

## Departure time versus departure rate: How to forage optimally when you are stupid

Frederick R. Adler<sup>1\*</sup> and Mirjam Kotar<sup>2</sup>

<sup>1</sup>*Departments of Mathematics and of Biology and* <sup>2</sup>*School of Medicine, University of Utah, Salt Lake City, UT 84112, USA*

---

### ABSTRACT

Foragers unable to leave a patch at the optimal moment must act as constrained foragers. Extending the results of Houston and McNamara (1985), we compare a blundering forager that leaves patches at a constant rate with an unconstrained optimal forager that leaves patches at the optimal time. When a dimensionless measure of environmental quality exceeds a particular value, the blundering forager remains in patches longer on average than the unconstrained optimal forager. The relative success of the blundering forager is, paradoxically, lowest when its average departure time exactly matches that of the unconstrained optimal forager. When foraging in two dimensions, blundering provides a robust spatial foraging strategy for dealing with unknown differences in patch size.

*Keywords:* blundering foragers, error-constrained foraging, Marginal Value Theorem, optimal foraging.

### INTRODUCTION

The Marginal Value Theorem states that an organism should leave a patch the instant the consumption rate drops below the average rate available in the environment (Charnov, 1976). Some organisms might not be clever enough to do this. When powers of assessment are limited, an organism might have to guess how bad things have become, as when a parasitoid cannot recognize parasitized hosts (Rosenheim and Mangel, 1994), or when a guinea pig takes time to assess patch quality (Cassini and Kacelnik, 1994). When knowledge of location is limited, an organism might have to guess whether it has in fact left the patch (Schmidt and Brown, 1996). When intelligence is limited, an organism might be unable to ‘decide’ to leave (Houston and McNamara, 1985; Crowley *et al.*, 1990), or have difficulty in estimating either residence or travel times (Brunner *et al.*, 1992; Bateson and Kacelnik, 1995).

In this paper, we study a model of a simple organism where the patch departure ‘decision’ is based on the probability of getting lost. The forager can adjust only its *rate* of getting lost, which controls only the *average* time it leaves a patch. Such a blundering forager cannot do as well as an unconstrained optimal forager (Houston and McNamara, 1985). Its behaviour

---

\* Author to whom all correspondence should be addressed. e-mail: [adler@math.utah.edu](mailto:adler@math.utah.edu)

will also be more variable. Several studies have observed coefficients of variation of departure time as large as 0.6 (Marschall *et al.*, 1989; Åström *et al.*, 1990; Cassini *et al.*, 1990; Crowley *et al.*, 1990). Of course, many other mechanisms can explain such variation, including differences in experience (Iwasa *et al.*, 1981) and changes in state (Newman, 1991).

Crowley *et al.* (1990) distinguish between 'inadvertent errors' and 'error-constrained optimization'. In the former case, organisms miss the optimal target, but do not take those errors into account to correct their foraging strategy. In the latter case, organisms are aware that they have bad aim and compensate to the best of their limited abilities.

The models presented here were inspired by observations of the nematode *Caenorhabditis elegans* foraging on patches of its bacterial food in the laboratory (M. Kotar, unpublished data). These worms, equipped with only 302 neurons (Wood, 1988), left discrete food patches when they blundered away and could not find the way back. No 'decision' was made to leave the patch; departure was a consequence of foraging within the patch.

Even organisms like *C. elegans*, which lack the spine to make decisions, can potentially adjust the rate at which they leave a patch in response to deteriorating conditions (Driessen *et al.*, 1995). This paper studies how well a forager can do without even this basic facultative adjustment. The underlying model thus has an exponential residence time distribution (Marschall *et al.*, 1989), which is a special case of the gamma distributions studied by Houston and McNamara (1985). The exponential distribution is 'memoryless', meaning that the probability of departure does not change with residence time, and thus models the behaviour of a blundering forager.

This paper extends and clarifies the results of Houston and McNamara (1985) in three ways. First, we compare the strategies of unconstrained optimal foragers and blundering foragers, finding that the mean residence time of the blundering forager exceeds that of the unconstrained forager when the product of the patch depletion rate and the travel time between patches exceeds a critical dimensionless value. Secondly, we show quite generally that the relative success of the blundering forager is *lowest* precisely at the point where its mean strategy matches that of the unconstrained optimal forager. Finally, we show that blundering foragers can cope with a range of patch sizes precisely as well as with a single patch size, with behaviour governed by the product of the harmonic mean of patch depletion rates with the travel time. Although never optimal, getting lost is a reasonably robust foraging strategy in the face of uncertainty about patch boundaries. The last result provides a hint of the connection between patch-based optimal foraging theory and the theory of area-restricted search (Bell, 1991; Benhamou, 1992; Focardi and Marcellini, 1995; Schmidt and Brown, 1996; Grünbaum, 1998).

### SINGLE PATCH SIZE

The framework is a special case of the Marginal Value Theorem (Charnov, 1976). The total amount of food collected from a patch by time  $t$  is:

$$G(t) = \frac{1 - e^{-at}}{a} \quad (1)$$

The initial consumption rate is scaled to 1 for later convenience. The travel time between patches is assumed to take the constant value  $T$ . Organisms seek to maximize the rate at which food is collected (Stephens and Krebs, 1986). The parameters used in the models are given in Table 1.

**Table 1.** Variables and parameters

| Symbol      | Description                                     |
|-------------|-------------------------------------------------|
| $a$         | Rate of depletion of patch                      |
| $T$         | Travel time between patches                     |
| $\hat{T}$   | Non-dimensionalized travel time $\hat{T} = aT$  |
| $t^*$       | Unconstrained optimal departure time            |
| $\hat{t}^*$ | Non-dimensionalized optimal departure time      |
| $\lambda$   | Departure rate of blundering forager            |
| $\bar{t}$   | Mean departure time of blundering forager       |
| $\hat{t}$   | Optimal mean non-dimensionalized departure time |

### Optimal departure time for an unconstrained forager

Assume first that all patches have the same value of  $a$ . The unconstrained optimal forager can choose its departure time  $t$  precisely. It collects an amount of food  $G(t)$  in time  $T + t$ , the sum of travel time and time in the patch. The intake rate is:

$$R_o(t) = \frac{G(t)}{T + t} = \frac{(1 - e^{-at})/a}{T + t}$$

$R_o(t)$  takes on its maximum when the strategy  $t^*$  satisfies  $G'(t^*) = R_o(t^*)$ , where  $G'(t)$  is the derivative of the gain function. To facilitate comparison with the blundering forager, we write this equation in non-dimensional form (Charnov, 1993; Stephens and Dunbar, 1993). Set

$$\hat{T} = aT, \quad \hat{t}^* = at^* \quad (2)$$

The non-dimensionalized travel time  $\hat{T}$  summarizes the quality of the environment, while the non-dimensionalized departure time  $\hat{t}^*$  summarizes the strategy. In terms of these dimensionless parameters, the maximization criterion  $G'(t^*) = R_o(t^*)$  can be rewritten as follows:

$$e^{-\hat{t}^*} = \frac{1 - e^{-\hat{t}^*}}{\hat{T} + \hat{t}^*} \quad (3)$$

The solution for  $\hat{t}^*$  depends only on  $\hat{T}$ . Although this equation cannot be solved algebraically, we can compare the solution with that of the blundering forager (for an approximate solution, see Stephens and Dunbar, 1993).

### Optimal departure rate for a blundering forager

To find the optimal departure rate, we must average over all possible outcomes of the process of getting lost (Houston and McNamara, 1985). Suppose the blundering forager gets lost at rate  $\lambda$ . The probability that it leaves the patch at time  $t$  follows the exponential distribution  $\lambda e^{-\lambda t}$  (Adler, 1998). The mean amount of food collected during a visit is:

$$\int_{t=0}^{\infty} \lambda e^{-\lambda t} G(t) dt = \int_{t=0}^{\infty} \lambda e^{-\lambda t} \left( \frac{1 - e^{-at}}{a} \right) dt = \frac{1}{\lambda + a}$$

The mean amount of time spent in a patch is  $\bar{t} = 1/\lambda$ , so the long-term rate of intake can be written in terms of the mean residence time as:

$$R_b(\bar{t}) = \frac{\bar{t}/(1 + a\bar{t})}{T + \bar{t}}$$

This is a special case of the form derived in Houston and McNamara (1985). This has the form of the intake rate for an unconstrained optimal forager, but the gain function  $G(t)$  (equation 1) has been replaced by

$$G_b(\bar{t}) = \frac{\bar{t}}{1 + a\bar{t}}$$

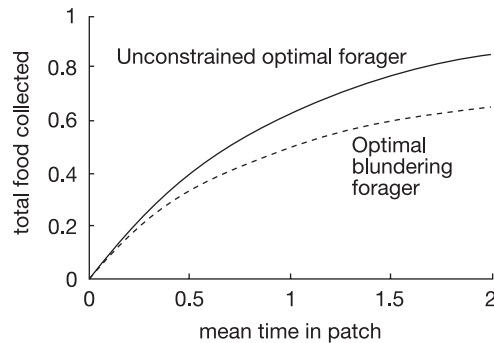
(Fig. 1). For a given mean residence time, the consumption by the blundering forager lies below that of the unconstrained optimal forager (and does so in general when the gain function  $G$  is concave down). The intake rate  $R_b$  has its maximum where  $\bar{t} = \sqrt{T/a}$ .

How does this strategy compare with that of the unconstrained optimal forager? We define the dimensionless average residence time  $\hat{t}$  as  $\hat{t} = a\bar{t}$ , which has its optimum where  $\hat{t} = \sqrt{aT} = \sqrt{\hat{T}}$  (the square root of the non-dimensionalized travel time). If  $\hat{t} = \hat{t}^*$ , the average residence time of the optimal blundering forager is equal to the residence time of the unconstrained optimal forager. We can check this condition by substituting  $\hat{t} = \sqrt{\hat{T}}$  into the optimization criterion for the unconstrained optimal forager (equation 3), or

$$\frac{1 - e^{-\sqrt{\hat{T}}}}{\hat{T} + \sqrt{\hat{T}}} = e^{-\sqrt{\hat{T}}}$$

This equation can be solved numerically for  $\hat{T} = 3.215$ . If  $\hat{T} > 3.215$ , the resource environment is poor, and a blundering forager must hedge its bets and risk remaining in patches longer than is optimal. When  $\hat{T} < 3.215$ , the resource environment is good, and the blundering forager does best by often remaining in patches shorter than is optimal (Fig. 2).

The analysis can be repeated to compare the median departure time of the blundering forager with that of the unconstrained optimal forager. The blundering forager is favoured to remain in the patch with a median time greater than the optimal time if  $\hat{T} > 22.50$ .



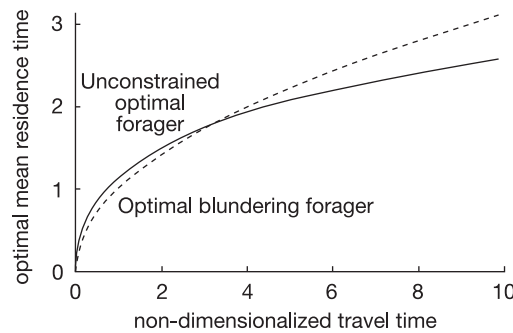
**Fig. 1.** Comparison of the gain as a function of residence time for the unconstrained optimal forager (solid line) with the gain as a function of mean residence time for the optimal blundering forager (dashed line). Parameter values are  $a = 1$  (depletion rate of patch) and  $T = 1$  (travel time between patches).

The blundering forager always has a lower payoff than the unconstrained optimal forager (Fig. 3a) ('too obvious to require much comment', according to Houston and McNamara, 1985). The ratio of fitnesses reaches a minimum of 0.7701, precisely at the critical value  $\hat{T} = 3.215$  (Fig. 3b). It is worst to be stupid precisely when your behaviour, on average, matches the unconstrained optimum. This result is demonstrated in general below.

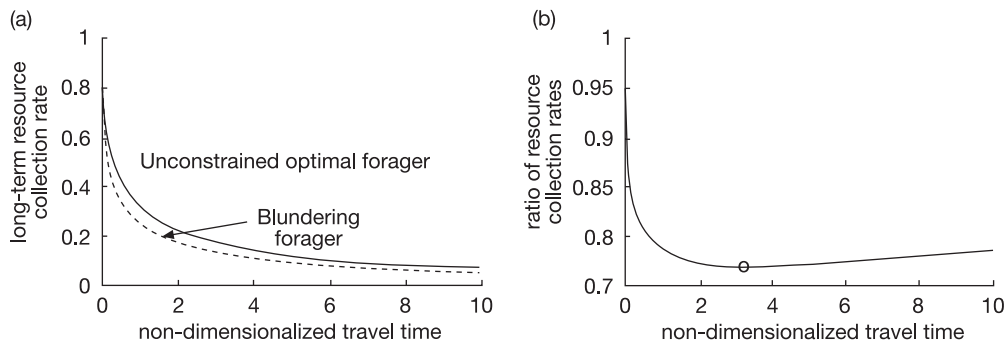
The above analysis used an exponential form for the gain function. With the alternative form

$$G(t) = \frac{t}{1 + at}$$

for the unconstrained optimal forager, the optimal departure time is  $t^* = \sqrt{T/a}$ . The optimal departure rate for the blundering forager must be found numerically. The qualitative pattern is identical to the exponential case, but the crossing point occurs instead at  $\hat{T} = 1.9336$ . With this gain function, the blundering forager should remain longer on average when  $\hat{T}$  exceeds this critical value.



**Fig. 2.** Dimensionless optimal residence time  $\hat{t}^*$  for the unconstrained optimal forager (solid line) and optimal mean residence time  $\hat{t}$  for the blundering forager (dashed line) as functions of the non-dimensionalized travel time  $\hat{T} = aT$ . The blundering forager remains longer on average when the environment is unfavourable (large values of  $\hat{T}$ ).



**Fig. 3.** (a) The payoffs to unconstrained optimal foragers (solid line) and blundering foragers (dashed line) as functions of the non-dimensionalized travel time  $\hat{T}$ . (b) The ratio of the payoff to a blundering forager to that of an unconstrained optimal forager as a function of  $\hat{T}$ . The blundering forager does relatively worst at the critical value  $\hat{T} = 3.215$ .

### When blundering foragers do the worst

In each case discussed above, the blundering forager has an effective gain function  $G_b(t)$  that lies below the true gain function  $G(t)$ . It is indeed too obvious to require much comment that the blundering forager does worse. But when does it pay the greatest cost for its stupidity?

Consider the general case illustrated in Fig. 4. A superior forager has gain function  $G$  with optimal strategy  $t^*$ , and an inferior forager has gain function  $G_b$  with optimal strategy  $t_b^*$ . These strategies must satisfy the Marginal Value Theorem requirements:

$$\frac{G(t^*)}{T + t^*} = G'(t^*), \quad \frac{G_b(t_b^*)}{T + t_b^*} = G'_b(t_b^*)$$

We have assumed that the two forager types have the same travel time  $T$ , meaning that differences in foraging within patches do not extend to differences in searching for patches (see Charnov and Parker, 1995, for a discussion of this case).

We can think of the optimal departure times  $t^*$  and  $t_b^*$  and the resulting intake rates as functions of the travel time  $T$ . The ratio of intake rates at these optimal times,  $r(T)$ , has derivative

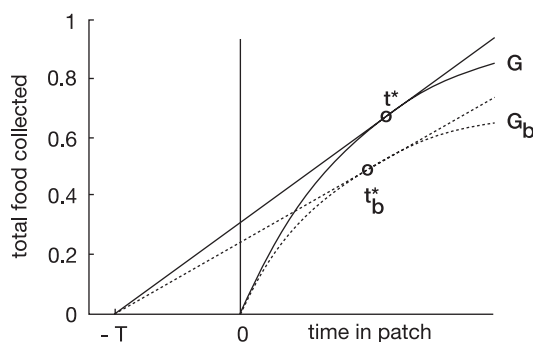
$$\frac{dr}{dT} = \frac{G'(t^*)}{G'_b(t_b^*)} \left( \frac{1}{t^* + T} - \frac{1}{t_b^* + T} \right)$$

This is zero if, and only if,  $t^* = t_b^*$ . All critical points, and potential minima, must occur when two optimal strategies match. Furthermore, the derivative is negative when  $t_b^* < t^*$  and positive when  $t_b^* > t^*$ , implying that  $t^* = t_b^*$  is a global minimum.

The global minimum always occurs when the average strategy of the blundering forager matches that of the optimal forager. The blundering forager does worst precisely when it might be thought to be doing the best.

### MULTIPLE PATCH SIZES

Suppose now that there are patches of a range of sizes, denoted by  $A_i$ , and that patches of size  $A_i$  are encountered with probability  $\beta_i$ . Assume that patch  $i$  is depleted at a rate inversely



**Fig. 4.** Optimal departure times for foragers with two different gain functions,  $t^*$  (marked with a circle on the solid gain function  $G$ ) and  $t_b^*$  (marked with a circle on the dashed gain function  $G_b$ ). The inferior forager with gain function  $G_b$  does relatively worst when  $t^* = t_b^*$ .

proportional to its size, or  $a_i = \rho/A_i$  for some constant  $\rho$  with units of area per time. The amount of food acquired from patch  $i$  by time  $t$  is:

$$G_i(t) = \frac{1 - e^{-a_i t}}{a_i}$$

As  $t$  becomes large, the food acquired approaches  $A_i/\rho$ . Large patches have greater potential resources and are depleted more slowly. The initial rate of intake is the same value (scaled to 1.0) in each patch, as in model 2 of Åström *et al.* (1990). Such a model corresponds to a case where a patch, like a tree, always has some highly available and desirable resource. Patches thus differ in size rather than quality.

### Optimal departure time for an unconstrained forager

To find the unconstrained optimal departure times, we maximize the average food per visit divided by the time per visit as a function of the departure time  $t_i^*$ . The payoff is

$$R_o = \frac{\sum_{j=1}^n (\beta_j/a_j)(1 - e^{-a_j t_j^*})}{T + \sum_{j=1}^n \beta_j t_j^*}$$

which has a maximum where  $e^{-a_i t_i^*} = R_o$  for each  $i$ . Therefore, the value

$$\hat{t}^* = a_i t_i^* \quad (4)$$

is the same for each patch. The optimal departure time is thus inversely proportional to  $a_i$ , and directly proportional to the patch size  $A_i$ .

As before, the equations can be simplified by rewriting them in dimensionless form. Define

$$\tilde{a} = \frac{1}{\sum_{j=1}^n (\beta_j/a_j)}$$

as the harmonic mean of the  $a$  values, and set  $\hat{T} = \tilde{a}T$ . The harmonic mean  $\tilde{a}$  is proportional to the reciprocal of the ordinary arithmetic mean of the patch sizes (see also Åström *et al.*, 1990). This equation generalizes the original definition of  $\hat{T}$  (equation 2). The optimal value of  $\hat{t}^*$  again satisfies equation (3), the equation for  $\hat{t}^*$  with a single patch size.

### Optimal departure rate for a blundering forager

Suppose that blundering foragers get lost from a patch at rate  $\lambda_i$ , which is inversely proportional to the size of the patch. This is the null model of departure rate from a patch for an organism following a random walk in two dimensions (Berg, 1993). Because depletion is inversely proportional to patch size,

$$\lambda_i = w a_i \quad (5)$$

for some constant  $w$ . The value of  $w$  represents the ‘wandering’ tendency and describes the strategy to be optimized. The expected amount of food gleaned from a patch, found by averaging the total intake over the exponential distribution of residence times, is:

$$G_{b,i}(\lambda) = \int_{t=0}^{\infty} \lambda_i e^{-\lambda_i t} \left( \frac{1 - e^{-a_i t}}{a_i} \right) dt = \frac{1}{a_i + \lambda_i} = \left( \frac{1}{1 + w} \right) \left( \frac{1}{a_i} \right)$$

The overall average intake rate is

$$R_b = \frac{(1/1 + w) \sum_{j=1}^n (\beta_j/a_j)}{T + (1/w) \sum_{j=1}^n (\beta_j/a_j)} = \frac{(1/1 + w) (1/\tilde{a})}{T + (1/w\tilde{a})}$$

The value of  $w$  that maximizes  $R_b$  is  $w = 1/\sqrt{\hat{T}}$ , which means that the average time spent in patch  $i$  is

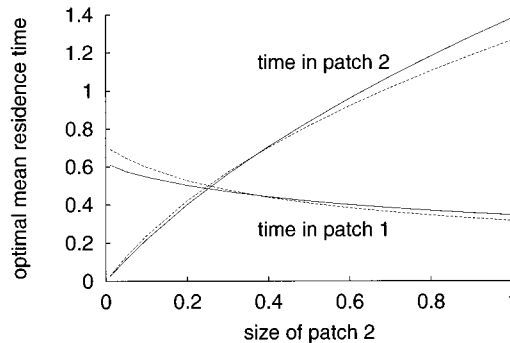
$$\bar{t}_i = \frac{1}{wa_i} = \frac{\sqrt{\hat{T}}}{a_i}$$

The non-dimensionalized residence time is  $\hat{t}_i = a_i t_i = \sqrt{\hat{T}}$ .

As in the single-patch case,  $\hat{t}$  will equal  $\hat{t}^*$  when  $\hat{T} = 3.215$  and will exceed  $\hat{t}^*$  if  $\hat{T} > 3.215$ . A few small values of  $a$ , corresponding to a few large patches, bring down the harmonic mean a great deal, potentially inducing blundering foragers to leave patches too early. In contrast, a few large values of  $a$ , corresponding to a few small patches, have little effect on the harmonic mean and the strategies of the foragers. In this case, a few bad  $a$ 's do not spoil the whole bunch.

Figure 5 compares the strategies for unconstrained optimal and blundering foragers in an environment consisting of two patches as a function of the size of the second patch. Below a critical value of  $A_2$ , the environment is perceived as poor and the blundering forager tends to remain in each patch longer than the unconstrained optimal forager. Above this value, the environment is good and the blundering forager tends to leave patches earlier than the unconstrained optimal forager.

A more general null model of path departure would set  $\lambda_i = wa_i^p$  for some power  $p$ . When the blundering forager follows a random walk in  $D$  dimensions, the value of  $p$  is  $2/D$  (Berg, 1993). Because the optimal strategy requires departure times proportional to patch size (equation 4), the blundering forager leaves at the appropriate rate only in two dimensions. Simulations with  $p < 1$  find that blundering foragers remain longer in small patches and shorter in large patches than they should.



**Fig. 5.** Optimal residence times in each of two patches as functions of the size of the second patch for the unconstrained optimal forager (solid lines) and optimal mean residence times for the blundering forager (dashed lines). The parameters are  $A_1 = 0.25$  and  $T = 1$ . The curves cross when  $\hat{T} = 3.215$ , which occurs at  $A_2 = 0.372$  in this case.

## DISCUSSION

We have seen that the stupidest error-constrained forager, which leaves patches only by accident when it gets lost, is favoured to remain in patches a shorter time when the world is good and a longer time when the world is bad. Paradoxically, the relative cost of stupidity is maximal precisely at the point where the mean strategy of the blundering forager matches that of the unconstrained optimal forager. This result is a general fact about foragers with different gain functions and the same travel time. When foragers show a significant degree of variability in residence times (Marschall *et al.*, 1989; Åström *et al.*, 1990; Cassini *et al.*, 1990; Crowley *et al.*, 1990), they pay the greatest cost for this variability when the average residence time matches that computed for an unconstrained optimal forager. Finding that a constrained forager achieves the optimal strategy on average does not indicate that fitness costs can be ignored.

Crowley *et al.* (1990) found that foraging sunfish remained in patches longer, on average, than the optimum predicted by the Marginal Value Theorem. The non-dimensionalized travel time  $\hat{T}$  is roughly 0.1 in their data (estimated from their figure 1). According to the theory presented here, fish getting lost at the optimal rate should remain in patches a *shorter* time on average in such a favourable environment. These data, however, are not an appropriate test of the theory for at least two reasons: the fish encounter prey discretely rather than continuously, and the fish are probably not leaving patches because they got lost.

Our observations of *C. elegans* indicate that it might provide a more appropriate test. Patches of bacteria are depleted continuously, and worms are not too intelligent. Even if individuals are not capable of learning the optimal rate of getting lost in a particular laboratory environment, strains from different environments could be programmed with different foraging behaviours that result in different rates of getting lost. These foraging behaviours should be part of an entire foraging syndrome, ostensibly optimal in the strain's ancestral habitat.

If *C. elegans* indeed lacks the ability to estimate parameters and to adjust behaviour accordingly, the difficulties in modelling cognition are not relevant (Yoccoz *et al.*, 1993; Bateson and Kacelnik, 1995). It would be interesting to test whether *C. elegans*, like the European starling, follows the apparently suboptimal strategy of maximizing food per patch rather than overall energy intake rate (Bateson and Kacelnik, 1996).

Differences in gain functions might result from mechanisms other than a blundering foraging strategy. Hosts or groups of hosts might be depleted both by consumption and by host defence (Adler and Harvell, 1990). Some foragers might induce defences more quickly through failure to suppress cues (Levin *et al.*, 1977; Adler and Grünbaum, 1999). The costs of this failure will again be most severe when the optimal strategies of odoriferous foragers exactly match those of scent-free foragers.

If one thinks of the 'patches' as having fuzzy boundaries (Schmidt and Brown, 1996), the blundering forager ceases to look quite so stupid. It may not know when it has left a patch because there are no boundary markers to indicate this. If foraging success is due to occasional prey capture rather than a constant rate of resource intake, a long period without finding food cannot be unambiguously interpreted (Iwasa *et al.*, 1981). The wandering strategy encoded in the value of  $w$  (the rate of getting lost defined by equation 5) can be a robust way to deal with this uncertainty.

We can think of  $w$  as the optimal diffusion coefficient. For a known distribution of patch sizes, an organism that encounters a resource should employ a strategy, such as walking

speed or turning angle, that creates this optimal diffusion coefficient (always under the assumption that the forager cannot find its way back after leaving a patch). Unlike a full model of area-restricted search (Focardi and Marcellini, 1995; Grünbaum, 1998), this model treats travel time  $T$  between patches as being independent of strategy. An organism with a wandering strategy that involves a large diffusion coefficient (or a small value of  $w$ ) will follow that strategy even after it leaves a patch, making itself inefficient at locating subsequent patches (Charnov and Parker, 1995).

### ACKNOWLEDGEMENTS

We thank S. Webb for useful discussion and logistical help. Thanks to E. Charnov, D. Grünbaum, S. Proulx and J. Seger for helpful comments on the manuscript, to Y. Iwasa for expert editing, and particularly to D. Stephens for an insightful review of both content and diction. This research was supported by the Hughes Foundation and the Biology Undergraduate Research Program at the University of Utah.

### REFERENCES

- Adler, F.R. 1998. *Modeling the Dynamics of Life: Calculus and Probability for Life Scientists*. Pacific Grove, CA: Brooks/Cole.
- Adler, F.R. and Grünbaum, D. 1999. Evolution of forager responses to inducible defenses. In *Ecology and Evolution of Inducible Defenses* (C.D. Harvell and R. Tollrian, eds), pp. 259–285. Princeton, NJ: Princeton University Press.
- Adler, F.R. and Harvell, C.D. 1990. Inducible defenses, phenotypic plasticity and biotic environments. *Trends Ecol. Evol.*, **5**: 407–410.
- Åström, M., Lundberg, P. and Danell, K. 1990. Partial prey consumption by browsers: Trees as patches. *J. Anim. Ecol.*, **59**: 287–300.
- Bateson, M. and Kacelnik, M. 1995. Preferences for fixed and variable food sources: Variability in amount and delay. *J. Exp. Anal. Behav.*, **63**: 313–329.
- Bateson, M. and Kacelnik, M. 1996. Rate currencies and the foraging starling: The fallacy of averages revisited. *Behav. Ecol.*, **7**: 341–352.
- Bell, W. 1991. *Searching Behaviour: The Behavioural Ecology of Finding Resources*. New York: Chapman & Hall.
- Benhamou, S. 1992. Efficiency of area-concentrated searching behaviour in a continuous patchy environment. *J. Theor. Biol.*, **159**: 67–81.
- Berg, H.C. 1993. *Random Walks in Biology*. Princeton, NJ: Princeton University Press.
- Brunner, D., Kacelnik, A. and Gibbon, J. 1992. Optimal foraging and timing processes in the starling, *Sturnus vulgaris*: Effect of inter-capture interval. *Anim. Behav.*, **44**: 597–613.
- Cassini, M.H. and Kacelnik, A. 1994. Patch choice by guinea pigs: Is patch recognition important? *Behav. Proc.*, **31**: 145–156.
- Cassini, M.H., Kacelnik, A. and Segura, E. 1990. The tale of the screaming hairy armadillo, the guinea pig and the marginal value theorem. *Anim. Behav.*, **39**: 1030–1050.
- Charnov, E.L. 1976. Optimal foraging: The marginal value theorem. *Theor. Pop. Biol.*, **9**: 129–136.
- Charnov, E.L. 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. New York: Oxford University Press.
- Charnov, E.L. and Parker, G.A. 1995. Dimensionless invariants from foraging theory's marginal value theorem. *Proc. Nat. Acad. Sci. USA*, **92**: 1446–1450.
- Crowley, P.H., Devries, D.R. and Sih, A. 1990. Inadvertent errors and error-constrained optimization: Fallible foraging by bluegill sunfish. *Behav. Ecol. Sociobiol.*, **27**: 135–144.

- Driessen, G., Bernstein, C., van Alphen, J. and Kacelnik, A. 1995. A count-down mechanism for host search in the parasitoid *Venturia canescens*. *J. Anim. Ecol.*, **64**: 117–125.
- Focardi, S. and Marcellini, P. 1995. A mathematical framework for optimal foraging of herbivores. *J. Math. Biol.*, **33**: 365–387.
- Grünbaum, D. 1998. Using spatially-explicit models to characterize foraging performance in heterogeneous landscapes. *Am. Nat.*, **151**: 97–115.
- Houston, A.I. and McNamara, J.M. 1985. The variability of behaviour and constrained optimization. *J. Theor. Biol.*, **112**: 265–273.
- Iwasa, Y., Higashi, M. and Yamamura, N. 1981. Prey distributions as a factor determining the choice of optimal foraging strategy. *Am. Nat.*, **117**: 710–723.
- Levin, S.A., Levin, J.E. and Paine, R.T. 1977. Snowy owl predation on short-eared owls. *The Condor*, **79**: 395.
- Marschall, E.A., Chesson, P.L. and Stein, R.A. 1989. Foraging in a patchy environment: Prey-encounter rate and residence time distributions. *Anim. Behav.*, **37**: 444–454.
- Newman, J.A. 1991. Patch use under predation hazard: Foraging behavior in a simple stochastic environment. *Oikos*, **61**: 29–44.
- Rosenheim, J.A. and Mangel, M. 1994. Patch-leaving rules for parasitoids with imperfect host discrimination. *Ecol. Entomol.*, **19**: 374–380.
- Schmidt, K.A. and Brown, J.S. 1996. Patch assessment in fox squirrels: The role of resource density, patch size and patch boundaries. *Am. Nat.*, **147**: 360–380.
- Stephens, D.W. and Dunbar, S.R. 1993. Dimensional analysis in behavioral ecology. *Behav. Ecol.*, **4**: 172–183.
- Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.
- Wood, W.B. 1988. *The Nematode Caenorhabditis elegans*. Cold Spring Harbor: Cold Spring Harbor Laboratory Press.
- Yoccoz, N.G., Engen, S. and Stenseth, N.C. 1993. Optimal foraging: The importance of environmental stochasticity and accuracy in parameter estimation. *Am. Nat.*, **141**: 139–157.