Optimal foraging and information gathering: how should animals invest in repeated foraging bouts within the same patch?

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ABSTRACT

Questions: How much should animals invest in information gathering when they have no prior information about the present state of the foraging patch, and does the ability to use information have an effect on the size of the investment?

Mathematical method: Optimization of the size of investment when animals use the same foraging patch repeatedly.

Key assumptions: Animals determine the size of their foraging investment before each foraging bout. They make a first investment without having any prior information. They then use information gained from the experience of the first bout to estimate patch profitability. (The larger the investment during the first bout, the more accurate the estimate.)

Predictions: When patch profitability can be correctly estimated irrespective of the size of investment, animals should invest as if they were at a patch of average profitability. If larger investments do produce more accurate estimates, animals should make a greater investment than that for average profitability in the environment. The more likely it is that information proves to be invalid, the smaller the optimal investment in gaining that information. Therefore, it is expected that the species that relocates its foraging patch frequently makes a relatively smaller investment in its first foraging bout, whereas the species that exhibits strong patch tenacity makes a relatively greater investment in its first bout. Animals should pay the cost of the non-maximized gain for information that will help them to estimate foraging patch profitability more accurately and to enhance their future foraging.

Keywords: environmental uncertainty, information gathering, optimal foraging, patch use, repeated foraging.

INTRODUCTION

Animals invest their time and energy in various activities including foraging, reproduction, and parental care, and this investment is critical to fitness. Animals must be able to assess

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their environment accurately to make optimal investments in these activities (Dall *et al.*, 2005). Therefore, it is important for individuals to be able to evaluate their environment and to adjust their investments as required to maximize their fitness.

Information about environmental conditions can be obtained from various cues. In the case of foraging, the result of the investment itself possibly provides a direct indicator of how much to invest. For example, the amount of food an animal obtains is an indicator of the food availability of that habitat. In this sense, animals invest their time and energy not only to gain immediate returns, but also to obtain information on food availability for future decision making by collecting samples of the environment (McNamara, 1982; Pierre *et al.*, 2003) when they forage under conditions of uncertainty.

Most studies about foraging decisions under uncertain conditions have been conducted in the framework of Bayesian foraging (for reviews, see McNamara *et al.*, 2006; Valone, 2006). A Bayesian forager is defined as an animal that updates its expectations of the state of the environment by combining prior expectations with sampling information and makes foraging decisions based on this information. A central issue in studies of Bayesian foraging has been how an animal uses sampling information in making foraging decisions, especially the decision of when to leave its current foraging patch (e.g. Iwasa *et al.*, 1981). Animals in these studies were assumed to use a foraging patch only once and to be able to adjust the size of their investment during the foraging bout.

However, these assumptions are not applicable to some animals. For example, sessile animals, sit-and-wait foragers, and animals that regularly use the same area (i.e. home range), including animals that have fixed foraging territories, use the same foraging patch repeatedly. They do so because their foraging activity does not affect food availability or because they live in environments where the food supply is renewed constantly. Their foraging decision will differ from the patch-leaving decision; they decide how much effort they should devote to each foraging bout, which occurs many times in the same foraging patch. In addition, their decision may be made at the beginning of a foraging bout, and it may be difficult to adjust the size of the investment during the foraging bout. For example, orb-web spiders, which are typical sit-and-wait foragers, remain at one web site for a long time. They reconstruct their webs many times in the same location, and each web construction is considered one foraging bout. They must decide how large a web to construct at each web-construction event prior to foraging because it is difficult to adjust the web size after construction is completed. Bees that have foraging territories around the nest are another example. As a whole colony, the bees must decide how many foragers to send to collect nectar and pollen every day (or many times on the same day) before foraging.

In a sense, such animals can also be Bayesian foragers because they can extract information from their foraging experiences, assemble expectations, and use these to make decisions (Inoue and Marsura, 1983; Nonacs and Soriano, 1998; Venner *et al.*, 2000). However, these animals sometimes must decide how much to invest in foraging without having any information from past foraging experiences. This is expected to occur in two cases: when animals change their feeding territory or foraging patch to a new location that has never been used before, and when information from past experience becomes irrelevant to the present state of the foraging patch because of disruptive changes in the environment or interruptions to foraging caused by factors such as predator avoidance or inclement weather (Dall *et al.*, 1999). The questions we address here are how much animals should invest in information gathering when they have no prior information about the present state of the foraging patch, and whether the ability to use information has an effect on the size of the investment.

We anticipate that even when animals do not have any sampling information, the optimal size of the foraging investment should be affected by the ability of the animal to use information, because even foraging activity made without any prior sampling information will provide information that can be used in future decision making. The size of the foraging investment is considered to determine how much information the animal gathers: the larger the investment, the more information the animal is expected to obtain. For example, by constructing larger webs or by sending more forager bees, spiders and bee colonies respectively can sample a wider area. Gathering more sample information at the cost of a greater foraging investment will lower the stochastic effect of food encounters (equivalent to sampling error) in assessing the state of the environment. In other words, it leads to a more correct assessment and may be beneficial for future decisions. Because accurate information is a benefit and the investment in obtaining that information is a cost in foraging, there should be an optimal amount of investment used for both information gathering and energy intake in foraging. This benefit of information or value of information gathering is a concept similar to the 'foraging benefit of information' (Olsson and Brown, 2006), which is the benefit acquired by spending time searching a patch in a Bayesian foraging model. In the present study, we discuss the optimal amount of investment incorporating information gathering and energy intake based on an extended marginal value theorem model (Charnov, 1976).

We consider a situation in which animals use the same foraging patch repeatedly. For the sake of simplicity, we constructed a mathematical model for animals conducting two foraging bouts after past information has become useless and we explored the optimal foraging investment during the first bout. It should be noted that in the first bout, the animals make investments without having prior information. During the second bout, they use information from the experience of the first bout to estimate patch profitability. The foraging investment corresponds to the size of a trap or territory in sit-and-wait foragers such as spiders. The size of such an investment is often determined at the beginning of a foraging bout and is difficult to change during the bout. Beachly *et al.* (1995) proposed a patch-use theory for sit-and-wait foragers that use information procured from foraging, assuming that the foraging gain is a linear function of the investment (because sit-and-wait foragers do not deplete the food resources in their foraging patches), and hence the optimal investment is indefinite. However, we made a different and likely more plausible assumption: in each foraging bout, there is an optimal size of foraging investment. For example, if trap-building sit-and-wait foragers build too large a trap, foraging efficiency or energy intake during a foraging bout will deteriorate because of the increased cost of building and maintaining the traps or the reduced food capture success at the periphery of the trap, as in orb-web spiders (Vollrath, 1992). Similarly, bees can deplete the nectar supply of a flower on a particular day; therefore, sending too many forager bees may be fruitless. However, the nectar will regenerate before the next morning to a level unrelated to how many bees visited it before; therefore, the bee colony can use the same foraging territory repeatedly.

Specifically, we focused on the effect on the optimal foraging investment of the frequency of foraging patch relocation and the change in patch profitability due to an environmental change. We anticipate that animals with less opportunity for patch relocation or animals in a more stable habitat invest more in foraging to obtain accurate information. This is because information is useful for longer periods of time and is thus more valuable.

MODELS

General assumptions

We assumed a foraging area that contains foraging patches in which food density varies, and animals make investments in foraging in each patch during a constant foraging bout. In our model, the amount of the foraging investment corresponds to trap size in sit-and-wait foragers. 'Currency maximized' in the model is the total net energy intake in a foraging area, and the decision variable is the amount of foraging investment in each patch during a foraging bout. Here, we assumed that the decision is made at the beginning of a foraging bout. As stated above, this is a plausible assumption in nature.

We assumed that gross energy intake in a foraging patch can be expressed as a product of initial prey density in the patch and prey encounter rate, which is a function of the amount of investment. Thus, the net energy intake in a foraging patch i is a function of the amount of investment in the patch, x, and can be expressed as $G_i(x)$:

$$G_i(x) = D_i \cdot f(x) - x, \tag{1}$$

where D_i is the initial food density in foraging patch i, and $f(x)$ is the prey encounter rate or energy intake per foraging bout at the investment of x. The investment of x, which can correspond to trap size in sit-and-wait foragers, is converted into energy expenditure in our model. We assumed that D_i was constant between foraging bouts. This assumption is applicable when foragers take a fraction of a portion of whole food or when food availability returns to the original level within a short time. Here, we assumed $f(x) > 0$, $f'(x) > 0$, and $f''(x) < 0$ when $x > 0$. That is, the prey encounter rate is an increasing but decelerating function of the amount of investment x. Thus, $G_i(x)$ first increases but eventually decreases with increasing x. We also assumed that an animal knows the $f(x)$ and average food density, D, of the foraging area.

If an animal knows the exact food density in foraging patch i, D_i, it should invest in the optimal amount of x_i, x_i^*, which maximizes equation (1) or satisfies $G'_i(x_i^*) = 0$. In this case, the total net energy intake the animal obtains in the foraging area is the maximum possible net energy intake in the foraging area G_{max}, and can be expressed as

$$G_{max} = \Sigma[h_i \cdot (D_i \cdot f(x_i^*) - x_i^*)],$$

where h_i is the frequency (or proportion) of D_i in the foraging area.

When an animal settles in a foraging patch without knowledge of the exact food density in the patch and always invests a constant amount x_0 in any patch, the total net energy intake the animal obtains in the foraging area is $\Sigma[h_i \cdot (D_i \cdot f(x_0) - x_0)]$, i.e. $D \cdot f(x_0) - x_0$. Therefore, the optimal amount of investment, x_0^*, should maximize $D \cdot f(x_0^*) - x_0^*$. As is clear from equation (1), this indicates that the optimal amount of investment in a patch in which exact food density is unknown should be the same as that for average food density in the foraging area. For convenience, hereafter we express $D \cdot f(x) - x$ as $G_0(x)$ and $D \cdot f(x_0^*) - x_0^*$ as G_0.

It should be noted that in this case, the animal foraging in patch i, in which food density at the beginning is D_i, obtains $D_i \cdot f(x_0^*) - x_0^*$, although the animal expects G_0. This indicates that an animal that knows the $f(x)$ and D can estimate the actual food density in the patch, D_i, after foraging with an investment of x_0^*, using the difference between expected energy intake (G_0) and that obtained in practice. It should also be noted that this estimation is not

based on and differs from Bayesian estimations and that Bayes' theorem is not incorporated in this estimation. Using this estimation, the animals can make an optimal investment in the next bout.

Information gathering to estimate food density based on investment size

Here, we consider an extended case in which an accurate estimate of food density in the patch is impossible, but the accuracy varies according to the amount of investment, such that a greater investment results in greater accuracy. In this case, the benefit of the estimate is incurred during the next foraging bout, so that we consider two successive foraging bouts.

Assume that an animal first settles in a foraging patch i, for which food density is unknown, and makes an investment of the amount x_1. If the animal estimates the food density of the patch accurately depending on the amount of x_1 and invests based on the estimate in the patch in the next foraging bout, net energy intake can be expressed as

$$D_i \cdot f(x_1) - x_1 + q(x_1) \cdot (D_i \cdot f(x_i^*) - x_i^*),$$

where $q(x)$ $(0 < q(x) < 1)$ is the degree of accuracy of the estimate and $q'(x) > 0$. In other words, $q(x)$ is a proportion of the maximum energy intake from the patch. By multiplying by $(D_i \cdot f(x_i^*) - x_i^*)$, $q(x)$ functions as a penalty for an inaccurate estimate, i.e. by estimating D_i less correctly [through smaller $q(x)$], the amount of food an animal obtains will be further from the optimal. Therefore, the total net energy intake in the foraging area is $\Sigma[h_i \cdot (D_i \cdot f(x_1) - x_1)] + q(x_1) \cdot \Sigma[h_i \cdot (D_i \cdot f(x_i^*) - x_i^*)]$, i.e.

$$D \cdot f(x_1) - x_1 + q(x_1) \cdot G_{\max}. \tag{2}$$

If the animal leaves the first patch i and settles in a new, unknown patch j during the next foraging bout due to reasons such as bad foraging conditions, avoidance of predators or interference by other animals, the animal should again invest an amount x_1 in the next period. In this case, net energy intake is $D_i \cdot f(x_1) - x_1 + D_j \cdot f(x_1) - x_1$ and the total net energy intake in the foraging area is $\Sigma[h_i \cdot (D_i \cdot f(x_1) - x_1)] + \Sigma[h_j \cdot (D_j \cdot f(x_1) - x_1)]$, or $2(D \cdot f(x_1) - x_1)$, i.e. $2G_0(x_1)$. This is applicable for a case in which the animal does not use the estimate and always invests an amount x_1.

Therefore, when an animal forages first with an investment of x_1 in patch i, for which the initial food density D_i is unknown to the animal, and then leaves the patch for a new patch with a probability p or remains at the same patch based on the estimate made during the previous period with a probability $(1 - p)$, the net energy intake will be $D_i \cdot f(x_1) - x_1 + (1 - p)[q(x_1) \cdot (D_i \cdot f(x_i^*) - x_i^*)] + p [D_j \cdot f(x_1) - x_1]$, and the total net energy intake in the foraging area is

$$G_0(x_1) + (1 - p) q(x_1) \cdot G_{\max} + p G_0(x_1). \tag{3}$$

If it exists, the x_1 maximizing expression (3), x_1^*, is greater than x_0^* (see Appendix 1). This means that the animal should invest more than the investment for average food density in the foraging area, x_0^*, when it settles in an unknown patch and uses the estimate for the next foraging bout. The use of the estimate is profitable only when

$$G_0(x_1^*) + (1 - p) q(x_1^*) \cdot G_{\max} + p G_0(x_1^*) > 2G_0(x_0^*) = 2G_0.$$

If this condition is not satisfied, the optimal investment in the foraging area is always x_0^*, which is the same as that for average food density in the foraging area.

ANALYSIS

Effect of food density instability: probability of patch change

Based on the model described above, we analysed the relationship between the probability of patch change p and the optimal investment x_1^* (Table 1, Fig. 1). General features of the results are: (1) when $p = 1$, the optimal amount of investment is x_0^*, which is the same as that for average food density in the foraging area; (2) when p is larger than a threshold, the optimal amount of investment remains x_0^*, but when p is less than the threshold, the optimal amount of investment 'jumps' from x_0^* to increase with the decline in p; and (3) the threshold at which this 'jump' in investment occurs depends on the maximum possible net energy intake in the foraging area, G_{max} (Fig. 1). These features are not parameter specific because the probability p is a decreasing function of x_1^* in our model (Appendix 2). This means that because the foraging investment in our model corresponds to the size of the trap or territory in sit-and-wait foragers, animals that do not change foraging patches frequently should have larger traps or territories in unfamiliar patches than animals that change foraging patches frequently, if the estimate is profitable.

Effect of food density instability: undetectable changes in the environment

The probability of p in the model is the probability that an animal will change its foraging patch, but it can also be considered to be the instability of food density in a patch. For example, even if the animal remains in a patch, the food density may change dramatically between successive foraging bouts because of factors such as weather. If the animal can detect the change in food density in a patch after the first foraging bout, then the above model is applicable and the animal should behave as if the patch were a new one. Here, we consider animals that cannot detect the change in food density. In this case, the total net energy intake in the foraging area for foragers that invest an amount x_1 to estimate food density and invest in the next foraging period according to that estimate is $G_0(x_1) + (1 - p)$ $q(x_1) \cdot G_{max} + p\, G_{rand}$, where G_{rand} is the expected energy gain when foragers invest randomly (Appendix 3). The difference between this expression and expression (3), which was used in the analysis in the above case, lies in the last term, $p\, G_{rand}$, and $p\, G_0(x_1)$. If it exists, the x_1 maximizing this expression, x_1^*, is the optimal amount of investment in an unfamiliar patch for animals that remain in a patch for successive foraging bouts, but cannot detect the change in food density between bouts.

   Based on the model using this expression, we analysed the relationship between the instability of food density in a patch, p, and the optimal investment, x_1^* (Table 1, Fig. 2).

Table 1. Functions and parameters used for the calculations [see text for details; note that x_0^* is determined by $f(x)$]

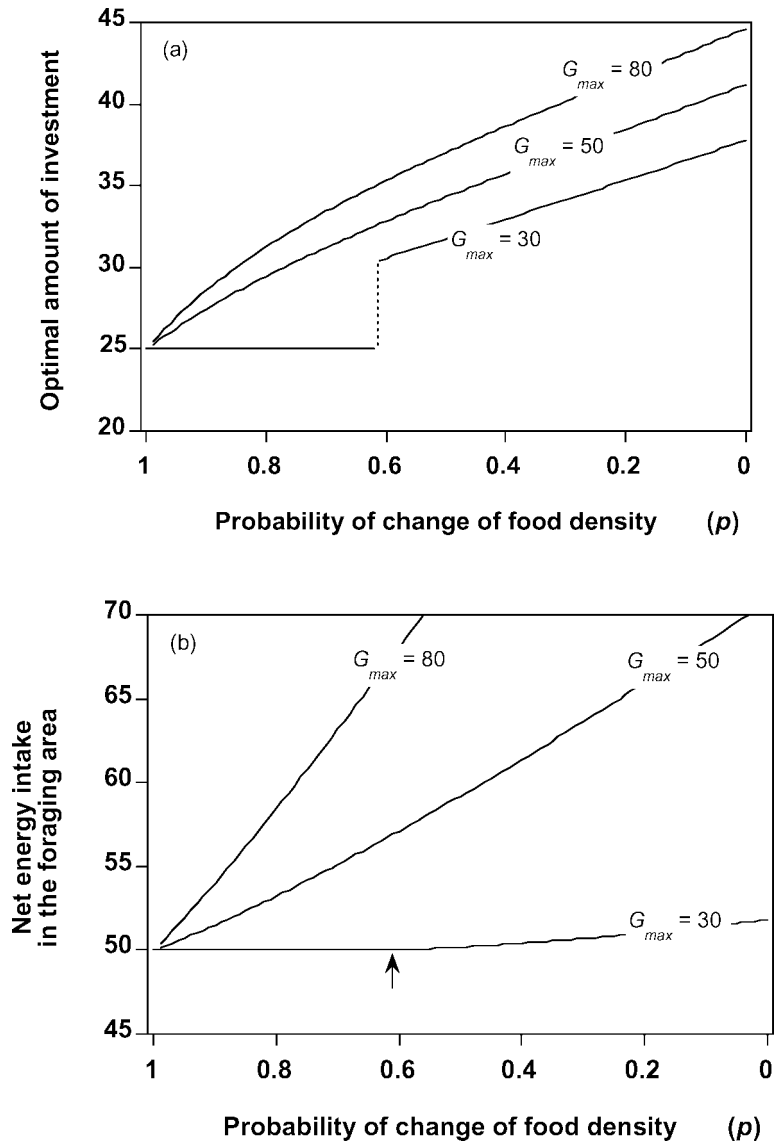|	
$f(x)$	$10\sqrt{[x]}$
$q(x)$	$1 - \exp(-0.1\,[x + 40])$
G_{max}	80, 50, 30
x_0^*	25
G_{rand}	5, 10

Fig. 1. The effect of the probability of patch change, p, on (a) the optimal amount of investment and (b) the net energy intake in the foraging area. Parameters and functions used for the calculation are provided in Table 1. Arrows in (b) indicate the point at which there is a 'jump' in the optimal amount of investment.

The general features of x_1^* for a given p are the same as those described above: (1) the optimal amount of investment is x_0^* when $p = 1$; (2) x_1^* is larger than x_0^* only when $G_0(x_1) + (1 - p) q(x_1) \cdot G_{max} + p G_{rand} > 2G_0$; (3) there is a threshold of p at which the optimal amount of investment 'jumps' from x_0^*, and then x_1^* increases with the decline in p; and (4) the threshold of p at which the 'jump' in investment occurs depends on G_{max} and G_{rand}.
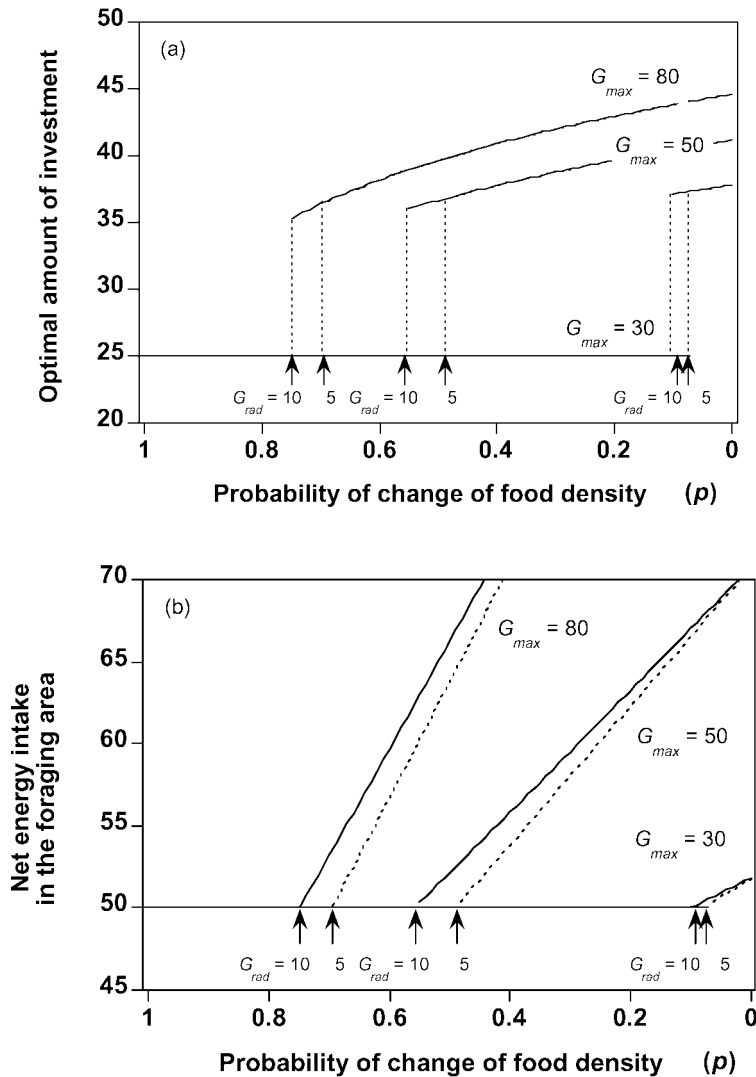
Fig. 2. Effect of food density instability in a patch, p, on (a) the optimal amount of investment and (b) the net energy intake in the foraging area. Parameters and functions used for the calculation are provided in Table 1. Arrows indicate the point at which there is a 'jump' in the optimal amount of investment. In our model, there is no effect of G_{rand} on the optimal amount of investment, although it affects the threshold at which the 'jump' occurs.

Compared with the case in which animals can detect changes in food density, the threshold of p at which the 'jump' in investment occurs is small when animals cannot detect this change. These results indicate that animals that use stable habitats should make a larger investment (e.g. larger size trap or territory) in unfamiliar patches than those that use unstable habitats, if the estimate is profitable.

DISCUSSION

We developed a model that predicts the optimal amount of foraging investment under conditions of incomplete information. Our model shows that animals should invest in foraging as if they were located in a patch of average profitability at the first bout when past information becomes useless and there is no environmental ambiguity. In contrast, animals should make a greater investment when the following two conditions are satisfied. First, the estimation of patch profitability from the foraging experience is imperfect and its accuracy is positively correlated with foraging investment, which we consider to be a plausible assumption in nature. Second, parameter p, which expresses the probability of foraging patch relocation or the probability of the change in profitability of the patch between the first and the second foraging bout (hereafter referred together as the fidelity of the foraging patch condition), is smaller than a threshold. Our model also showed a positive relationship between optimal foraging investment and the fidelity of the foraging patch condition, as well as the threshold of the fidelity where animals should increase investment levels away from the average when they are aware of a change in patch condition.

In our model, foraging investment is related to information gathering or information use. Therefore, our model concerns information value and predicts how much information should be used or how high a cost should be paid for information gathering under conditions of incomplete information. Unfortunately, few models have considered these issues directly (but see the following discussion), although many Bayesian foraging studies have considered the optimal or most effective foraging decisions under conditions of incomplete information.

Our results suggest that it can be adaptive for animals to pay the cost of the non-maximized gain in the first foraging bout to obtain information that will help them estimate foraging patch profitability more correctly, which will enhance their foraging gain during the second bout. This result is not surprising, and this 'non-maximized gain in the first foraging bout to obtain information' is a similar concept to the 'foraging benefit of information' (Olsson and Brown, 2006), which is derived from a Bayesian foraging model, although our model is not based on the Bayesian theorem, but is a kind of extended marginal value theorem, maximizing a static function. In addition, our model assumes that information on food availability obtained during a foraging bout is not used in the present but in the next foraging bout, whereas Bayesian foraging and other information-use models assume that the information obtained is used in the present foraging bout. It is interesting that these two different principles yield similar results.

Our model also suggests that animals should make a larger investment to obtain more valuable information. In general, there are two types of costs in estimating the foraging environment: the cost of sampling and the cost due to inaccurate estimation. Both patch-condition fidelity and awareness of change in the environment affect the estimation cost. Patch-condition fidelity determines the opportunity that animals have to enhance foraging gains in the second bout using information from the first bout. It means that the value of information (Stephens, 1989) is positively correlated with patch-condition fidelity. Similarly, whether animals are aware of the change affects the value of the information: when patch quality changes, information from past foraging experiences is irrelevant for future decisions. Nevertheless, when animals are not aware of the change, they could wrongly adjust their investment according to irrelevant information and thus decrease any foraging

gains during the second bout. In this case, the information gained from the first foraging bout is actually detrimental.

Stephens and Krebs (1986) and Stephens (1987) used mathematical models to examine how often an animal should sample information in a changing environment. They found that information sampling intensity is higher when the relative value to the cost of information sampling is higher. In our model, the value of sampling is affected by the probability of a change in food density (the parameter p in our model) because the information sampled during a current bout is used in the next bout, and the value of sampling is higher when the probability of a change in food density is lower. In such a case, our model predicts that the sampling intensity should be greater (Fig. 2a), which is consistent with previous models.

In empirically testing the predictions from our study, food acquisition and the sampling of food availability cannot always be distinguished easily in a field study (Naef-Daenzer, 2000). In practice, it will be important to determine whether foraging activity increases as patch-condition fidelity increases over time. Evidence to support our results can be found in the trap-building behaviour of orb-web spiders and ant-lions after nest-site relocation. These trap builders are not completely sedentary animals, but sometimes move their traps to new locations that they have never used before (Riechert and Gillespie, 1986; Scharf and Ovadia, 2006). Thus, after nest-site relocation, they must construct their traps without prior information about the profitability of the new patch, as modelled in our study. We propose that our model can be applied to empirically test how they invest in trap building after nest-site relocation. Nakata and Ushimaru (2004) observed web construction behaviour in newly located foraging patches in two orb-web spider species that exhibit different web-site tenacity. They found that the species that relocates its webs frequently made smaller webs than usual, but the species that exhibits strong patch tenacity did not exhibit any reduction in web size. Heinrich and Heinrich (1984) reported that the ant-lion *Myrmeleon immaculatus* tends to build smaller pits in newly located foraging patches when it exhibits a high pit relocation rate. In contrast, *M. immaculatus* that relocate their pits less frequently increase the pit size in new foraging patches. This evidence is consistent with the results of our model.

In conclusion, our model shows that animals should make a greater investment than that for average profitability when the accuracy of the estimation of patch profitability is positively correlated with the size of the investment, and the optimal investment should be negatively correlated with the probability of information proving to be invalid, indicating that animals should pay the cost of the non-maximized gain for information that will help them to estimate foraging patch profitability more accurately and enhance their future foraging gain, and animals should pay more to obtain more valuable information. These results highlight the importance of examining the effect of information gathering in the study of foraging ecology. When, how, and to what extent animals devote their activity to obtaining information that will be used later should be examined more extensively both theoretically and empirically in future studies.

REFERENCES

Beachly, W.M., Stephens, D.W. and Toyer, K.B. 1995. On the economics of sit-and-wait foraging: site selection and assessment. *Behav. Ecol.*, **6**: 258–268.

Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.*, **9**: 129–136.

Dall, S.R.X., McNamara, J.M. and Cuthill, I.C. 1999. Interruptions to foraging and learning in a changing environment. *Anim. Behav.*, **57**: 233–241.

Dall, S.R.X., Giraldeau, L.-A. and Olsson, O. 2005. Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.*, **20**: 187–193.

Heinrich, B. and Heinrich, M.J.E. 1984. The pit-trapping foraging strategy of the ant lion, *Myrmeleon immaculatus* De Geer (Neuroptera: Myrmeleontidae). *Behav. Ecol. Sociobiol.*, **14**: 151–160.

Inoue, T. and Marsura, T. 1983. Foraging strategy of a mantid, *Paratenodera angustipennis* S.: mechanisms of switching tactics between ambush and active search. *Oecologia*, **56**: 264–271.

Iwasa, Y., Higashi, M. and Yamamura, N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *Am. Nat.*, **117**: 710–723.

McNamara, J. 1982. Optimal patch use in a stochastic environment. *Theor. Popul. Biol.*, **21**: 269–288.

McNamara, J.M., Green, R.F. and Olsson, O. 2006. Bayes' theorem and its applications in animal behaviour. *Oikos*, **112**: 243–251.

Naef-Daenzer, B. 2000. Patch time allocation and patch sampling by foraging great and blue tits. *Anim. Behav.*, **59**: 989–999.

Nakata, K. and Ushimaru, A. 2004. Difference in web construction behavior at newly occupied web sites between two *Cyclosa* species. *Ethology*, **110**: 397–411.

Nonacs, P. and Soriano, J.L. 1998. Patch sampling behaviour and future foraging expectations in Argentine ants, *Linepithema humile. Anim. Behav.*, **55**: 519–527.

Olsson, O. and Brown, J.S. 2006. The foraging benefits of information and the penalty of ignorance. *Oikos*, **112**: 260–273.

Pierre, J.-S., van Baaren, J. and Boivin, G. 2003. Patch leaving decision rules in parasitoids: do they use sequential decisional sampling? *Behav. Ecol. Sociobiol.*, **54**: 147–155.

Riechert, S.E. and Gillespie, R.G. 1986. Habitat choice and utilization in web-building spiders. In *Spiders: Webs, Behavior and Evolution* (W.A. Shear, ed.), pp. 23–48. Stanford, CA: Stanford University Press.

Scharf, I. and Ovadia, O. 2006. Factors influencing site abandonment and site selection in a sit-and-wait predator: a review of pit-building antlion larvae. *J. Insect Behav.*, **19**: 197–218.

Stephens, D.W. 1987. On economically tracking a variable environment. *Theor. Popul. Biol.*, **32**: 15–25.

Stephens, D.W. 1989. Variance and the value of information. *Am. Nat.*, **134**: 128–140.

Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.

Valone, T.J. 2006. Are animals capable of Bayesian updating? An empirical review. *Oikos*, **112**: 252–259.

Venner, S., Pasquet, A. and Leborgne, R. 2000: Web-building behaviour in the orb-weaving spider *Zygiella x-notata*: influence of experience. *Anim. Behav.*, **59**: 603–611.

Vollrath, F. 1992. Analysis and interpretation of orb spider exploration and web-building behaviour. *Adv. Study Behav.*, **21**: 147–199.

APPENDIX 1: PROOF FOR $x_1^* > x_0^*$

Let the total energy intake in a foraging area be

$$y = G_0(x_1) + (1 - p) \cdot q(x) \cdot G_{max} + p \cdot G_0(x_1),$$

when the accuracy of estimation depends on the amount of the investment (see text). We

assume that $G_0(x_1)$ is a convex function of x_1. The optimal x_1, x_1^*, maximizing y should then satisfy

$$y' = (1 + p) \cdot G_0'(x_1^*) + q'(x_1^*) \cdot G_{max} = 0.$$

Because $q'(x) \cdot G_{max} > 0$, to satisfy this equation, $G_0'(x_1^*)$ must be negative, which means that the x_1^* satisfying the equation is larger than the x_0^* that satisfies $G_0'(x_0^*) = 0$.

APPENDIX 2: PROOF THAT PARAMETER p IS A DECREASING FUNCTION OF x_1^*

Let expression (3) be $G(x_1)$. Then x_1^* satisfies $G'(x_1^*) = 0$, or $(1 + p)\ G_0'(x_1^*) + (1 - p)\ q'(x_1^*) \cdot G_{max} = 0$. Transforming this equation, we obtain

$$p = - [G_0'(x_1^*) + q'(x_1^*) \cdot G_{max}]/[G_0'(x_1^*) - q'(x_1^*) \cdot G_{max}] \tag{4}$$

and

$$dp/dx_1^* = -2G_{max} [G_0'(x_1^*) \cdot q''(x_1^*) - G_0''(x_1^*) \cdot q'(x_1^*)]/[G_0'(x_1^*) - q'(x_1^*) \cdot G_{max}]^2. \tag{5}$$

For the optimal x_1, x_1^*, that maximizes $G(x_1)$ to exist, $G(x_1)$ must be a convex function within the range of reasonable x_1. The necessary condition for this is $G''(x_1) < 0$, and therefore $G''(x_1^*) < 0$. Because $G''(x_1^*)$ is $p\ [G_0''(x_1^*) - q''(x_1^*) \cdot G_{max}] + G_0''(x_1^*) + q''(x_1^*) \cdot G_{max}$, from equation (4) this condition can be expressed as $-[G_0''(x_1^*) - q''(x_1^*) \cdot G_{max}][G_0'(x_1^*) + q'(x_1^*) \cdot G_{max}]/[G_0'(x_1^*) - q'(x_1^*) \cdot G_{max}] + G_0''(x_1^*) + q''(x_1^*) \cdot G_{max} < 0$, i.e.

$$2G_{max} [G_0'(x_1^*) \cdot q''(x_1^*) - G_0''(x_1^*) \cdot q'(x_1^*)]/[G_0'(x_1^*) - q'(x_1^*) \cdot G_{max}] < 0. \tag{6}$$

Because x_1^* is larger than x_0^*, if it exists, $G_0'(x_1^*)$ should be negative and $q'(x_1^*) \cdot G_{max} > 0$, which then leads to $2G_{max} [G_0'(x_1^*) \cdot q''(x_1^*) - G_0''(x_1^*) \cdot q'(x_1^*)] > 0$. This indicates that equation (5) is negative, which means that p is a decreasing function of x_1^*, if x_1^* exists.

APPENDIX 3: TOTAL ENERGY INTAKE FOR ANIMALS THAT CANNOT DETECT THE CHANGE

Let an animal that forages first at patch i, in which the initial food density D_i is unknown to the animal, invest an amount x_1 to estimate food density and invest $x_i^{*\prime}$ in the next foraging period according to the initial estimate. Assuming that the change in food density is random in the next bout with a probability of p, the net energy intake the animal obtains will be $D_i \cdot f(x_1) - x_1 + (1 - p)[q(x_1) \cdot (D_i \cdot f(x_i^*) - x_i^*)] + p\ [D_j \cdot f(x_i^{*\prime}) - x_i^{*\prime}]$, and the total net energy intake in the foraging area is $G_0(x_1) + (1 - p)\ q(x_1) \cdot G_{max} + p\ \Sigma[h_j \cdot (D_j \cdot f(x_i^{*\prime}) - x_i^{*\prime})]$. The last term, $\Sigma[h_j \cdot (D_j \cdot f(x_i^{*\prime}) - x_i^{*\prime})]$, can be considered not to be a function of x_1 because if the food density changes randomly, the accuracy of the investment for the previous density has no effect on the energy intake at the present time. Therefore, we assume that $\Sigma[h_j \cdot (D_j \cdot f(x_i^{*\prime}) - x_i^{*\prime})]$ can be expressed as G_{rand}, and the total net energy intake in the foraging area is

$$G_0(x_1) + (1 - p)\ q(x_1) \cdot G_{max} + p\ G_{rand}. \tag{7}$$