

An individual's gain in a foraging group

Hannu Rita & Esa Ranta

Rita, H. & Ranta, E., Integrative Ecology Unit, Division of Population Biology, Department of Ecology and Systematics, P.O. Box 17, FIN-00014 University of Helsinki, Finland

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By modelling an individual's gain through waiting times between subsequent prey encounters we characterise its performance when foraging alone or in a group. The larger the group, the longer the time between successful prey captures. The waiting times also depend on how the grouping behaviour affects foraging efficiency of individuals, when joining a group. With full additivity ($A = 1$) grouping has no effect on an individual's foraging efficiency, while with larger values of additivity individuals co-operate. When A is below one subadditivity occurs and individuals interfere each other when foraging in the patch. With $A < 0$ competition in the group is so hard that the intake-rate for the group is less than the rate of gain of a solitary forager. When additivity equals zero the patch corresponds to a system with continuous input and immediate consumption of the arriving prey items. The model, via waiting times, renders it possible to examine different foraging scenarios. For example, assuming that the forager already has gained k prey, for solitary foragers waiting times for the $(k + 1)^{\text{th}}$ prey are not affected by time in the patch, whereas for an individual in a group the waiting times get longer with increasing time. This is because other individuals affect the prey availability by their foraging activity. Using the model we were able to uncover that in depleting patches under resource matching distribution of foragers food-intake rates of individuals differed in groups of different size. Finally, via modification of waiting times the finder's advantage (the gain accumulated before others in the group arrive) can be implemented into group foraging.

1. Introduction

That individuals of a great variety of taxa exhibit grouping behaviour is commonplace (Wilson 1975). As everything in life of animals is based on gain in foraging it is no wonder that there exists a rich literature of both theoretical and em-

pirical arguments favouring evolution of grouping behaviour also due to benefits achieved in foraging (Bertram 1978, Caraco 1981, Clark & Mangel 1984, Magurran 1990, Pitcher & Parrish 1993). Our focus is in performance — in terms of gain accumulation — of individuals foraging either alone or as a member in a group of others. As

done earlier (Ranta 1993, Ranta *et al.* 1993, 1994, 1995, Rita *et al.* 1997, Rita & Ranta 1998b), we shall assume a foraging environment where discrete prey items are found aggregated in food-patches while the areas between the patches are void of prey. Foraging behaviour in such a system has traditionally been approached with the help of the marginal value theorem (Charnov 1976) addressing how long an optimally foraging long-term energy maximizer should spend per patch. A somewhat differing approach to group foraging is taken in the theory of ideal free distribution (Fretwell & Lucas 1970, Sutherland 1996) focusing on how foraging individuals should distribute themselves over patches differing in food availability. A third approach, a game theoretical one, addresses payoff an individual receives from joining a foraging group, a decision made also perhaps by other foragers thus affecting group size and the payoff endcome of all foragers (Parker 1974, Barnard & Sibly 1981, Maynard Smith 1982, Axelrod 1984). Our task is to provide tools — in the framework of group foraging — for these approaches (Rita *et al.* 1996, Rita & Ranta 1998a, 1998b).

Earlier — using stochastic processes — we (Rita & Ranta 1998a) have modelled accumulation of gain of a solitary forager. The distribution of the gain process is derived from differential equations for the corresponding probabilities of k prey items being eaten after foraging a given time in the patch. The accumulation of gain is characterized through transition intensities, which serve as parameters for the distribution. Later, the model was generalised giving the gain distribution of a member in a foraging group (Rita & Ranta 1998b). We now want to further the intensity characterisation of the process, and especially answer the question: How does the foraging activity of the group affect the actual foraging situation of a single member in the group, as compared to that of a solitary forager?

2. A model on individual's gain in a foraging group

Let $G_{\text{sol}}(t)$ be the number of prey items gained by a solitary forager after exploiting the patch for t time units. The distribution of the gain $G_{\text{sol}}(t)$ can

be characterised by a differential equation system (Rita & Ranta 1998a)

$$p'_k(t) = -\lambda_k p_k(t) + \lambda_{k-1} p_{k-1}(t) \quad (1)$$

where $p_k(t) = P(G_{\text{sol}}(t) = k)$, $k = 0, 1, \dots, X$ is the probability that the solitary forager — of which we are interested in — has obtained exactly k prey items after t time units in the patch, X being the number of discrete prey items in the patch. The transition intensities λ_k , $k = 0, 1, \dots, X$, are the parameters of the gain distribution. Using these elements the distribution of gain $G_{\text{mbr}}(t)$ of a member of the foraging group can be derived (Rita & Ranta 1998b). Here we want to find a characterisation corresponding to Eq. 1 to the gain of a member in a foraging group. Using this result we can then answer the question: How does the gain of a member in a foraging group differ from that of a solitary forager?

Let $\tilde{p}_k(t)$ be the probability that a member of the foraging group has obtained exactly k prey items after t time units in the patch:

$$\tilde{p}_k(t) = P(G_{\text{mbr}}(t) = k), \quad k = 0, 1, \dots, X.$$

Define for each k function $\tilde{\lambda}_k$ of patch time t by setting

$$\tilde{\lambda}_k(t) = \frac{-\sum_{j=0}^k \tilde{p}'_j(t)}{\tilde{p}_k(t)} \quad (2)$$

Note that $\tilde{\lambda}_X$ is identically zero, because the corresponding numerator is zero as the derivative of a constant (sum of probabilities being one). It is an easy task to see that the probabilities $\tilde{p}_k(t)$ satisfy the differential equations

$$\tilde{p}'_k(t) = -\tilde{\lambda}_k(t)\tilde{p}_k(t) + \tilde{\lambda}_{k-1}(t)\tilde{p}_{k-1}(t) \quad (3)$$

for $k = 0, 1, \dots, X$.

These equations have the same structure as the solitary forager's in Eq. 1. But, in contrary to them, the coefficient intensities in Eq. 3 are not constant but depend on the elapsed time t in the patch.

The intensities in Eq. 1 have the following interpretation: assume that the solitary forager has, after t time units in the patch, obtained k prey items, i.e., $G_{\text{sol}}(t) = k$. The conditional probability that, during a short time interval of length h , an additional prey item will be obtained from the $X - k$

remaining in the patch can be approximated by $\lambda_k h$ (Cox & Isham 1980). Because the transition intensities λ_k in Eq. 1 are constant with respect to time t , this approximation is the same irrespective of the time t spent in the patch. This reflects the fact that the forager is solitary being the only cause to changes in the amount of prey in the patch, which, in turn, call out the effects of depletion. The amount eaten by time t completely determines the foraging situation, i.e., how much there is left in the patch, as we assume here immobile prey that can not escape. For a member in a foraging group the conditions are quite different.

Let us assume that the focal individual in the group has gained k prey items by time moment t . The probability that it will obtain an additional item during a short time interval $(t, t + h)$ can be

approximated by the integral $\int_t^{t+h} \tilde{\lambda}_k(r) dr$, which in turn, can be approximated by $\tilde{\lambda}_k(t)h$ (Collett 1991). Note that if the integrand is constant — as with the solitary forager — the integral and its approximation perfectly coincide.

As $\tilde{\lambda}_k$ depends on time point t , the approximation is valid on time interval of length h and starting from t , not on any interval of length h as was the case with solitary forager. This is because knowing the amount the focal individual has obtained by time t , $G_{mbr}(t) = k$, does not tell how much the rest of the group has gained up to that point of time. It is the modification of the patch profitability the rest of the group does “behind” our focal individual that causes the time dependency of the intensities $\tilde{\lambda}_k(t)$. These intensities are averages across the foraging activity of the other individuals in the group.

From the interpretation of $\tilde{\lambda}_k(t)h$, one may see that $\tilde{\lambda}_k(t)$ is the instantaneous food-intake rate of the forager (per unit time) conditional on the amount of prey k it already has gained. By weighting these conditional intake rates with the corresponding probabilities $\tilde{p}_k(t)$ one obtains average intake rate of the member of the foraging group. In Appendix it is shown that

$$(EG_{mbr})'(t) = \sum_{k=0}^X \tilde{p}_k(t) \tilde{\lambda}_k(t), \quad (4)$$

i.e., the derivative of the average gain $EG_{mbr}(t)$ gives the food-intake rate.

With solitary forager, the waiting time between the k^{th} and the $(k + 1)^{\text{th}}$ prey encounter has exponential distribution, with parameter λ_k (Rita & Ranta 1998a). Thus the probability that the waiting time exceeds s time units is $\exp(-\lambda_k s)$. This probability does not depend on the time point t where the k^{th} incidence took place. Let us calculate the corresponding probability for a member of the foraging group. Assume that the individual obtained its k^{th} prey item at time point t . The probability that the waiting time U_k between the k^{th} and the following prey item is more than s time units is

$$P(U_k > s | k^{\text{th}} \text{ at } t) = \exp\left(-\int_t^{t+s} \tilde{\lambda}_k(r) dr\right) \quad (5)$$

(Collett 1991).

Before the behaviour of $\tilde{\lambda}_k(t)$ and $E(G_{mbr})'(t)$ can be exemplified one has to specify the transition intensities that characterise the behaviour of the group gain.

There are — in addition to group size n — X parameters, which determine the gain distribution of the group: $\Lambda_k, k = 0, 1, \dots, X$. These parameters also determine the distribution of the gain $G_{mbr}(t)$ of a member in the group (Rita & Ranta 1998b). To keep things simple, we assume, in what follows, that the intensity sequence Λ_k is linear with respect to the number of prey still remaining in the patch, i.e., $\Lambda_k = (X - k)\Lambda$. From this it follows (Appendix) that the sequence $\tilde{\lambda}_k(t)$ is linear, too, i.e., $\tilde{\lambda}_k(t) = (X - k)\tilde{\lambda}(t)$ for $k = 0, 1, \dots, X$, where the “basic” intensity $\tilde{\lambda}(t) = \tilde{\lambda}_{X-1}(t)$ has the form

$$\tilde{\lambda}(t) = \frac{\left(\frac{1}{n}\right)\Lambda e^{-\Lambda t}}{1 - \left(\frac{1}{n}\right)(1 - e^{-\Lambda t})}. \quad (6)$$

Thus, to illustrate the time dependency of the member gain intensities, it is enough to visualise $\tilde{\lambda}(t)$. In addition, assume that the effect of group size is determined through the additivity parameter A , i.e., $\Lambda = n^A \lambda$, where λ is the basic intensity of a solitary forager (Rita & Ranta 1998b).

With linear group intensities, the group gain is binomial, which implies that the member gain has expectation (Rita & Ranta 1998b)

$$EG_{mbr}(t) = \frac{X}{n} \left(1 - e^{-n^A \lambda t}\right) \quad (7)$$

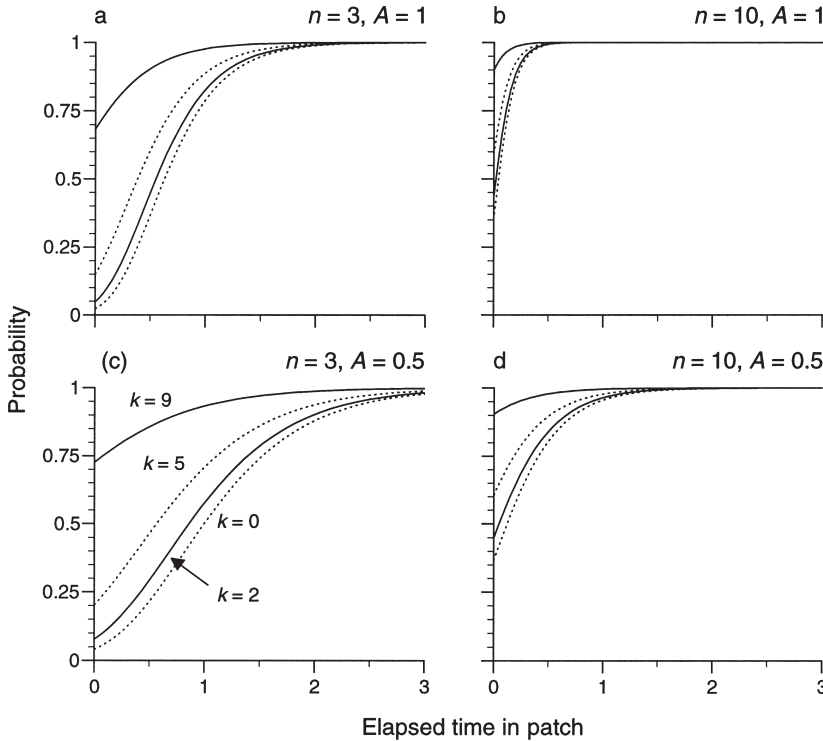


Fig. 1. The probability Eq. 5 that waiting time between the k^{th} and the subsequent prey item encounter is larger than $s = 1$ as function of patch time t . Patch size is always $X = 10$. Additivity parameter A and group size n as well as the number of prey k eaten by time t are inserted.

from this it follows that

$$(EG_{\text{mbr}})'(t) = \left(\frac{X}{n}\right) n^A \lambda e^{-n^A \lambda t}. \quad (8)$$

3. The model behaviour

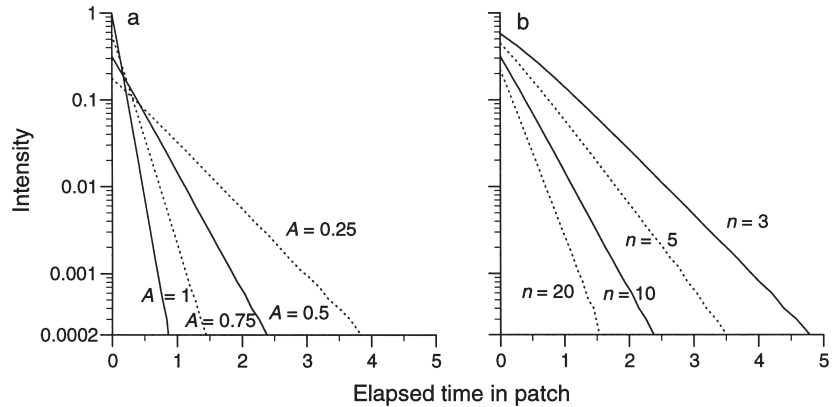
In what follows we shall, to some extent, go through main features of the model. We shall emphasize that the concept of additivity has an important bearing to how an individual “sees” the world when foraging in a group, as compared to solitary foraging. In the present context the term additivity is introduced to take care how individuals, when joining together, might affect each other while harvesting prey in the patch (Rita & Ranta 1998b). In short, full additivity $A = 1$ is achieved when the gain of the group accumulates as fast as the gains of n solitary foragers added together. Note that full additivity is assumed in many classical foraging models (Stephen & Krebs 1986, clear exceptions being, e.g., Sutherland 1983, Sutherland & Parker 1985, 1992, Parker & Suth-

erland 1986). Value $A = 0$ corresponds to drift-food as group size has no effect on the intensities affecting the waiting time between subsequent deliveries of prey. With $A > 1$ there is co-operation in foraging among the individuals in the group. Finally, negative values of A describe extreme competition as the whole group gains slower than a solitary forager would. Let us now exemplify how level of additivity affects performance of an individual foraging as a member in a group of n equal individuals. While commenting the effects of additivity we shall also rephrase the key elements in our model.

3.1. Waiting times and intensities

Let us first explore the meaning of the waiting time Eq. 5 from a group member’s point of view. For example (Fig. 1c), after gaining exactly five prey items with $A = 0.5$ by time $t = 1$ the probability not to gain the sixth one before $t = 2$ is ca. 0.7, whereas the corresponding value with full additivity $A = 1$ is close to 0.9 (Fig. 1a): with full additivity there is less prey left. An other way of

Fig. 2. The basic intensities Eq. 6 as function of patch time t . The basic intensity λ of a solitary forager is always 1.0. — a: group size is $n = 10$, the effect of different values of the additivity parameter A are explored. — b: additivity parameter is $A = 0.5$, while the foraging group size n varies. The combination $A = 0.5$ and $n = 10$ is in both panels.



looking at the waiting times (Fig. 1) goes as follows: the more the focal individual has gained (large k), the less there are prey remaining in the patch and the waiting times to gain yet another prey get longer. These probabilities increase also as function of time t : the longer the group has been exploiting the patch, the less prey there is left.

With a high level of additivity the patch of prey is exploited faster than with smaller values (Fig. 2). A similar effect is achievable via increased group size. In these cases the time in the patch for an individual forager appears to go faster — in terms of gain accumulation — than in smaller groups, or in groups where individuals disturb each other more in foraging. Naturally, time in the patch goes slower for a solitary forager, but it may go even more slowly for members in a group where each and every prey item is heavily scrambled for, i.e., $A < 0$.

The basic intensity Eq. 6 for a group member at $t = 0$ is $\tilde{\lambda}(0) = n^A \lambda / n$. In the full additive situation $A = 1$ this equals λ , which means that a member's gain resembles that of a solitary forager in a patch of size X . That is, with full additivity each member of the group can forage undisturbed as if foraging alone. Note, however that this is the situation only at time $t = 0$. With increasing time in patch, the intensities of a member soon get smaller than those of a solitary forager. When additivity is less than one, even at $t = 0$ interference decreases the intensity from solitary's λ (Fig. 2).

We have selected four different foraging scenarios, all with linear intensities (Fig. 3). First, with a solitary forager the intensities remain un-

affected as function of time in patch t (Fig. 3a). This is natural as food level in the patch is not affected by anyone else than the one and only solitary forager. When this is contrasted with the intensities of a group member (Fig. 3b), one can see a pronounced effect of the presence of other foraging individuals of the group, decreasing the food level in the patch.

Individuals in foraging groups commonly use of public information of food patch locations (Ward & Zahavi 1973, Valone 1989, Vickery *et al.* 1991) and as a consequence a patch found by a member of the foraging group will often be exploited by other individuals in the group. Finding a patch of prey leads to apparent asymmetries in foraging success, the finder and the rest of the foraging group having different opportunities to exploit prey in the patch (Giraldeau *et al.* 1990, 1994, Mangel 1990, Vickery *et al.* 1991). Two different views can be taken. First, the finder's time (Rita & Ranta 1998c) is assumed to be constant f (Fig. 3c). Up to the end of this time, the intensities remain constant as the finder foragers as a solitary individual, but after the entry of rest of the group, they start decreasing. Second, the finder's time is stochastic (Rita & Ranta 1998c) having exponential distribution (Fig. 3d; we have here assumed expectation 1.5 to make the stochastic finder's time comparable with that of the fixed time, i.e., in both cases the average finder's times are equal). As a notable difference to the fixed finder's time, the intensities start decreasing from the very beginning (Fig. 3d). This reflects the possibility that due to variability in the finder's time it may be very short (or as well

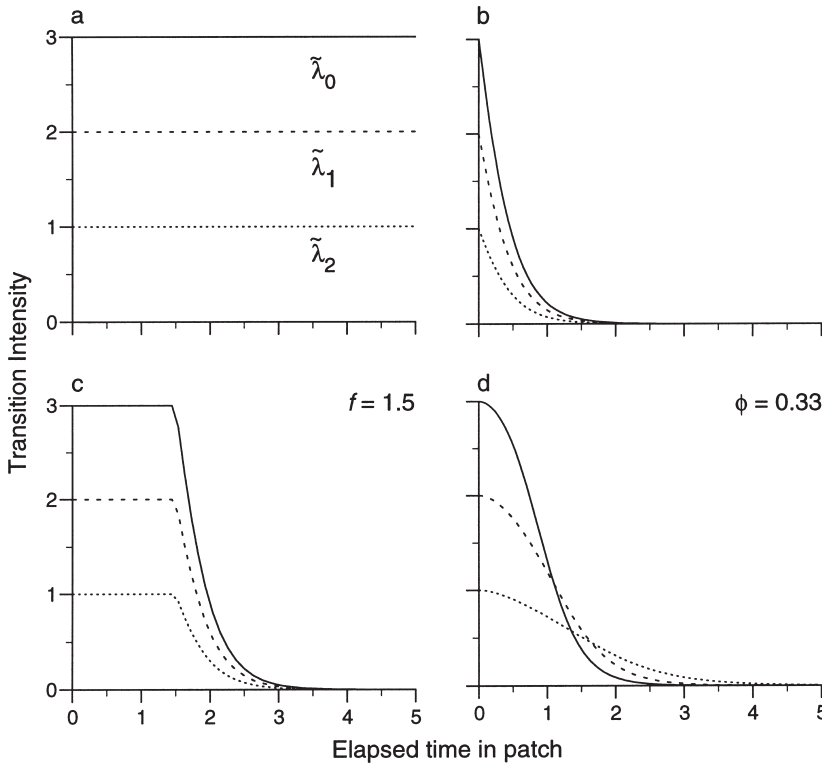


Fig. 3. Transition intensities Eq. 2 for different foraging scenarios. For simplicity of the graph patch size is always $X = 3$ (basic intensity of solitary $\lambda = 1.0$). Group intensities are linear with $A = 0.5$. — a: solitary forager. — b: member in a group of size $n = 3$. — c: finder with fixed finders time $f = 1.5$, $n = 3$. — d: finder in a group of size $n = 3$ with exponentially distributed finders time, the expectation being 1.5.

very long) and the others in the group may arrive soon to take their benefit of the food in the patch found.

In passing, our scenarios (Fig. 3c and d) also give a striking example of the fallacy of the averages: This fallacy means that if the value of a variable (here finder's time) is replaced with its average in a formula (Eq. 2), the resulting functions may differ considerably. For the concept of the fallacy of averages, see Templeton and Lawlor (1981), although the fallacy they detected did not exist (Turelli *et al.* 1992).

3.2. Food-intake rate

We have defined average food-intake rate for an individual in a foraging group to be the derivative of a member's average gain at time t , Eq. (4). Let us first assume that the foraging environment is the same for a solitary forager and the foraging group. Comparing intake rate of a solitary forager to that of a member in a foraging group merits a few comments. Only when group members co-operate ($A > 1$), the intake rate at $t = 0$ is higher

for a group member than for a solitary forager (Fig. 4a and b). However, the intake rate per individual in a co-operative group rather soon goes below that of a solitary forager. With full additivity ($A = 1$) the intake rates of a member and a solitary forager — hunting in the same environment — meet only at $t = 0$. The higher the value of A is the faster the intake rate slows down. This is natural, because the more co-operation there is, the faster the group exploits the patch. When the scramble is tight ($A = 0$), group intake rate equals that of a solitary forager, but as there are several to divide the prey in the patch, the intake rate of a member at $t = 0$ has to be divided by n .

Our next comparison scores performance of a solitary forager and an individual foraging in a group of n in a foraging environment where the number of prey available per patch for the solitary forager is x , while the prey per patch for the group is $X = xn$. In such an environment the intake rate of a member is larger at the beginning of patch exploitation (as long as A is positive), but eventually decreases below that of a solitary forager (Fig. 4c and d). With $A = 0$, the patch corresponds to a flow of prey in a drift, and the group size has no effect on the intake rate of the group.

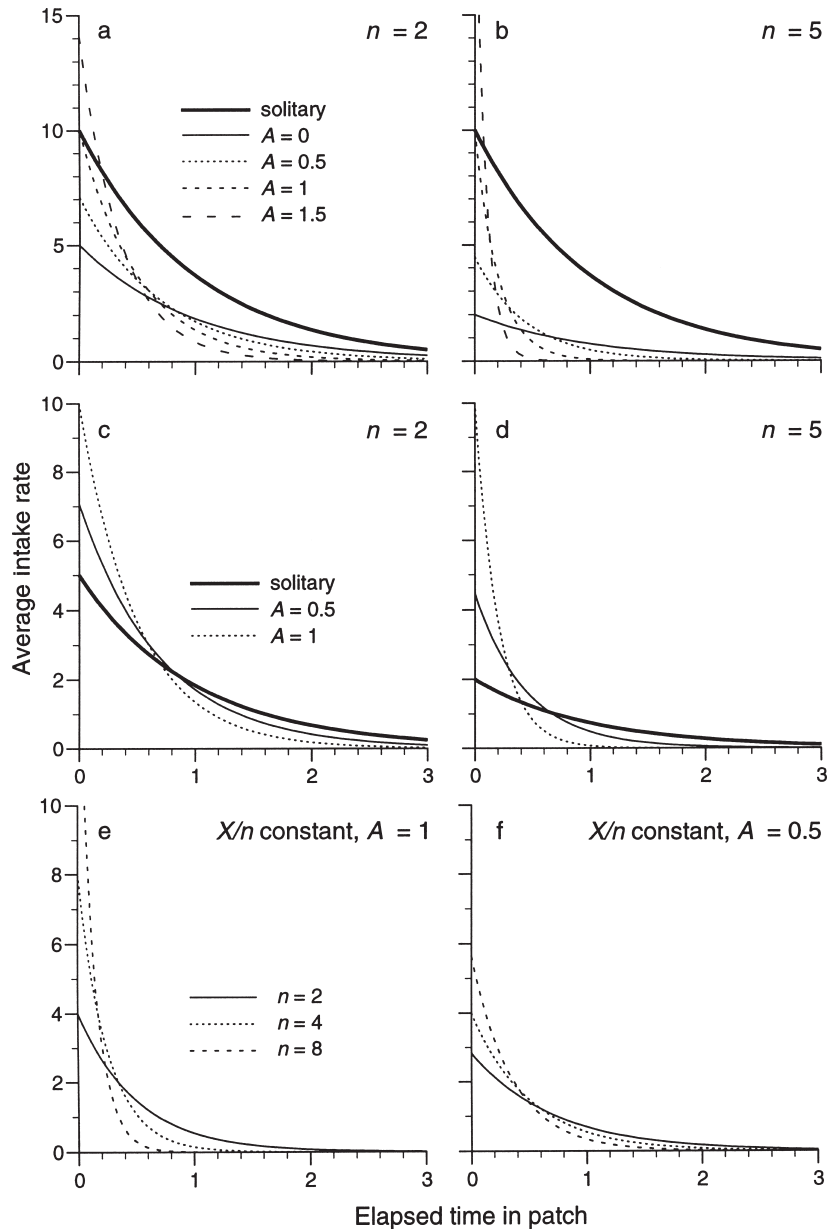


Fig. 4. Average intake rate Eq. 4 as function of patch time t . The group intensities are linear with basic intensity λ having value 1.0 in all panels. In panels *a* and *b*, values of the additivity parameter A are shown, and patch size is $X = 10$. In panels *c* and *d*, patch size is $X = 10$ except for solitary who has X/n . In panels *e* and *f*, the ratio X/n has constant value of 2, i.e., the average share per member is equal in all situations. Value of additivity A is shown.

In this case, a solitary forager in a flow of size x has equal intake rate with a member of a group of size n foraging in flow of size X for any time t in the patch. Note, however, that this is true only with linear intensities $\Lambda_k = (X - k)\Lambda$.

The final foraging scenario is an environment where the ratio X/n is kept constant, i.e., the average share of each member is equal regardless the group size. However, even with full additivity, ($A = 1$), the intake rates of individuals in groups of dif-

ferent size are not equal (Fig. 4e and f). It is noteworthy that the dependency of the intake rates of patch time t is quite different in groups differing in size, even though each group has constant ratio X/n . It should be remembered that only with $A = 0$, i.e., in a flow are the intake rates equal irrespective of the values of X and n giving constant ratio X/n . This resembles Milinski's (1979) classical test of Fretwell and Lucas' (1970) theory on ideal free distribution.

4. Discussion

The theory on ideal free distribution (Fretwell & Lucas 1970, Parker 1970) has stimulated a rich set of empirical and theoretical research on distribution of competing individuals in a patchy world (recent reviews by Milinski & Parker 1991, Tregenza 1995, Sutherland 1996). Theories on social foraging (e.g., Sibly 1983, Pulliam & Caraco 1984, Clark & Mangel 1984, Giraldeau 1988, Giraldeau & Livoreil 1997) concern also the same question, but concentrating on an individual member in a foraging group. When merged, they can be seen from the point of view of the marginal value theorem addressing whether to persist utilising a patch of prey (Charnov 1976, Stephen & Krebs 1986).

In both systems an individual's intake rate is reduced due to exploitation depleting the standing crop level in the patch and due to interactions among individuals. These processes operate by increasing time between subsequent successful encounters. We have modelled an individual's gain in a foraging group precisely through these waiting times (Rita & Ranta 1998a, 1998b). Under this domain the distribution of the gain process can be derived from differential equations for the gain probabilities. The accumulation of gain is characterized through transition intensities, which serve as parameters for the distribution. Here we focused to further the intensity characterisation of the foraging process from an individual's point of view.

One of the central concepts in our patch-foraging model is additivity. This is our way to measure to what extent an individual disturb each other when exploiting prey in a patch. Additivity functions via affecting the distribution of the waiting times. Our additivity differs from Sutherland's (1983) interference concept in that it is based on changes in search efficiency when an individual is foraging in a group, whereas Sutherland's interference parameter m describes the intake rate of a group member. We feel, a conceptual clarification to distinguish between search and share is badly needed. We shall here restrict *additivity* to how individuals affect each others' search performance.

Contrary to solitary foraging the intensities affecting the development of gain of a member in a

group decrease with increasing time in the patch. This is natural, as an individual's gain process is affected by what others in the group have achieved. In foraging groups obeying information sharing (Ward & Zahavi 1973, Valone 1989, Vickery *et al.* 1991) the decrease can be slowed down — for a limited period of time — for one individual at a time, the patch-finder (Giraldeau *et al.* 1990, 1994, Mangel 1990, Vickery *et al.* 1991, Rita & Ranta 1998c). Unless individuals permanently differ in their patch-searching abilities (Ranta *et al.* 1996), this process, however, does not give rise to long-term gain differences among individuals as they level off with increasing number of prey patches (Rita *et al.* 1996, Rita & Ranta 1998c). If there are phenotype-specific differences in patch-finding abilities among individuals the gain process is likely to create phenotype assorted foraging groups (e.g., Ranta & Lindström 1990, Ranta 1993, Ranta *et al.* 1993, 1994, Rita *et al.* 1996)

By defining average food-intake rate for an individual in a foraging group at any point of time in the patch we have been able to uncover the following key features of group foraging. First, not so surprisingly, if solitary individuals and individuals foraging as a member in a group are living in the same environment, food-intake rate of solitary foragers exceeds that of an individual in a group. Second, in environments where patch size is scaled by foraging group size ($X = xn$) the expected equal payoff is not reached but rather, the average intake rate is higher for group members in the beginning of time in the patch than for a solitary forager.

Finally, and perhaps most interestingly, assume a foraging scenario after the theory on ideal free distribution (Fretwell & Lucas 1970) with patches differing in food availability. We find that with standing crop, or rather, with depleting food patches, there is no unequivocally definable equal average food-intake rate. Matching intake-rate over patches differing in productivity (when foragers are distributed over the patches after IFD) is reached only with systems of continuous food-input, as especially emphasized by Tregenza (1994) and Lessells (1995). We definitely agree with Tregenza (1994) who claimed that continuous input of food into patches is but one foraging situation, and perhaps also a rather uncommon in the wild. To echo him we suggest that, in the distribution

of foragers over food patches, focus should be turned to study patch types more commonly encountered by foraging animals: patches with aggregated prey not renewing while being exploited.

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Appendix

We shall first show that linear group intensities imply linear $\tilde{\lambda}_k$. Assume that the group gain intensities have the linear form $\Lambda_k = (X - k)\Lambda$. This implies (Rita & Ranta 1998b) that the gain $G_{\text{mbr}}(t)$ has binomial distribution with parameters X and

$$\pi(t) = \binom{X}{n} (1 - e^{-n\Lambda t})^n. \quad (\text{A1})$$

Inserting the corresponding binomial probabilities to Eq. 2 gives — after straightforward calcu-

lation — the desired Eq. 6.

Next, task is to show that derivative of the expected gain is the average intensity. Using Eq. 3 and doing some calculation one can see that

$$\begin{aligned} (EG_{\text{mbr}})'(t) &= \frac{d}{dt} \sum_{k=0}^X k \tilde{p}_k(t) \\ &= \sum_{k=0}^X k \tilde{p}'_k(t) \\ &= \sum_{k=0}^X k \left[-\tilde{\lambda}_k(t) \tilde{p}_k(t) + \tilde{\lambda}_{k-1}(t) \tilde{p}_{k-1}(t) \right] \quad (\text{A2}) \\ &= \sum_{k=0}^X \tilde{\lambda}_k(t) \tilde{p}_k(t). \end{aligned}$$