

# Optimal foraging: Lévy pattern or process?

M. J. Plank and A. James\*

*Department of Mathematics and Statistics, University of Canterbury, Private Bag 4800, Christchurch, New Zealand*

Many different species have been suggested to forage according to a Lévy walk in which the distribution of step lengths is heavy-tailed. Theoretical research has shown that a Lévy exponent of approximately 2 can provide a higher foraging efficiency than other exponents. In this paper, a composite search model is presented for non-destructive foraging behaviour based on Brownian (i.e. non-heavy-tailed) motion. The model consists of an intensive search phase, followed by an extensive phase, if no food is found in the intensive phase. Quantities commonly observed in the field, such as the distance travelled before finding food and the net displacement in a fixed time interval, are examined and compared with the results of a Lévy walk model. It is shown that it may be very difficult, in practice, to distinguish between the Brownian and the Lévy models on the basis of observed data. A mathematical expression for the optimal time to switch from intensive to extensive search mode is derived, and it is shown that the composite search model provides higher foraging efficiency than the Lévy model.

**Keywords:** Brownian random walk; foraging behaviour; foraging efficiency; Lévy random walk; power law; stochastic differential equation

## 1. INTRODUCTION

The observed foraging behaviour of many different species has been found to fit closely to a power law distribution with an exponent close to 2, for example grey seals (Austin *et al.* 2004), spider monkeys (Ramos-Fernández *et al.* 2004) and even human tribes (Brown *et al.* 2007). That is, the observed distribution has a probability density function (PDF)

$$f(x) = Cx^{-\mu}, \quad x > x_{\min}, \quad (1.1)$$

where  $\mu \approx 2$ . The common assumption is that this pattern of observations is generated by a Lévy random walk, i.e. the forager is selecting movement distances directly from a distribution of the form (1.1). If  $\mu \leq 3$ , this distribution is heavy-tailed, meaning that there is a significant probability of extremely large values of  $x$  occurring, and the distribution does not have a finite variance.

Viswanathan *et al.* (2000) proposed a Lévy walk model for the random search problem of locating randomly located search targets and examined the relationship between foraging efficiency and power-law exponent  $\mu$ . Two types of foraging were considered: non-destructive, in which the forager may visit and feed at the same target site many times; and destructive, in which the forager may feed at a given target site only once.

In destructive foraging, after a food item has been consumed, the individual is effectively placed randomly among randomly scattered food items to begin the next search. In this case, the most efficient search strategy is

often a ballistic one, i.e. to move in a straight line until food is found. Indeed, Viswanathan *et al.* (2000) showed that decreasing  $\mu$  always increases efficiency. For equation (1.1) to be a valid PDF,  $\mu$  must be greater than 1, so the optimal strategy occurs as  $\mu \rightarrow 1$ , which is tending towards ballistic motion. Optimal strategies for destructive foraging have also been investigated by Bartumeus *et al.* (2002), Condamin *et al.* (2006) and Shlesinger (2006). Some of these studies have compared Lévy and Brownian motion strategies, but restricted to the case where step lengths are drawn from a power law distribution ( $\mu < 3$  for Lévy;  $\mu \geq 3$  for Brownian). This gives no indication as to whether alternative strategies that are not based solely on a power law can provide a higher efficiency. In contrast, Bénichou *et al.* (2005, 2006) and Lomholt *et al.* (2007) looked at strategies for searching for non-revisitable targets (i.e. a form of destructive foraging), in which the searcher switches intermittently between two different search modes. As well as presenting expressions for the mean optimal switching times, it was shown that this intermittent searching can lead to higher efficiencies than purely ballistic or power law-based searching.

The question of optimal strategies for non-destructive foraging is a separate problem. The forager begins each search in the knowledge that there is another food item in close proximity, but in an unknown direction. This can be thought of as modelling a patchy environment, where the finding of one food item implies an increased likelihood of other food items locally in the same patch. Unlike purely ballistic movement, an efficient strategy will make use of this knowledge. In the power law model of Viswanathan *et al.* (2000), it was shown that the maximum efficiency occurs when  $\mu \approx 2$

\*Author for correspondence (a.james@math.canterbury.ac.nz).

(i.e. a Lévy walk), provided that the distance between food items is large relative to the distance at which the forager can detect food. The model was extended in Santos *et al.* (2004) to include scenarios, intermediate between the destructive and non-destructive extremes, in which a target site may be revisited only after a certain period of time has elapsed. Again, these studies consider only walks with power law-distributed step sizes.

Raposo *et al.* (2003) claimed that the optimal search strategy for the random search problem is always a Lévy walk. Recently, however, the paradigm of a Lévy process corresponding to an optimal foraging strategy has come under closer scrutiny. Edwards *et al.* (2007) showed that the original findings of Viswanathan *et al.* (1996), which fitted power law distributions to data for flight lengths of wandering albatrosses, were incorrect. Additionally, Benhamou (2007) demonstrated that a Brownian random walk model (i.e. one in which step lengths are selected from a distribution with finite variance) for non-destructive foraging can produce data that appear to fit a power law distribution. The model consists of a composite random walk—the forager initially moves according to a Brownian random walk with a relatively small mean step size (intensive search). However, after searching for a prescribed length of time without finding any food, it switches to a larger mean step size (extensive search) until it finds a food item. It then reverts to the original intensive search method. Not only did simulations of this model produce what could be interpreted as a Lévy pattern from a non-Lévy process, the efficiency of the composite search strategy was shown to be significantly higher than for a Lévy walk. This is in agreement with the results of Bénichou *et al.* (2006) for destructive foraging.

In this paper, a one-dimensional model for non-destructive foraging movements based on a stochastic differential equation (SDE) for the location of the forager is presented. One-dimensional models are a common tool for studying foraging in this way (Bartumeus *et al.* 2002; Bénichou *et al.* 2005; Lomholt *et al.* 2007). They capture the essence of a search strategy but are often amenable to analytical manipulation. Most of the qualitative results obtained from one-dimensional models can be seen in two-dimensional simulations. In particular, Viswanathan *et al.* (2000, 2001) carried out extensive numerical explorations of power law random walks and showed a good correspondence between the one- and two-dimensional cases.

Similarly to Benhamou (2007) the basis of the model is a combination of Brownian intensive and extensive search modes, and a rule for when to switch from one to the other. The efficiency of the model and the observed distributions of movements it produces are compared with a Lévy random walk. Both this approach and that of Benhamou (2007) use the same underlying scenario. However, the advantage of the continuous SDE model over the discrete random walk model is that of higher tractability to analytical manipulation. The use of SDEs allows analytical expressions to be derived for the observed distributions and for the foraging efficiency, rather than relying on purely numerical simulations.

SDEs have been used previously for understanding foraging strategies. Condamin *et al.* (2006) examined the mean first passage time for SDEs in a range of geometries and the consequences of this work for foraging strategies were discussed by Shlesinger (2006). Our work looks at a slightly more specialized case but presents expressions for the distribution of the encounter time in addition to the mean. We also give distributions of other commonly measured distributions observed in foraging data. These analytical results highlight the important parameters (e.g. average distance between food items within a patch, average distance between patches and average search velocity) involved in factors such as foraging efficiency, and in determining optimal strategies, thus allowing for improved insight into the observed data.

## 2. THE COMPOSITE SEARCH MODEL

Consider an individual who displays two distinct types of behaviour. The first mode is a local, area-intensive search with frequent turning and a mean velocity  $v_I$ . The second mode is far more extensive with few turns and potentially a much higher velocity  $v_E$ . Composite search behaviour of this type gives movement patterns similar to the observed data, particularly for individuals in patchy environments. For example, Klaassen *et al.* (2006) studied swans and typical foraging paths showed short intrapatch movements connected by longer interpatch movements.

In this work, the individual is modelled by a forager searching for a food item on a one-dimensional line. The individual starts at position  $x_0$ , the point at which the previous food item was found. In one direction, the next food item is close by at  $x=0$ ; in the other direction, the food item is much further away. This scenario represents a forager in a patchy environment with only limited knowledge of its surroundings, and is very similar to the non-destructive foraging scenario of Viswanathan *et al.* (2000). If the forager chooses the correct direction, it will stay in the patch and find its next food item quickly. If it chooses the other direction, it will move out of the patch and potentially have to travel a large distance to the next item.

Presume that the forager follows a composite search strategy. It starts by carrying out an intensive local search, characterized by frequent changes of direction. However, if, after time  $\tau$ , this strategy has not been successful, the forager abandons the intensive search and simply runs in a straight line (ballistic motion), in a randomly chosen direction, until it finds food. As a simplifying assumption, it is assumed that the distance the forager must travel before finding a food item in this second phase is exponentially distributed with mean  $d/2$ , independently of the position  $X(\tau)$  after the intensive phase. (Note that this travel distance is due to the distribution of food items rather than to any decision by the forager.) In fact this is a reasonable assumption since, in an environment where food patches are distributed randomly (i.e. according to a Poisson process), the distance travelled before the next patch is encountered is exponentially distributed and the mean distance is the mean free path (Viswanathan *et al.* 2000). Hence  $d$  is a

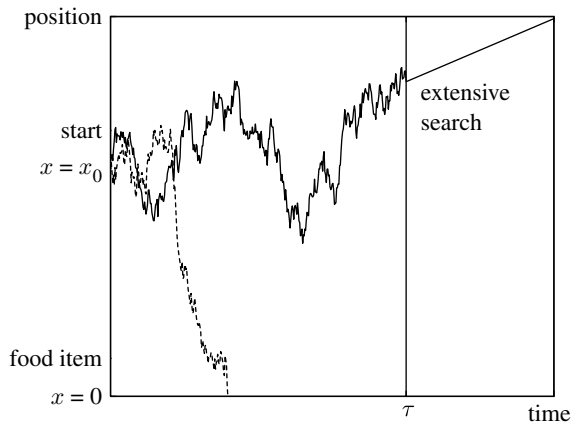


Figure 1. Two sample foraging paths, both starting at  $x = x_0$ . On the path represented by the dashed line, the forager finds the food item at  $x = 0$  during the intensive search phase; on the path represented by the solid line, the forager fails to find food during the intensive phase and would continue to perform an extensive search.

measure of the average distance between food patches, while  $x_0$  is a measure of the average distance between items in the same patch; it is assumed that  $x_0 \ll d$ . Figure 1 shows two sample foraging paths: on one path, the forager only carries out an intensive search as the food item at  $x = 0$  is found before  $t = \tau$ ; on the other path, the forager would continue to do an extensive search at a constant velocity.

Once a food item is found, it is assumed that the forager resumes a new search, restarting in the original configuration, i.e. a distance  $x_0$  from a food item. This scenario describes a patchy environment, in which food items within a patch are spaced at distance  $x_0$  apart, and the patches themselves are an average distance  $d$  apart.

In the intensive phase, the forager's movement is described by Brownian-type random motion in one dimension and follows the SDE:

$$dX = \sigma dW(t), \quad (2.1)$$

where  $X(t)$  is the forager's position at time  $t$ , and  $\sigma dW(t)$  is a standard white noise process. Equation (2.1) is written in the standard notation of SDEs (see Grimmett & Stirzaker (2001) for details) and represents a stochastic process in which a series of small steps ( $dX$ ) are drawn from a normal distribution with mean 0 and variance  $\sigma^2$ . The forager starts at  $X(0) = x_0$  and reaches the food item at  $x = 0$  at time  $T$ , the shortest value of  $t$  such that  $X(t) = 0$ . This corresponds to the Brownian motion of a particle along a line with an absorbing barrier at  $x = 0$ .

The PDF  $f_X(x, t)$  of the position of a searcher moving according to (2.1) with an absorbing barrier at  $x = 0$  is given by Grimmett & Stirzaker (2001) as

$$f_X(x, t) = \frac{1}{\sqrt{2\pi t\sigma}} \left( \exp\left(-\frac{(x-x_0)^2}{2\sigma^2 t}\right) - \exp\left(-\frac{(x+x_0)^2}{2\sigma^2 t}\right) \right), \quad x > 0, t \geq 0.$$

Integrating this PDF over  $0 < x < \infty$  for a fixed value of  $t$  gives the total probability of being at any positive  $x$  value (i.e. of not having been absorbed by time  $t$ ). From this, the probability of having been absorbed before time  $t$  (i.e. the cumulative distribution function (CDF)  $F_T$  of the random variable  $T$ ) is

$$F_T(t) = P(T \leq t) = 1 - \int_0^\infty f_X(x, t) dx, \quad t \geq 0. \quad (2.2)$$

The PDF  $f_T(t)$  may be found by differentiating  $F_T(t)$  with respect to  $t$ .

The central limit theorem predicts that the discrete random walk model of Benhamou (2007) will converge to the continuous model provided a large enough number of independent steps have been taken, and the distribution of the step lengths has finite variance.

## 2.1. Comparisons with observed distributions

Many studies have observed individual foraging behaviour and fitted the observed distributions to a number of statistical models. However, field studies use a wide range of observation techniques, resulting in a variety of observed distributions. Here, we examine some of the more common observation methods and find the corresponding analytical solutions of the SDE model. In all cases, the predicted distributions were verified with the results from  $10^5$  individual-based simulations of the SDE using the Euler–Maruyama method (Higham 2001).

**2.1.1. Distance travelled between food items.** Viswanathan *et al.* (1996) observed the foraging patterns of wandering albatross. Individuals were tracked over a period of days and the times between immersions in water were recorded. A constant velocity was presumed and this gave a distribution of distances between immersions, which was assumed to be the distribution of distances between food items. Similar data were recorded by Klaassen *et al.* (2006) for foraging swans in a patchy food environment—the position of a swan was recorded every time it submerged its head, giving both time and position data at food sites. Both these recording methods give no information of the individual's path from one food item to the next. The distance travelled between food items is inferred by measuring the time between food items and assuming a constant velocity. The continuous model presented here can be used to give an analytical form for the distribution of the time spent and hence the distance travelled between food items.

The mean instantaneous speed of the intensive search process described by (2.1) is  $v_I = \sqrt{2/\pi}\sigma$ , and the total distance travelled during this phase is  $v_I T$ . If a time  $\tau$  has elapsed (i.e.  $T > \tau$ ), the intensive search is abandoned and an additional straight-line distance  $R$  is travelled, which is a random variable from an exponential distribution  $R \sim \exp(2/d)$ . The mean speed of the forager during the extensive search period is  $v_E$ .

The distance travelled between successive food items,  $L$ , has a distribution that must be found in the two separate cases. If the item is found in the intensive

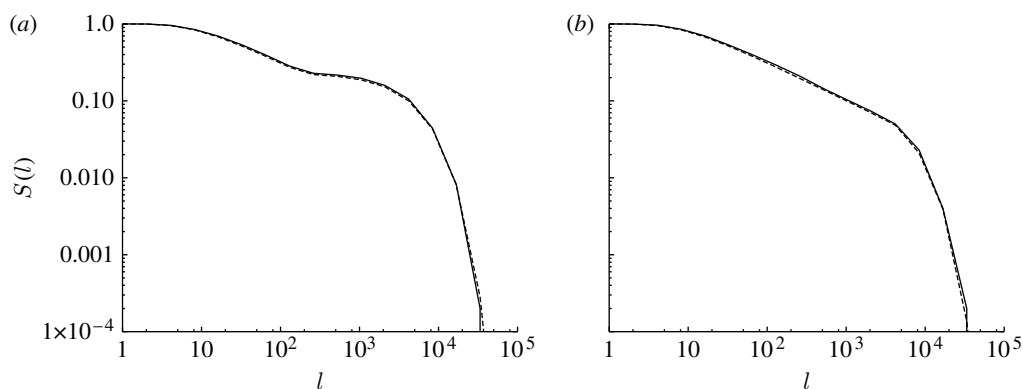


Figure 2. Distribution of distance travelled  $L$  before finding food ( $S(l) = P(L > l)$ ), calculated from SDE simulations and analytically from equation (2.4). (a) Early changeover from intensive to extensive search mode ( $\tau = 50$  s). (b) Late changeover ( $\tau = 1000$  s). Other parameter values:  $v_I = 4 \text{ ms}^{-1}$ ,  $x_0 = 10$  m and  $d = 10\,000$  m. Solid line, SDE simulations; dashed line, analytic.

search period,  $L$  has, essentially, the same distribution as the time to absorption. If the item is found during the extensive search period, the distance is the sum of the distance travelled in the intensive period and a distance  $R$  taken from an exponential distribution.

$$L = \begin{cases} v_I T & \text{if } T \leq \tau, \\ v_I \tau + R & \text{if } T > \tau. \end{cases} \quad (2.3)$$

Hence the PDF of the total distance travelled before finding food is

$$f_L(l) = \begin{cases} \frac{1}{v_I} f_T\left(\frac{l}{v_I}\right) & l \leq v_I \tau, \\ (1 - F_T(\tau)) f_R(l - v_I \tau) & l > v_I \tau. \end{cases} \quad (2.4)$$

Figure 2 shows the distribution of distances travelled before finding food, with an early changeover from an intensive to an extensive search (small  $\tau$ ) and with a late changeover (large  $\tau$ ). The analytical distribution (calculated using (2.4)) shows excellent agreement with the results of simulations. The parameter values used in figure 2 were chosen, for illustrative purposes, to be approximately representative of wandering albatross foraging—Weimerskirch *et al.* (2007) reported a minimum flying speed and an overall mean speed of approximately 3 and  $10 \text{ m s}^{-1}$ , respectively, and a maximum patch diameter of 1 km. The qualitative results shown in figure 2, and the agreement of the analytical and numerical results, are the same for a wide range of parameter values.

**2.1.2. Observed distance travelled in a given time interval.** An alternative method of observing foraging paths is to measure the position of an individual at a series of fixed time intervals and to calculate the straight-line distance between successive points to give a distribution of move lengths. Data of this type are usually combined with observations of wait times, i.e. time intervals in which the individual does not move and is presumed to have arrived at a food item. Observation intervals for this type of data cover a wide range depending on the method of observation and the type of individual. For example, Mårell *et al.* (2002) observed reindeer at 30 s intervals, Ramos-Fernández *et al.* (2004)

observed the positions of spider monkeys at 5 min intervals and Austin *et al.* (2004) observed seals at daily intervals. Clearly, the exact shape of the observed distribution will depend on the relative sizes of the observation interval and the average time taken to move between food items.

Initially, to obtain a distribution of the movement lengths in a given time interval, it is presumed that the observation interval  $t_s$  is smaller than the changeover time between the intensive search phase and the extensive phase so that, during any one interval, the behaviour observed is either entirely intensive or entirely extensive, rather than a mixture of the two. The SDE model predicts that the observed distance moved during a time interval of length  $t_s$  in the intensive phase,  $Y_I = |X(t + t_s) - X(t)|$ , follows an absolute Gaussian distribution with PDF

$$f_{Y_I}(y) = \frac{2}{\pi v_I \sqrt{t_s}} \exp\left(-\frac{y^2}{\pi v_I^2 t_s}\right). \quad (2.5)$$

It should be noted that, in a Brownian process of this type, the actual distance travelled by an individual is  $v_I t_s$ , as the individual is moving at a constant speed  $v_I$ . However, observations at discrete intervals will record only the net distance of the individual from its previous point.

In a foraging sequence, the individual either finds the food item during the intensive search ( $T < \tau$ ) and the number of observed move lengths is approximately  $T/t_s$ , or it finds food during the extensive search ( $T \geq \tau$ ) and there will be approximately  $\tau/t_s$  observed move lengths during the intensive phase, followed by a number of observations during the straight-line run. As previously, during the extensive search phase, the forager travels a random distance  $R \sim \exp(d/2)$ . It is assumed that the mean speed during each observed interval also follows a Gaussian distribution with mean  $v_E$  and variance  $\sigma_E^2$ , so the distance travelled  $Y_E$  during each interval is distributed according to

$$f_{Y_E}(y) = \frac{1}{\sqrt{2\pi}\sigma_E t_s} \exp\left(-\frac{(y - v_E t_s)^2}{2\sigma_E^2 t_s^2}\right). \quad (2.6)$$

The proportion  $q$  of move length observations drawn from the intensive distribution (2.5) can be approximated by the proportion of the foraging cycle spent in



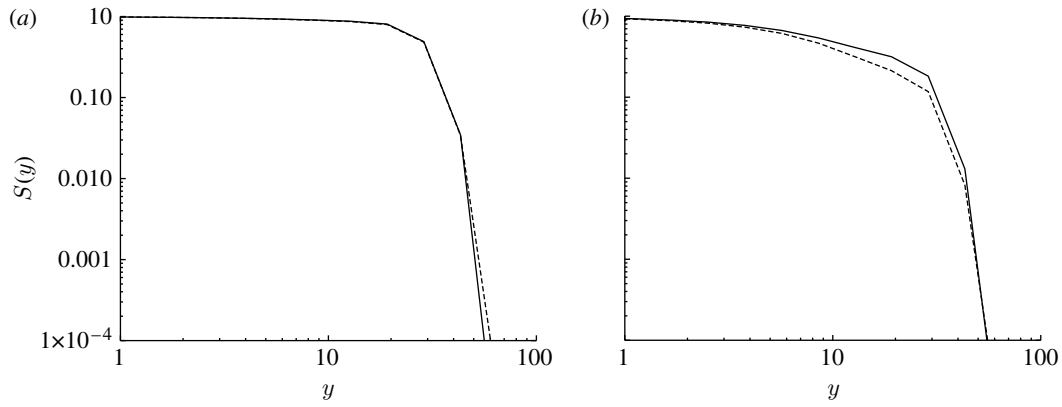


Figure 3. Distribution of observed step lengths  $Y$  ( $S(y) = P(Y > y)$ ), calculated from SDE simulations and analytically from equation (2.8). (a) Early changeover from intensive to extensive search mode ( $\tau = 50$  s). (b) Late changeover ( $\tau = 1000$  s). Other parameter values are  $v_I = 4 \text{ m s}^{-1}$ ,  $v_E = 10 \text{ m s}^{-1}$ ,  $\sigma_E = 2.5 \text{ m s}^{-1}$ ,  $x_0 = 10 \text{ m}$ ,  $d = 10\,000 \text{ m}$  and  $t_s = 3 \text{ s}$ . Solid line, SDE simulations; dashed line, analytic.

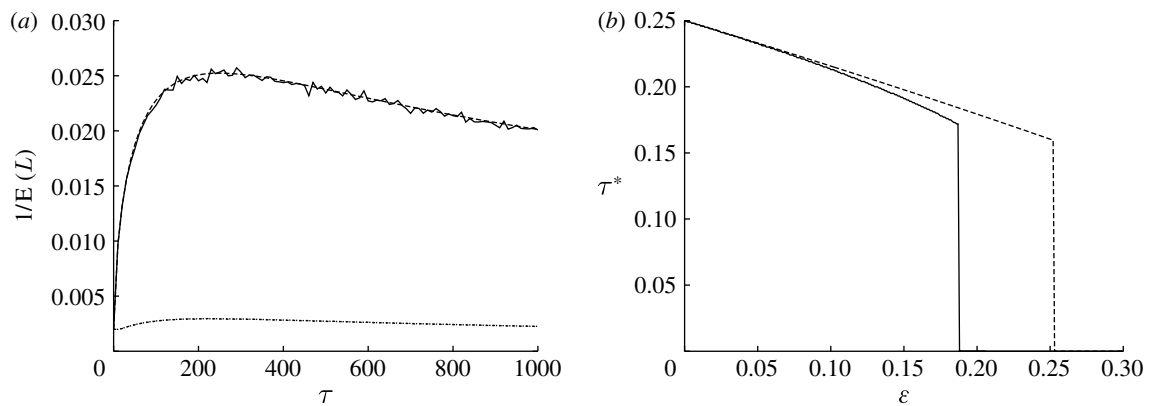


Figure 4. (a) Mean efficiency (reciprocal of distance travelled to find food) against  $\tau$ , calculated from SDE simulations and analytically from equation (2.9):  $v_I = 1$ ,  $d = 1000$  (solid line, SDE simulations  $x_0$ ; dashed line, analytic  $x_0$ ; dot-dashed line, SDE simulations  $x_0$ ; dotted line, analytic  $x_0$ ). (b) Optimal switching time  $\hat{\tau}^* = v_I \tau^* / d$  against  $\epsilon$  (solid line, numerical; dashed line, analytical). The curves are calculated by numerical minimization of  $E(L)$  according to equation (2.9) and using the approximation (2.10). If  $\epsilon < 0.19$ , there is a global minimum in  $E(L)$  at a value of  $\tau$  closely approximated by (2.10). If  $\epsilon > 0.19$ , this local minimum ceases to be a global minimum—the optimal value of  $\tau$  is zero.

the intensive search mode,

$$q = \frac{\text{intensive time}}{\text{intensive time} + \text{extensive time}} = \frac{\int_0^\tau t f_T(t) dt + \tau \int_\tau^\infty f_T(t) dt}{\int_0^\tau t f_T(t) dt + \left(\tau + \frac{d}{2v_E}\right) \int_\tau^\infty f_T(t) dt}, \quad (2.7)$$

and the remaining proportion  $1 - q$  is from the extensive distribution (2.6). Note that this formulation for  $q$  does not depend on the sampling frequency  $t_s^{-1}$ , but it does presume a zero handling time for each food item.

Hence, the PDF  $f_Y$  of observed step lengths is

$$f_Y(y) = q f_{Y_I}(y) + (1 - q) f_{Y_E}(y). \quad (2.8)$$

Figure 3 shows examples of this distribution for two different values of the changeover time  $\tau$  and the sampling time  $t_s$ . Again the analytical values agree well with those generated from the simulations of the SDE.

### 2.2. Optimal foraging theory

Of particular interest in any model of foraging behaviour is the optimal foraging strategy. This is the strategy that maximizes the net energy gain—the

energy intake from food minus the energy expended during the search. In simple mathematical models, finding the optimal strategy usually corresponds to optimizing the values of one or more parameters. For example, in the Lévy walk model of Viswanathan *et al.* (2000), the value of the power law exponent  $\mu$  is optimized; in the present model, it is the optimal value of the changeover time  $\tau$  which is of primary interest.

It is assumed that energy expenditure is proportional to distance travelled, and that the energy obtained from each food item found is the same. Thus by minimizing the mean distance travelled between food items, the forager will maximize its net energy gain. From equation (2.4), the expected distance travelled  $E(L)$  before finding a food item is

$$E(L) = \int_0^\infty l f_L(l) dl = v_I \int_0^\tau t f_T(t) dt + (1 - F_T(\tau)) \times \left( v_I \tau + \int_0^\infty s f_R(s) ds \right). \quad (2.9)$$

This expression for  $E(L)$  can be written in closed form (see appendix A), and is valid for any distribution of extensive travel distances with mean  $d/2$ . Hence the

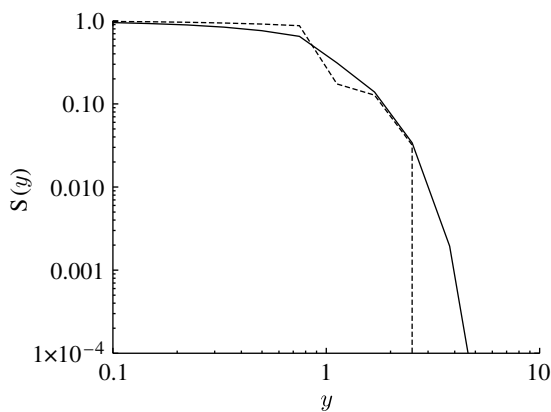


Figure 5. Distribution of step lengths  $Y$  ( $S(y) = P(Y > y)$ ), under the SDE model ( $\tau = 1000$ ) and the Lévy random walk model with  $\mu = 1.9$  and  $x_{\min} = 0.01$ . For both curves,  $v_I = v_E = 1$ ,  $\sigma_E = 0.1$ ,  $x_0 = 10$ ,  $d = 1000$  and  $t_s = 1$ . Solid line, SDE simulations; dashed line, analytic.

results of this section are independent of the assumption that the length of the extensive movement follows an exponential distribution. Figure 4a shows the mean efficiency  $1/E(L)$  against  $\tau$  calculated using equation (2.9) and from simulations. The optimal value of  $\tau$  is the one that minimizes  $E(L)$  and can be approximated by

$$\tau^* = \frac{d}{4v_I} \left( 1 - \frac{4}{3}\epsilon - \frac{2}{5}\epsilon^2 \right), \quad (2.10)$$

where

$$\epsilon = \frac{2x_0^2}{\pi v_I d} < 0.19.$$

If  $\epsilon > 0.19$  then the minimum value of  $E(L)$  occurs at  $\tau = 0$  (see appendix A). Figure 4b shows the optimal value of  $\tau$  against  $\epsilon$ , calculated both from numerical minimization of equation (2.9) and using the analytical approximation (2.10). These two show excellent agreement provided  $\epsilon < 0.19$ . Efficiency drops significantly as  $x_0$  increases.

These results show that if food patches are distributed sufficiently densely relative to the density of items within a patch (i.e. a relatively unpatchy environment,  $\epsilon > 0.19$ ), then the optimal strategy is always to move in a straight line ( $\tau = 0$ ) until food is encountered. This strategy is often termed ballistic foraging (Santos *et al.* 2004) and the mean distance travelled is  $d/2$ . On the other hand, if intrapatch distances are much smaller than interpatch distances (i.e. a very patchy environment,  $\epsilon < 0.19$ ), then efficiency is improved by performing an intensive search. The optimal duration of this intensive period increases almost linearly with decreasing  $\epsilon$ .

The SDE model highlights a case of the marginal value theorem (MVT) of Charnov (1976). The MVT states that a forager in a patchy environment will move on from a patch when the average gain from that patch falls below the average gain from the overall area (Stephens & Krebs 1986). The SDE model presented here presumes that the forager has recently consumed a food item and continues to search the patch using an intensive search mode. While in this mode the energy gain per unit time will decrease steadily if no food is

found. The MVT states that the forager should change modes when the expected energy gain from changing patches is equal to the expected gain from the current patch. This result predicts that the optimal time to switch strategies will be such that the average distance travelled in intensive mode is equal to the average distance travelled in extensive mode. The optimal time found here corresponds well to that predicted by the MVT (found by equating average distance travelled in the intensive and extensive search phases via equation (2.7)), provided the initial starting position of the forager is close to the food item (i.e.  $x_0$  is small). In the limit  $\epsilon \rightarrow 0$ , i.e. the forager starts in the patch as required by the MVT, both times are identical,  $d/4v_I$ . As  $\epsilon$  increases and the forager starts further away from the patch, the switching time predicted by equating intensive and extensive distances increases, whereas the time predicted by minimizing  $E(L)$  decreases. The optimal switching time (2.10) can, therefore, be thought of as a generalization of Charnov's theorem to situations where each search begins a significant distance away from the nearest food item.

### 3. COMPARISONS TO OTHER DISTRIBUTIONS AND PROCESSES

Recent work on foraging behaviour has often focused on fitting power law distributions to observed step length distributions (Viswanathan *et al.* 1996; Mårell *et al.* 2002; Austin *et al.* 2004; Ramos-Fernández *et al.* 2004; Weimerskirch *et al.* 2005; Brown *et al.* 2007). However, as has been pointed out previously (Benhamou 2007), one must not confuse pattern with process. For example, if the best-fit model to an observed distribution is a power law distribution, this does not automatically imply that the individual is taking steps from a power law distribution (i.e. performing a Lévy walk). Conversely, an individual who is performing a Lévy walk may have an observed distribution of step lengths which is not a power law.

To illustrate this point, simulations of a Lévy random walk were also carried out. Step lengths were drawn from the distribution (1.1), and each step was randomly chosen to be left or right. The forager began each search at  $x = x_0$ , and food items were assumed to be positioned at  $x = 0$  and  $x = d$ . Figure 5 shows the distribution of observed step lengths  $Y$  (as described in §2) under both the composite search model and the Lévy random walk model (under the assumption that the Lévy forager always travels with instantaneous velocity  $v_I$ ). By eye the two distributions are quite similar, despite being produced from two different mechanisms. If these results were observed field data, a standard technique would be to try a range of common candidate models to find the best-fit distribution. Using the appropriate technique of maximum-likelihood estimation (Newman 2006), an exponential and a power law distribution were trialled as candidates for the results shown in figure 5. For both underlying mechanisms, composite search and Lévy walk, the best-fit parameters were found for both these candidate models. The log likelihood  $\mathcal{L}$  was also found for each model and, in both cases, the exponential model

Table 1. Statistical results of fitting candidate distributions to the distributions of observed step lengths of the SDE and Lévy models.  $\mathcal{L}$ =log likelihood.

candidate distribution		
exponential	power law	
$f_Y(y) = \lambda e^{-\lambda(y-x_{\min})}$	$f_Y(y) = Cy^{-\mu}$	
underlying model		
SDE	$\lambda=0.83, \mathcal{L}=-1.2,$	$\mu=1.1, \mathcal{L}=-3.2$
Lévy	$\lambda=0.78, \mathcal{L}=-1.2$	$\mu=1.1, \mathcal{L}=-3.3$

provided a better fit to the observations (higher log likelihood) than the power law model. The best-fit parameter values were notably similar for both underlying mechanisms. These results are summarized in table 1. Similar conclusions can be drawn by examining the distribution of travel distances,  $L$  (as described in §2.1.1), from the two underlying processes.

These results complement those of Benhamou (2007), which showed that it is possible for both a Lévy and a non-Lévy process to produce an apparent Lévy pattern. Here it has been shown that both a Lévy and a non-Lévy process can produce a non-Lévy pattern. In fact, the non-Lévy process of Benhamou (2007) produces a non-Lévy pattern, because the step lengths are drawn from an exponential distribution, which is not heavy-tailed. Nevertheless, owing to the relatively large mean step length in the extensive search mode, the pattern may appear to be Lévy, especially when working with a limited sample size. In the present model, where both the Lévy and the non-Lévy processes produce a non-Lévy pattern, this is, in large part, a consequence of observing the position of the forager at fixed time intervals, which effectively provides an upper limit on the observed step lengths, thus precluding the observation of a truly heavy-tailed distribution. Likewise, the assumption that the length of the extensive search phase is exponentially distributed means that the distribution of distances travelled cannot be heavy-tailed.

Figure 6 shows the mean maximum efficiency for the Lévy model and the SDE model over a range of starting positions,  $x_0$ . The efficiency of the SDE model at the optimal switching time was calculated using (2.9) and (2.10). For the Lévy model, the efficiency was maximized over all values of the exponent  $1 < \mu \leq 3$ , for each particular value of  $x_0$ . The optimal SDE model consistently gives higher efficiency values than the optimal Lévy model. Again, this is in agreement with Benhamou (2007), whose composite Brownian random walk search was more efficient than a Lévy walk. As  $x_0$  increases the efficiency of the two strategies tends towards  $d/2$  which is the efficiency of a ballistic strategy in a random (i.e. non-patchy) environment. For smaller values of  $x_0$ , the efficiency of the SDE strategy is significantly higher than that of the Lévy strategy because the latter does not take effective advantage of a starting position that is close to a food item. Note that altering the value of  $x_{\min}$  in the Lévy model can change

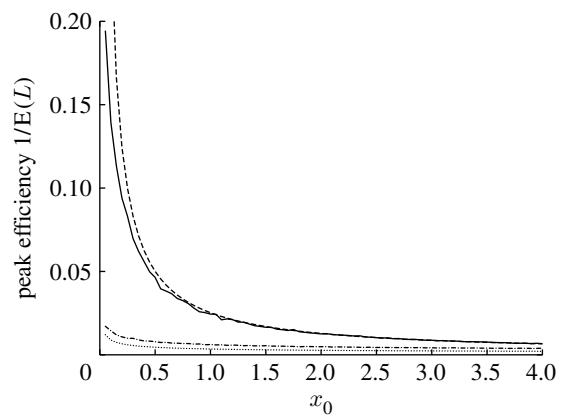


Figure 6. Mean maximum efficiency (reciprocal of distance travelled to find food) against  $x_0$ , for the composite strategy and the Lévy strategy. The analytical results for the SDE model were calculated using equations (2.9) and (2.10). The analytical results for the Lévy model were calculated according to equation (2.1) of Viswanathan *et al.* (2000) (with  $r_v = x_{\min}$ ), maximized over all values of  $\mu$ . Parameter values:  $x_{\min} = 0.01$ ,  $d = 1000$ . Solid line, SDE simulations; dashed line, SDE analytic; dot-dashed line, Lévy RW simulations; dotted line, Viswanathan analytic.

the efficiency, but a wide range of values of  $x_{\min}$  were tested, and the efficiency of the SDE model was always significantly higher, as shown in figure 6.

#### 4. DISCUSSION

A model of animal foraging movements has been presented, based on a one-dimensional Brownian-type intensive search, followed by a straight-line movement if the intensive search fails to find food inside a prescribed time. The intensive search may be described by a simple SDE, while the length of the straight-line movement is assumed to be exponentially distributed. This is a toy model in the sense that it is a simplification of the true situation and does not attempt to replicate accurately real-world foraging behaviour. Nevertheless, a series of one-dimensional searches captures the essence of the decision facing a forager—how far to move in a particular direction before changing direction? One-dimensional foraging models have been employed in a similar way previously (Bartumeus *et al.* 2002; Lomholt *et al.* 2007) and been shown to produce results consistent with two-dimensional simulations (Viswanathan *et al.* 2000, 2001). The assumption of an exponentially distributed straight-line running distance to a food item is realistic in the sense that, for uniformly distributed food patches in a two-dimensional area, the distance travelled in a straight line before hitting a patch is exponentially distributed, the mean of the distribution being the mean free path (Viswanathan *et al.* 2000).

Working from the probability distribution of the position of the forager after a given amount of time, analytical expressions have been found for the mean foraging efficiency (number of food items found per unit distance travelled), and the distributions of the total distance travelled before finding food and the observed movement lengths in a fixed time interval. In addition, an approximation to the optimal switching time  $\tau^*$  has

been derived. All of these results have been shown to match closely with data generated from the simulations of the search process. It is this analytical tractability that distinguishes the SDE model from the more usual random walk models (Viswanathan *et al.* 2000). Provided the step distribution has a finite variance the results of a random walk model will converge to the SDE presented here as a large number of steps are taken. However, most random walk models can be explored only through numerical simulation.

It was found that, although the mechanisms in the search process are Brownian in nature (i.e. step lengths have finite variance), the resulting observed distributions could feasibly be fitted to a power law distribution, especially under the limitation of a relatively small sample size. It should be noted, however, that a power law may not provide the best fit of the common candidate distributions. In the scenario shown here, an exponential distribution provided a better fit. Klaassen *et al.* (2006) fitted two separate normal distributions to their data on inter-patch and intrapatch swan movements. The model presented here would be an excellent choice for data of that form in which there are two distinct types of behaviour being exhibited.

Under the models of Viswanathan and co-workers (Viswanathan *et al.* 2000; Bartumeus *et al.* 2002; Raposo *et al.* 2003), all movements are drawn from an underlying power law distribution (1.1). With this constraint, the optimal strategy is always  $\mu \leq 3$ , corresponding to a Lévy rather than a Brownian random walk. In contrast, the present model and the model of Benhamou (2007) allow the forager to switch between two distinct types of foraging behaviour (intensive and extensive search), each with its own distribution of step lengths. The intensive search is Brownian in nature; the extensive search is ballistic, which is equivalent to a power law distribution as  $\mu \rightarrow 1$ , although the truncation of the ballistic movement at the next food item results in a non-heavy-tailed distribution of step lengths. This additional flexibility in the search strategy increases the efficiency of the search and removes the need for the forager to choose its movements by sampling directly from a power law distribution. There is a clear intuitive reason for this. Although both models consist of a mixture of short and long step sizes, the composite search model has an inbuilt mechanism for focusing the intensive search phases in areas known to be close to food items, especially when the food items within a patch are close together (small  $x_0$ ). In contrast, the Lévy model intersperses short and long steps randomly, so intensive search effort is potentially wasted in the areas distant from food. This is in agreement with the results of Benhamou (2007).

Overall, these findings suggest that data on foraging movements should be treated with caution. An apparent fit to a power law distribution does not necessarily imply that the movement was based on a Lévy process. Furthermore, recent work (Clauset *et al.* 2007; Edwards *et al.* 2007; James & Plank 2007) has shown that some of the foraging datasets proposed to fit to Lévy distributions can be equally, or in some cases

better, fitted to non-heavy-tailed distributions with finite variance, such as the exponential distribution. The model presented in this paper reinforces the findings of Edwards *et al.* (2007) by giving an analytical example in which a Lévy process is not the most efficient strategy. However, it also provides an example in which the underlying process is based on a Lévy walk, but the observed patterns are not best described by a Lévy (i.e. power law) distribution. This corresponds with the work of Sims *et al.* (in press), who claim to have evidence of Lévy distributions in marine predators. One reason that the Lévy and composite search models can produce observed distributions that are similar in certain respects is that both have the common feature of a mixture of short and long step lengths.

In agreement with an increasing number of other studies (Bénichou *et al.* 2005, 2006; Benhamou 2007), this model has shown that, frequently, there are simple composite search strategies that are more efficient than ballistic or Lévy strategies. This is particularly so in the less well-studied case of non-destructive foraging (corresponding to a patchy food environment) considered in this paper.

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## APPENDIX A. MAXIMIZING MEAN EFFICIENCY

From equation (2.9) for  $E(L)$ , we may write

$$\frac{E(L)}{d} = \sqrt{\frac{2\epsilon\hat{\tau}}{\pi}} e^{-\epsilon/2\hat{\tau}} + \left(\epsilon + \hat{\tau} + \frac{1}{2}\right) \operatorname{erf}\left(\sqrt{\frac{\epsilon}{2\hat{\tau}}}\right) - \epsilon,$$

where

$$\hat{\tau} = \frac{v_I \tau}{d}, \quad \epsilon = \frac{2x_0^2}{\pi v_I d}.$$

If there is a local minimum in  $E(L)$  for a positive value of  $\hat{\tau}$ , it will occur where the derivative of this function with respect to  $\hat{\tau}$  is zero, i.e.

$$0 = F(\hat{\tau}) - G(\hat{\tau}), \quad (\text{A } 1)$$

where

$$F(\hat{\tau}) = \operatorname{erf}\left(\sqrt{\frac{\epsilon}{2\hat{\tau}}}\right), \quad G(\hat{\tau}) = \frac{\epsilon^{1/2}}{2^{3/2}\pi^{1/2}} \hat{\tau}^{-(3/2)} e^{-(\epsilon/2\hat{\tau})}.$$

This is a transcendental equation for  $\hat{\tau}$  for which there is no closed-form solution. However, by considering the functions  $F$  and  $G$ , it may be seen that there are two possibilities, depending on the value of  $\epsilon$ .

$F(\hat{\tau})$  is monotonic decreasing in  $\hat{\tau}$ ,  $F(0) > 0$  and  $F(\hat{\tau}) \rightarrow 0$  as  $\hat{\tau} \rightarrow \infty$ .  $G(\hat{\tau})$  has a unique local maximum at, say,  $\hat{\tau} = \hat{\tau}_m$ ,  $G(0) = 0$  and  $G(\hat{\tau}) \rightarrow 0$  as  $\hat{\tau} \rightarrow \infty$ .  $G$  decays to zero more rapidly than  $F$  so, for sufficiently large  $\hat{\tau}$ ,  $G(\hat{\tau}) < F(\hat{\tau})$ . There are thus two possibilities: (a)  $G(\hat{\tau}) < F(\hat{\tau})$  for all  $\hat{\tau} \geq 0$ ; or (b)  $G(\hat{\tau}) > F(\hat{\tau})$  for some  $\hat{\tau}$  (see figure 7). In case (a),  $E(L)$  is a monotonic increasing function of  $\hat{\tau}$ , hence the optimal value of  $\hat{\tau}$  is zero. In case (b), there is a range of  $\hat{\tau}$  for which  $E(L)$  is a decreasing function of  $\hat{\tau}$ . There is hence a local maximum and a local minimum in  $E(L)$ ; the local



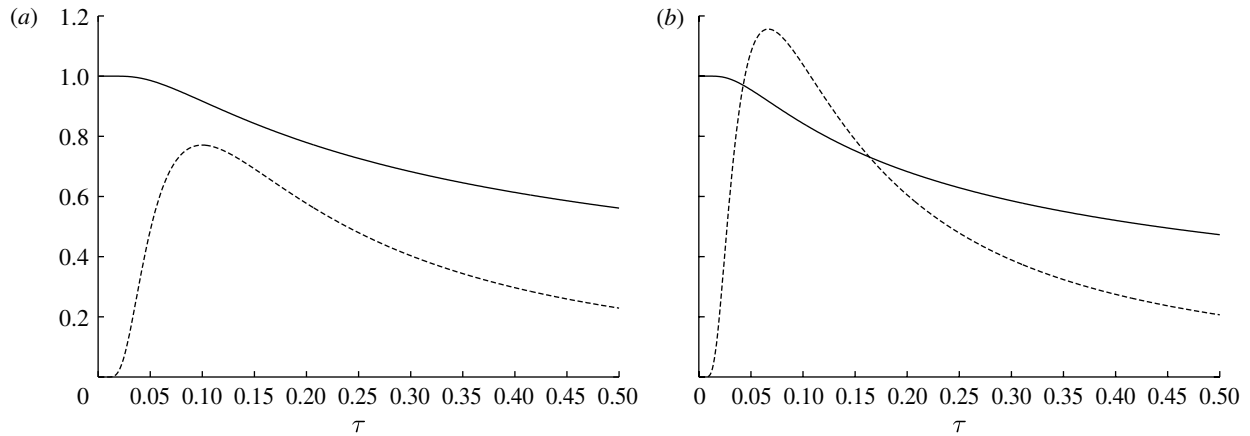


Figure 7. Graphs of  $F(\hat{\tau})$  (solid lines) and  $G(\hat{\tau})$  (dashed lines) against  $\hat{\tau}$  for (a)  $\epsilon = 0.3$  and (b)  $\epsilon = 0.2$ . In case of (a),  $(dE(L))/(d\hat{\tau}) > 0$  for all  $\hat{\tau}$ . In case of (b), there is a range of  $\hat{\tau}$  (between the two roots of  $F(\hat{\tau}) = G(\hat{\tau})$ ) for which  $(dE(L))/(d\hat{\tau}) < 0$ .

minimum is a global minimum if it is smaller than the value of  $E(L)$  at  $\hat{\tau} = 0$ .

Case (b) is guaranteed to occur if  $G(\hat{\tau}) > F(\hat{\tau})$  at  $\hat{\tau} = \hat{\tau}_m$  (the local maximum of  $G$ ). Solving the equation  $G'(\hat{\tau}_m) = 0$  shows that  $\hat{\tau}_m = \epsilon/3$ . Hence  $G(\hat{\tau}_m) > F(\hat{\tau}_m)$  if and only if

$$\frac{3^{3/2}}{2^{3/2}\pi^{1/2}e^{3/2}\epsilon} > \operatorname{erf}\left(\frac{3^{1/2}}{2^{1/2}}\right), \quad (\text{A } 2)$$

i.e.  $\epsilon_m < \epsilon \approx 0.25$ . To find an approximation to the solution to equation (A 1), we let  $s = \hat{\tau}^{-1}$  and expand  $F$  and  $G$  as power series in  $s$ . Equation (A 1) then reads

$$0 = \frac{2^{1/2}}{\pi^{1/2}} \left( (\epsilon s)^{1/2} - \frac{(\epsilon s)^{3/2}}{6} + \frac{(\epsilon s)^{5/2}}{40} + O((\epsilon s)^{7/2}) \right) - \frac{\epsilon^{1/2}}{2^{3/2}\pi^{1/2}} s^{3/2} \left( 1 - \frac{\epsilon s}{2} + \frac{(\epsilon s)^2}{8} + O((\epsilon s)^3) \right).$$

Collecting powers of  $s$  gives

$$0 = 1 - \left( \frac{\epsilon}{6} + \frac{1}{4} \right) s + \epsilon \left( \frac{\epsilon}{40} + \frac{1}{8} \right) s^2 - \frac{\epsilon^2}{24} s^3 + O((\epsilon s)^3). \quad (\text{A } 3)$$

In case (b), where there is a solution to equation (A 1),  $\epsilon \ll 1$  by (A 2). We thus seek a solution as a power series in  $\epsilon$

$$s = \sum_{n=0}^{\infty} s_n \epsilon^n. \quad (\text{A } 4)$$

Substituting this series into equation (A 3) and equating coefficients of  $\epsilon^n$  ( $n=0, 1, 2$ ) give the coefficients in the series for  $s$  as follows:

$$s_0 = 4, \quad s_1 = \frac{16}{3}, \quad s_2 = \frac{392}{45}.$$

Hence, provided that condition (A 2) is satisfied, there is a local minimum of  $E(L)$  with respect to  $\tau$ , which occurs at

$$\begin{aligned} \tau^* &= \frac{d}{v_I} \left( 4 + \frac{16}{3}\epsilon + \frac{392}{45}\epsilon^2 + O(\epsilon^3) \right)^{-1} \\ &= \frac{d}{4v_I} \left( 1 - \frac{4}{3}\epsilon - \frac{2}{5}\epsilon^2 + O(\epsilon^3) \right). \end{aligned} \quad (\text{A } 5)$$

Numerical explorations indicate that if  $\epsilon < 0.19$ , then this local minimum is also the global minimum. If  $0.19 < \epsilon < 0.25$  then the local minimum still exists, but the global minimum is at  $\tau = 0$ . If  $0.25 < \epsilon$  then there is no solution to equation (A 1) and the global minimum is at  $\tau = 0$ .

Disregarding terms of order  $\epsilon^3$  in or higher in (A 5) yields the approximation (2.10). It is straightforward to calculate more terms in the series (A 4), but the approximation provided by calculating terms up to order  $\epsilon^2$  was judged to be sufficiently accurate.

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