, assuming it leaves when the food value $F(t)$ falls to v . By analogy with the previous models, this is given by

$$\tau_x = \frac{1}{\alpha(2 + \pi\lambda x_c^2)} \ln\left(\frac{V_{xc}}{v}\right). \quad (20)$$

Again, by analogy with the previous models, we can see that the uptake rate to our focal individual (R_x) from exploiting this patch until this time is given by

$$R_x = \left(\frac{1}{\frac{x_c}{S} + \tau_x} \right) \left(\frac{V_{xc} - v}{2 + \pi\lambda x_c^2} \right). \quad (21)$$

We now need to find the value of v (v^*) that maximises R_x . Again, using working similar to the previous models, this is given by

$$\ln\left(\frac{V_{xc}}{v^*}\right) = \frac{V_{xc}}{v^*} - 1 - \alpha(2 + \pi\lambda x_c^2) \left(\frac{x_c}{S}\right), \quad (22)$$

where V_{xc} is given by (19).

The long term average uptake rate of the focal individual is no longer the same as in models 1 & 2, because now other foragers can take advantage of discoveries made by the focal individual. Once a patch has been discovered, then the total amount of time for which it is exploited (t_f) is given by

$$t_f = \frac{x_c}{S} + \frac{1}{\alpha(1 + \pi\lambda x_c^2)} \ln\left(\frac{V_{xc}}{v_x^*}\right). \quad (23)$$

Notice the term $(1 + \pi\lambda x_c^2)$ rather than $(2 + \pi\lambda x_c^2)$ used in the preceding equations, since we have switched our attention back to the general experience of a forager, rather than the special case of a forager placed exactly at a distance x_c from the patch. During this time t_f , all the individuals that were within x_c of the patch when it was discovered are either travelling to the patch or feeding within it. We assume that patches are sufficiently challenging to find that the zones of radius x_c surrounding two discovered patches never overlap while those patches are being exploited. The number of individuals involved in exploiting a patch (N) will on average be $1 + \pi\lambda x_c^2$. The average time required for one individual to find a patch is E . Thus each individual finds a patch at rate $1/E$; if there are N individuals searching, new patches are found at rate N/E , with expected time E/N . For every patch found, a searching time E/N times N has been spent in total by the population. Then the group of $1 + \pi\lambda x_c^2$ individuals each spend an amount of time t_f travelling to and exploiting a patch. The amount of food taken from a patch is $V - v_x^*$. Hence the long-term food uptake rate of the group is given by

$$R = \frac{V - v_x^*}{E + t_f(1 + \pi\lambda x_c^2)}. \quad (24)$$

In order to forage optimally, individuals should leave when their feeding rate falls to the average of the whole population, and hence the optimal feeding rate αv_x^* equals R :

$$\alpha v_x^* = \frac{V - v_x^*}{E + t_f (1 + \pi \lambda x_c^2)}. \quad (25)$$

If we substitute for t_f using (23) and for V_{xc} using (19), this gives another relation between x_c and v_x^* :

$$\left(\frac{\alpha v_x^*}{V} \right) \left(E - \frac{x_c}{S} \right) = 1 - \exp \left(- \frac{\alpha x_c}{S} \left(1 + \frac{\pi \lambda x_c^2}{3} \right) \right), \quad (26)$$

Combining (22) & (26), we get

$$\ln \left(\frac{V}{v_x^*} \right) = \frac{V}{v_x^*} - 1 - \alpha E - \frac{2\alpha \pi \lambda x_c^3}{3S} \quad (27)$$

Comparison with (4), demonstrates that since x_c must be positive, then v_x^* must be less than v^* for a single forager, and the long-term food uptake rate is always lower for an individual foraging with others than for one able to exploit the same environment on its own. The reason for this is the time spent in travelling to join discovered patches. Despite this, it is not advantageous to entirely give up joining if others will still join your discoveries, and similarly in a population of non-joiners an individual that switched to joining and sharing nearby discoveries would do better than non-joining individuals, so joining is the evolutionarily stable strategy for selfish individuals, even though not joining would yield higher long-term reward rates if such a strategy could be cooperatively adopted and maintained.

For specific values of λ , α , E , S and V , then (26) and (27) can be solved simultaneously to give v_x^* and x_c .

An example situation of Model 3

For notational convenience, let us imagine that we measure food value in kJ, space in metres and time in seconds. Let us imagine that all patches have initial food value of 100kJ,

and that an individual on its own would take 10 seconds to find a patch. Individuals can travel at 5ms^{-1} to reach the discovery of another. The density of individuals while searching is 0.001m^{-2} , that is there are on average 10 individuals in a square of length 100m. The initial rate at which food can be extracted from the patch is 5kJ per second. These assumptions translate into the parameter values ($V=100$, $E=10$, $S=5$, $\lambda=0.001$, $\alpha=0.05$). These values might be appropriate for birds searching grassland for small patches of invertebrates. An approximate energy density for earthworm and snails is 3KJ per g, so a patch would contain approximately 30 g of prey, and the uptake rate of an individual in a full patch would be about 1.7gs^{-1} . If we simultaneously solve (26) and (27) for these values, we get $x_c=13.54\text{m}$, $v_x^*=40.87\text{kJ}$. Hence, foragers will invest up 2.71 seconds in travelling to share the discovery of another; this is 27% of the time it would take them to find a patch on their own. Once a patch has been discovered, it is exploited by on average 1.58 individuals, for 8.40 seconds, during which time 59.13% of its food value is consumed. The average food intake rate of an individual is simply $\alpha v_x^*=2.04\text{kW}$. Had the individual been on its own, then (using eqn 4), its intake rate would have been 2.12 kW. Hence, the evolutionarily stable joining strategy causes only a slight reduction in long-term average reward rate over a single individual exploiting the same environment. The cost is likely to be kept relatively low by the infrequency of joining, with roughly only one in every two patches being shared with only one joining individual.

Sensitivity analysis

We now explore how the values assigned to parameters affect model predictions, by varying one parameter whilst holding all the others at their default values. We begin with the value of a patch when it is first discovered (V). From the form of (26) and (27), we can see that as V changes so v_x^* is changed such that the ratio V/v_x^* is constant and the value of x_c remains unaffected. These predictions were confirmed by numerical solution of the equations (not shown). These predictions make intuitive sense, since all patches start with the same value (V), so changing the value of V should not change the attractiveness of one patch compared to another: thus it has no effect on the critical joining distance (x_c), or the time that the foragers remain on one patch before quitting it for another (t_f and hence V/v_x^*). However, since x_c must be greater than zero, we can see that the ratio of v^*/V for a single forager must be greater than the ratio v_x^*/V for a joiner, and so the difference between the

average food consumption rates of a joiner and a singleton increases as V increases. Again this was confirmed by numerical methods.

We next turn to the density of foragers (λ). As λ increases, the average number of foragers nearer to a discovered patch than a focal individual increases. Thus the attractiveness of joining (and so x_c) decreases. Since more individuals will now share any discovery (although patches will be found more quickly), efficiency will decline because of time invested in travelling to discovered patches. Hence as λ increases, so v_x^* and R_x decrease. The length of time for which patches are exploited (t_f) declines with increasing λ , because larger numbers of foragers exploit any given patch. These results are illustrated in Figure 2.

We now turn to the speed at which joiners can travel to a discovered patch (S). Increasing S makes joining more attractive (increasing x_c). This increased frequency of joining can be expected to decrease the amount of time that patches are exploited (decreasing t_f). The increased occurrence of joining causes a decrease in the long term consumption rate. All these effects are illustrated in Figure 3.

As the time taken for a singleton to find a patch (E) increases, so the attractiveness of joining (and so x_c) increases. Patches are exploited for longer, because patches are harder to come by and so must be exploited more fully. One would expect that the long term food uptake rate would decline both for singletons and joiners with increasing E ; this does occur, although the drop is greater for joiners, because as E increases the frequency of joining increases. These results are illustrated in Figure 4.

As the efficiency with which food can be exploited within a patch increases, joining becomes less attractive (x_c decreases), because more food will be consumed from the patch in the time it takes a joiner to reach it. The increased speed with which food is removed from the patch decreases the time spent exploiting each patch (decreases t_f) and increases overall long-term food uptake rate (R_x). These results are illustrated in Figure 5.

Discussion

Here we have produced the first quantitative predictions for a flexible joining strategy in situations that are well described by the information-sharing paradigm. We confirm

rigorously the previous suggestion that there should be a critical joining distance, with all joining opportunities within that distance being accepted and all others being declined. Further, we predict that this distance should be unaffected by the total availability of food in the environment, but increase with decreasing density of other foragers, increasing speed of movement towards joining opportunities, increased difficulty in finding undiscovered food patches and decreasing speed with which discovered patches can be harvested. We are further able to make predictions as to how fully discovered patches should be exploited before being abandoned as unprofitable, with discovered patches being more heavily exploited when patches are difficult to find, patches can be searched for remaining food more quickly, forager density is low and foragers are relatively slow in travelling to discovered patches. All these predictions should be amenable to empirical testing. Common species that have been used in laboratory experiments of social foraging are small passerine birds and shoaling freshwater fish (see Krause & Ruxton 2002 for an overview), searching for experimentally manipulated patches of food distributed in their environment. Both of these groups should be suitable for study of the predictions of the theory presented here. In both fish (Krause & Godin 1996) and birds (Templeton & Giraldeau 1995a&b) characteristic feeding behaviour can sometimes (but not always: Coolen et al. 2001) be detected by other foragers, even while searching for food themselves, and so the key requirements of the information-sharing paradigm are likely to be met (see below). However, experiments would need to be on appropriate temporal and spatial scales to avoid travel times being trivial and many joining opportunities being simultaneously available. The need for large spatial scales may argue for field based rather than laboratory based studies. In testing the model, it will be important to determine at what distances individuals can perceive the discoveries of others. The fact that patches outside the predicted radius are not exploited to the same extent as closer ones may be due to sensory limitations: either the patch is too far to see or detection of the patch is obstructed by the presence of others. The challenge for empiricists here is to determine whether a distant joining opportunity is not detected by a focal bird, or is actually detected but the opportunity to join is spurned.

It is always important to consider the limitations on the generality of a model's predictions imposed by the assumptions of the model. There are two types of assumptions to consider here, the assumptions of the information-sharing scenario, and further assumptions that we have had to make in our analytic derivations. The key requirement for foraging situations to be modelled by either producer-scrounger or information sharing models is that food (or

any resource) is distributed in patches that are challenging to find (in that foragers cannot go immediately from one patch to the next), that the food in such patches occurs in such a way that several individuals can feed simultaneously in the same patch, and that this feeding leads to depletion and eventual exhaustion of the patch. These conditions are met in many natural situations. The additional specific requirement of information-sharing models is that an individual's ability to discover food patches is not adversely influenced if they also search for joining opportunities. Foragers may sometimes alert other foragers to a discovery that they have made, in order to gain anti-predatory benefits from feeding as a group (e.g. Elgar 1986). However, from a foraging economics viewpoint, they should be selected to make detection of their food discovery as challenging for other foragers as possible. That said, the discoverer will likely have to adopt characteristic behaviours that are different from those associated with searching in order to exploit the food resource themselves, and these characteristic behaviours can often be readily identified by other nearby foragers (e.g. Brockman & Barnard 1979; Pitcher & Magurran 1983). However, it seems almost inevitable that the demand for sensory processing combined with cognitive limitations would mean that adding an extra task (searching for joining opportunities) would lead to at least some degradation of performance at another task (searching for undiscovered food). This is likely to be dependent on how challenging the tasks are (Milinski & Heller 1978; Dukas & Ellner 1993; Dukas & Kamil 2001). Finding undiscovered food patches can be challenging because it requires movement around the environment rather than because it is sensorially challenging (a human example might be searching for your car in a large car park compared with looking for a dropped contact lens). In this case, if each task does not require a substantial investment in cognitive processing, then information sharing may be a closer approximation to reality than the mutual-exclusion of producer-scrounger theory. Evidence of similar multi-tasking has been shown in, for example, flocking birds (Lima 1995) that can both feed on grains from the substrate and detect the predator-induced departures of flockmates (differentiating these from departures for other reasons). Hence, there is reason to expect that situations that can be well described by the information-sharing paradigm should be relatively common in the natural world, although further empirical exploration of the relationship between efficiency of looking for joining opportunities and undiscovered food would be welcome. There will however be situations where detecting joining opportunities and searching for undiscovered food are incompatible (e.g. Coolen et al. 2001).

There are further specific assumptions that we made to gain analytic tractability. We assume that prey decision making is based solely on their own distance to a patch and the average distribution of other foragers. Hence, decision-making in our model is not based on the specific distances of all other potential joiners from the patch at the specific instance of patch discovery. This may be a reasonable description of the reality facing foragers in circumstances of limited sensory range where foragers more distant than the patch from a focal individual may be difficult to detect or where small animals on a flat substrate do not have the elevation that would give them the perspective to make accurate estimates of the angle of trajectory that its neighbours would take to the patch. Freshwater fish may provide examples of the first condition and ground feeding birds of the second. For some foraging situations, such detailed information of the positioning of others may be available, and it would be particularly valuable to act on this in situations where average behaviour is a poor description in individual patch-finding incidents. Such strong stochastic fluctuations will be most evident in cases where the density of foragers is very low, such that sometimes there will be a single individual nearer the discovered patch than the focal individual and sometimes there may not be. In such cases, a conditional strategy should provide advantages over the strategy developed in this paper, although we would expect these advantages to be slight and the predictions of both of our joining models to provide a good guide to the likely form and consequences of such a conditional strategy.

We assume that foraging occurs in a two-dimensional space. Whilst this is likely to be appropriate for many natural systems, especially in terrestrial ecosystems, foraging in the open ocean may well more appropriately be considered as a three-dimensional environment. Recasting our theory for this case should be relatively straightforward, and we would expect little loss of analytic tractability and no qualitative change in our conclusions. We further assume that when a patch is discovered, that nearby foragers are distributed uniformly throughout the environment. This is unlikely to hold in circumstances where food patches are relatively densely distributed in the environment (i.e. the time to find a patch (E) is small). This problem arises because the process of joining and then simultaneously dispersing from a patch naturally leads to clumping of individuals. However, after dispersal from a patch, individuals should seek to spread out so as to minimise the risk of searching parts of the environment already unsuccessfully searched for food by other individuals. Hence, providing food patches are relatively scarce, so that substantial dispersal of individuals from one patch occurs before any of these individuals

finds another patch, then our assumption of uniformly distributed foragers may be a fair approximation to reality. A further assumption is again one relating to the scarcity of patches. This is that the zones of attraction surrounding two patches that are being exploited simultaneously do not overlap. This assumption was introduced to avoid considering more complex strategies involving not only deciding whether to join or not, but which patch to join from a number of simultaneous choices (as well as complex functions of distance and expected number of individuals). Hence, again we see that the key assumption underlying our theory is one of patch scarcity. Relaxing the requirement is likely to require numerical simulation methods and require consideration of how individuals choose between simultaneously available joining opportunities (see Ruxton et al 1995 for further consideration of this). It is worth remembering however that if patches are relatively easy to find then joining becomes an unattractive tactic, and so our theory is least applicable under conditions where the underlying behaviour of interest (joining) is least frequent in occurrence. Further, we expect our predictions to remain qualitatively intact in simulations that relax the assumptions considered above, and exploration of the effect of our quantitative predictions would be welcome.

Another consideration that simulation models would have to consider is appropriate search trajectories for a group of individuals simultaneously leaving a depleted patch. We would expect selection pressure for these individuals to adopt trajectories that minimise the overlap between their individual search fields. Further, in producer-scrounger models both theory (Barta et al. 1997) and laboratory experiments (Flynn & Giraldeau 2001) have demonstrated that producers and scroungers take up characteristically different positions with respect to other individuals. Scroungers seek to be near to producers so as to take best advantage of joining opportunities; whereas producers seek to distance themselves so as to allow them as much time as possible to exploit their discoveries before joiners arrive. These predictions become less clear if animals can switch state from producing to scrounging over short time scales. In information-sharing models where each searching individual can become either a joiner or a discoverer, there is a trade-off between positions (with respect to other individuals) that are most advantageous to each potential outcome. The density of groups of foragers is likely to impact on other aspects of their fitness, such as thermoregulatory costs and predation risk. Hence, the evolutionarily stable search trajectories and consequent distribution of individuals within the local environment, is not completely obvious and worthy of further research. Although our work can be used to form

initial expectations for this research: in that our arguments that all joining leads to reduced food uptake rates compared to solitary foragers, suggests that individuals should minimise the extent of joining by adopting search trajectories that achieve high spatial separation between individuals. Again, such theoretical work would greatly benefit from simple empirical work that mapped the trajectories of foragers as they leave depleted food patches.

Producer-scrouter models of joining behaviour have been subject to more theoretical development than information-sharing models, but this theory has rarely included an explicit cost of travelling to a patch discovered by others. However, this cost is implicit in many producer-scrouter models through the producer's share (sometimes called producer's advantage), which is defined as the proportion of each patch that the finder obtains before other foragers join (see Giraldeau & Caraco 2000). With higher costs of travelling leading to a higher producer's share. A high producer's share has commonly been associated with reduced use of scrounging. Spatially explicit producer-scrouter models (for instance Beauchamp et al. 1997) incorporate the time cost of travelling and again increased cost of travel leads to reduced scrounging. However, in producer-scrouter models to date, scrounging is assumed to be inflexible and adjusted only to the average gain of joining a patch regardless of the distance a particular patch is away. That is, in these models, while the frequency with which foragers use the scrounger tactic takes into account the time cost of travelling (indirectly or not), the actual decision to join a particular patch is independent of the distance to that patch. In contrast, this paper explores flexible strategies where information on distance to a particular patch is used in making a joining decision. However, the extent of any advantage conferred by a flexible strategy has yet to be assessed, and this should make an interesting development of the results presented here. In considering the advantages of different strategies, both mean and variance in uptake rates may have to be considered. Another potential use for the methodology developed here is in exploring the utility of flexible kleptoparasitic strategies, where individuals are more likely to steal resources when they are required to invest less time and energy in reaching nearby current holders of the resource compared to more distance ones.

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Figure 1: Clearly $v^* < V$ and so V/v^* is greater than unity and increases the longer the forager remains on the patch. If we consider first the left side of (4) as a function of V/v^* : when V/v^* is one, then the left side is zero, it then increases as V/v^* increases, the gradient being the inverse of V/v^* . In contrast, when V/v^* is one, then the right side of (4) starts below the left side at value $-\alpha E$. In this case, we have used the values $\alpha = 1$ and $E = 1$. The right side also increases with increasing V/v^* , having a constant gradient of unity. Since, the left side starts above the right side but increases at an ever slower rate with increasing V/v^* , the right side must eventually take to the same value as the left side, then overtake it. Hence, there is always one solution to (4).

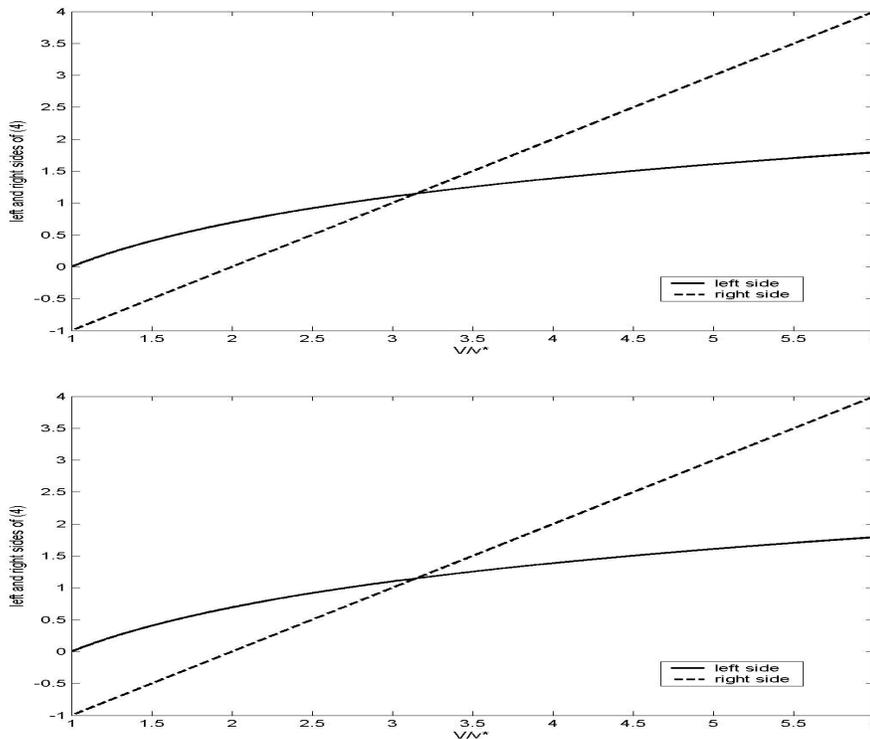


Figure 2: **a:** The maximum distance at which joining will occur (x_c) calculated from equations (26) and (27); **b:** The amount of time spend on a patch (t_f) calculated from (23); and **c:** the long term food uptake rate (calculated from (24), (26) and (27) for a joiner and (4) and (5) for single individual in the same environment). All as a function of the density of foragers (λ). Other parameter values $E = 10$, $S = 5$, $V = 100$, $\alpha = 0.05$

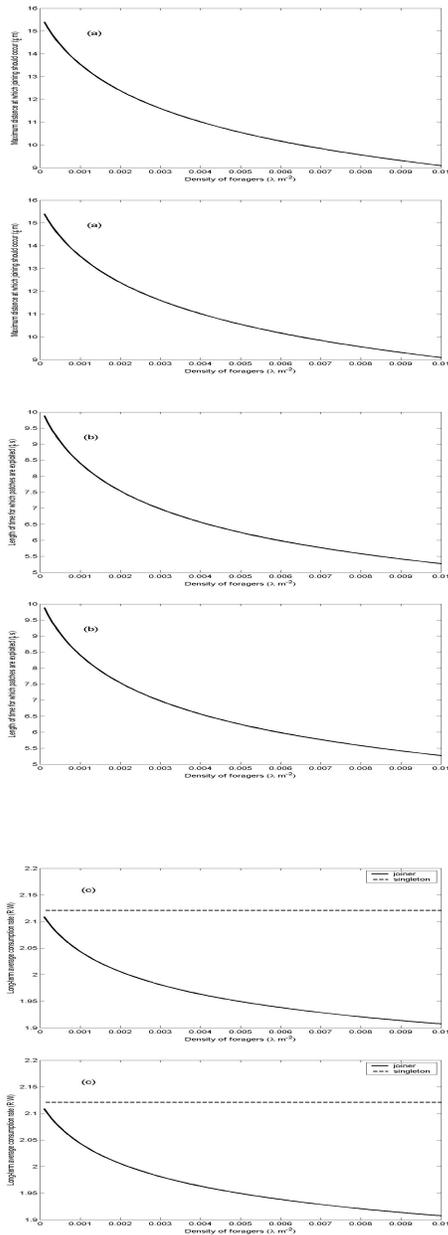


Figure 3: **a:** The maximum distance at which joining will occur (x_c) calculated from equations (26) and (27); **b:** The amount of time spend on a patch (t_f) calculated from (23); and **c:** the long term food uptake rate (calculated from (24), (26) and (27) for a joiner and (4) and (5) for single individual in the same environment). All as a function of the speed of joining (S). Other parameter values $E = 10$, $\lambda = 0.001$, $V = 100$, $\alpha = 0.05$

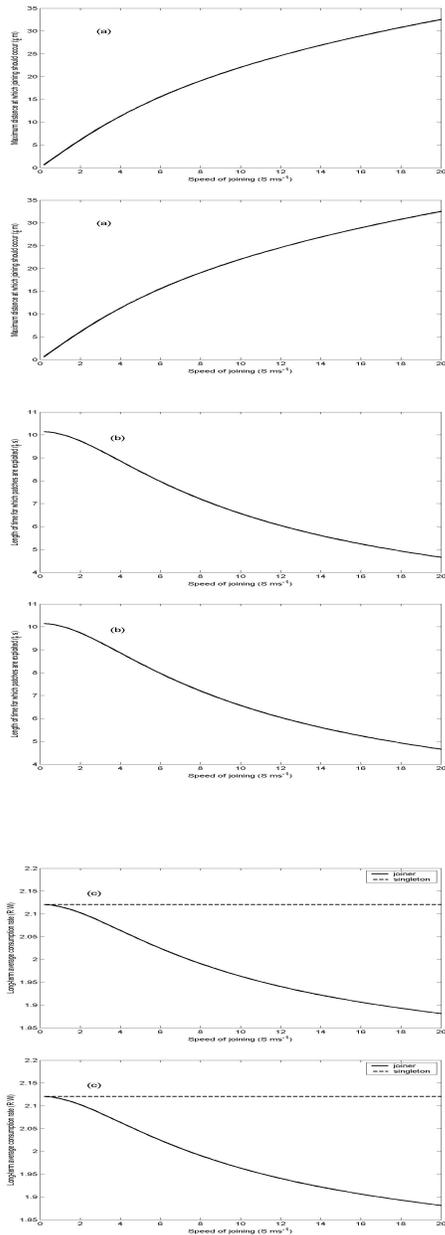


Figure 4: a: The maximum distance at which joining will occur (x_c) calculated from equations (26) and (27); **b:** The amount of time spend on a patch (t_f) calculated from (23); and **c** the long term food uptake rate (calculated from (24), (26) and (27) for a joiner and (4) and (5) for single individual in the same environment). All as a function of the speed with which an individual finds patches (E). Other parameter values $\lambda = 0.001$, $S = 5$, $V = 100$, $\alpha = 0.05$

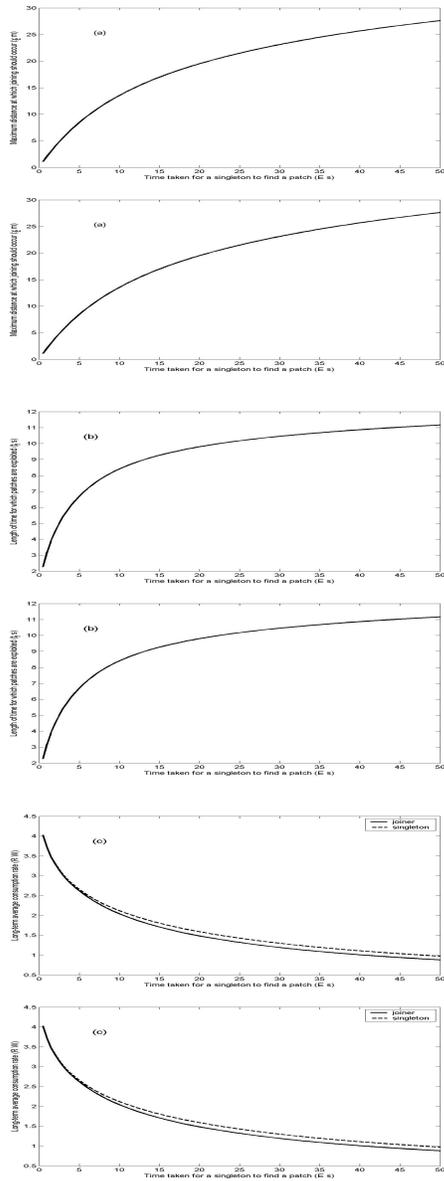


Figure 5: **a:** The maximum distance at which joining will occur (x_c) calculated from equations (26) and (27); **b:** The amount of time spend on a patch (t_f) calculated from (23); and **c** the long term food uptake rate (calculated from (24), (26) and (27) for a joiner and (4) and (5) for single individual in the same environment). All as a function of the efficiency with which patches are searched for food (α). Other parameter values $\lambda = 0.001$, $S = 5$, $V = 100$, $E = 10$.

