

Managing uncertainty: information and insurance under the risk of starvation

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In an uncertain world, animals face both unexpected opportunities and danger. Such outcomes can select for two potential strategies: collecting information to reduce uncertainty, or insuring against it. We investigate the relative value of information and insurance (energy reserves) under starvation risk by offering model foragers a choice between constant and varying food sources over finite foraging bouts. We show that sampling the variable option (choosing it when it is not expected to be good) should decline both with lower reserves and late in foraging bouts; in order to be able to reap the reduction in uncertainty associated with exploiting a variable resource effectively, foragers must be able to afford and compensate for an initial increase in the risk of an energetic shortfall associated with choosing the option when it is bad. Consequently, expected exploitation of the varying option increases as it becomes less variable, and when the overall risk of energetic shortfall is reduced. In addition, little activity on the variable alternative is expected until reserves are built up early in a foraging bout. This indicates that gathering information is a luxury while insurance is a necessity, at least when foraging on stochastic and variable food under the risk of starvation.

Keywords: uncertainty; information; sampling; starvation risk; dynamic programming; energy reserves

1. INTRODUCTION

Many things in life are uncertain. To be competitive in the evolutionary market place, organisms must respond adaptively to multi-dimensional problems with components that vary over a range of time-scales. Consider a caricature of a foraging bird; whilst searching, it must distinguish food from non-food, and, upon finding food, decide whether to eat now or hold out for more profitable fare that may turn up in the meantime. All the while, it must also consider whether to remain in the locale, move on to 'pastures greener', or into 'safer waters' (see Stephens & Krebs (1986) for a review of foraging problems in general). Moreover, wherever the bird decides to forage, it must navigate and be on the lookout for potential competitors, predators and future mates, to which it must also respond adaptively.

Almost all of the key components of the type of problems outlined above are likely to have uncertainty associated with them; for our purposes, uncertainty is the degree to which events are determined by factors that are out of an individual's knowledge ('chance'). For effective decision-making, the current state of an animal's environment is critical, which includes the range of options open to it, the likely consequences of each option, and the probable behaviour and states of others. However, such features are likely to be changing continuously due to changes in weather, the behaviour of other organisms, or other factors that are out of the animal's direct control. This means

that any time spent in one area, or attending to a particular task, will increase uncertainty about the rest of the world. In addition, an animal may never be able to eliminate the uncertainty associated with environmental features: for instance, parts of food patches are likely to be empty, and the proportion of such parts determines patch quality. In other words, many features of the world are inherently probabilistic, or stochastic in nature. We focus here on potential strategies for coping with what must therefore be a pervasive problem of uncertainty in evolutionary and behavioural biology, and present an initial attempt to characterize the conditions under which two probable solutions will be selected.

(a) *Information and insurance*

As one solution to the problem of uncertainty, organisms can attempt to reduce the uncertainty associated with key features of their environments by collecting and storing information. By sampling each of its options regularly, an animal gains from being able to exploit them when they are productive and avoid them otherwise. In this way, collecting information can be thought of as a solution to the uncertainty problem that maximizes potential opportunities (Stephens 1989; Mangel 1990). However, doing so may entail costs because valuable resources, including energy, time and attention, must be redirected to this end at the expense of other biological demands such as growth and reproduction. Formal analysis of the problem of tracking a changing environment has shown that the optimal level of sampling depends on the ratio of the costs of missing productive opportunities ('sampling error costs') to the costs of sampling unproductive options ('overrun error costs'), and the rate at which options change states (see Stephens & Krebs (1986) and Krebs & Inman (1992)

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for reviews). Acquiring information socially, however, can improve the efficiency of the sampling process by mitigating some of the costs (see Valone & Templeton (2002) for a review), although it is not without its own potential pitfalls (Giraldeau *et al.* 2002).

Alternatively, animals can minimize the consequences of uncertainty by insuring themselves against its potential dangers. One way that organisms can insure themselves against uncertainty is to develop and maintain a range of options; the more flexible or generalist an organism is, the less likely it is to be caught out when conditions change unpredictably. However, to reap such insurance benefits from flexibility, organisms must develop and maintain the ability to exploit alternatives that are unlikely to covary positively with each other; in other words, alternatives that are unlikely to depend on the same ecological factors (Wilson & Yoshimura 1994). This dependence on a spread of options underlies the costs associated with developing and maintaining flexibility as a solution to the uncertainty problem (see Dall & Cuthill (1997) and DeWitt *et al.* (1998) for further discussion).

Another way that organisms can insure themselves against uncertainty is to buffer themselves against it. For instance, many organisms have evolved defensive morphologies that act to minimize the consequences of predator activity. In doing so, however, such organisms may limit their ability to respond adaptively in other contexts (e.g. DeWitt 1998). Another form of buffer against risk that has received much attention in the behavioural ecology literature is the development and maintenance of energy reserves. Animals can minimize their risks of starving to death when foraging returns are uncertain by putting on fat, or storing food in caches. However, caches can be pilfered, spoil, or be forgotten (Lucas *et al.* 2001), and being fatter makes it relatively difficult to move around, which can increase the risk of injury or predation (Witter & Cuthill 1993). The implications of the trade-offs between such costs and the insurance benefits of storing energy are relatively well understood under a wide range of circumstances (Houston *et al.* 1993; Cuthill & Houston 1997; Lucas *et al.* 2001). To date, however, no one has attempted to explore when foragers should cope with uncertainty in foraging returns by insuring themselves against it rather than exploiting potential opportunities by attempting to collect information.

(b) On economically tracking a variable environment, revisited

We extend the model of Stephens (1987) of economic sampling in a changing environment to include energy reserves and the risk of starving to death over a finite foraging bout. We develop a dynamic programming model of the choice between two foraging options that differ in the variability of their returns: one provides a consistent alternative to an option that is sometimes better and sometimes worse. All foraging returns are stochastic: in this way the foragers are always at risk of an energetic shortfall, the magnitude of which is specified by the current probability of not gaining food after choosing an option. Our goal is to explore formally the relative value of information and insurance as strategies for coping with uncertainty in a context for which their consequences for fitness are well understood in isolation.

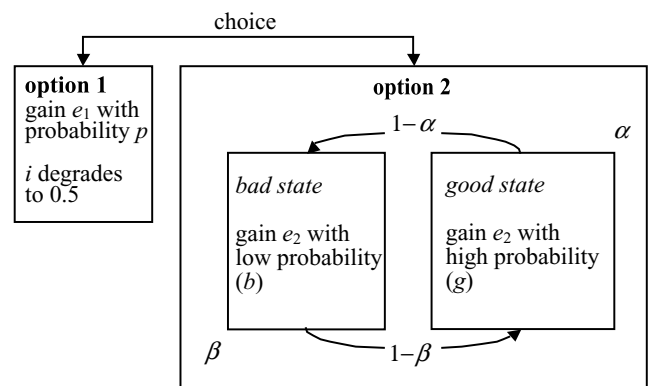


Figure 1. A schematic of the situation characterized by the model. See table 1 for definitions of the variables.

2. THE MODEL

Figure 1 is a schematic diagram of the model with terms defined in table 1, along with their baseline values. Behaviour is modelled as a sequence of decisions made at times $t = 1, 2, \dots$. An animal is characterized by the state of its energetic reserves at t , $X(t) = x$. If, at any point, this variable drops to its critical value, X_{crit} , the forager is assumed to have died of starvation. Likewise, the state variable cannot exceed X_{max} , which represents the maximum level of reserves that can be maintained. We assume that the foraging animal behaves so as to maximize its fitness F at T , the end of a foraging bout (e.g. at dusk for a diurnal animal). Specifically, the terminal fitness pay-off is a function of the forager's final state:

$$F(x, T) = \begin{cases} 0, & x \leq X_{crit} \\ \Omega \frac{x - X_{crit}}{x - X_{crit} + x_0}, & X_{crit} < x \leq X_{max} \end{cases} \quad (2.1)$$

As is evident from the bottom portion of equation (2.1), we assume that the pay-off from surviving the foraging period is an increasing, if decelerating, function of the forager's state at T . $\Omega = 1$ is the limit $x \rightarrow \infty$ of this function, thus representing the maximum fitness value of carrying reserves into the immediate future, with $F(x, T) = 0.5\Omega$ when $x = X_{crit} + x_0$ (Clark & Mangel 2000). In this way, we model the very general situation where condition at the end of a foraging period, as well as survival, has significant consequences for lifetime reproductive success (Cuthill & Houston 1997).

At each decision point t during the foraging period, the model animal must decide whether to forage on one of two foraging options (e.g. prey or patch types). If it chooses option 1, we assume that the forager will find food of expected energetic value e_1 with probability p in a time-period, and no food otherwise ($1 - p$). If, alternatively, the forager chooses option 2, it will find food of expected energetic value e_2 , also with a certain probability. However, the probability of finding food in a time-step does not remain constant on option 2. Rather, it changes over time such that the expected gain varies between two states: good (probability of finding food = g) > bad (probability = b), and hence the respective probabilities (risks) of finding no food $1 - g < 1 - b$. If the probability

Table 1. State-dependent sampling.

term and baseline value	definition
$T = 60$	length of foraging period
t	unit of time at which behavioural decisions are made
$X(t) = x$	state of energy reserves of the forager at t
$X_{\text{crit}} = 0$	levels of reserves at which starvation occurs
$X_{\text{max}} = 100$	maximum levels of reserves that can be stored
$I(t) = i$	state variable representing information about the system, it is the expectation that option 2 is in its good state
$X_{\text{init}} = 5, I_{\text{init}} = 0.5$	initial states for computation of expected optimal behaviour
e_1, e_2	net energy gained per food encounter from options 1, 2
p	probability of encountering food on option 1
g, b	probabilities of finding food on option 2 when in good, bad state: $g > p > b$
$\mu_1 = pe_1 = 15, \mu_2 = [(g + b)e_2]/2 = 13.5$	mean amount of food obtainable per time-step from options 1 and 2
$\alpha, \beta = 0.8$	probability that option 2 remains in good, bad state
$C(x)$	metabolic cost to forager of carrying x reserves specified in equation (2.2)
$r = 0.0339$	rate at which metabolic costs accrue with x

of finding food at t is g we assume that it will remain g with probability α or change to b at $t + 1$ with probability $1 - \alpha$. Likewise, if the probability of finding food on option 2 is b at t then we assume it remains so at $t + 1$ with probability β , or changes to g with probability $1 - \beta$. In this way, the model forager is offered a choice between two options, both with returns that are stochastic, but that differ in the variability of this stochasticity: one is stochastic consistently (option 1), the other varies over time in its stochasticity (option 2).

Whenever it has not chosen option 2, the animal has incomplete information about the current state of the option, and can gain information only by sampling it. Following Stephens (1987), we assume that the forager can easily discriminate between the good and bad states of option 2 once it has been chosen. In other words, we ignore the recognition problem that stochasticity poses (McNamara 1996; Dall *et al.* 1999), and assume instant recognition of ‘subtypes’ (Stephens & Krebs 1986). We represent the animal’s current information on the system by a value $I(t) = i$, which is the expectation that the probability of finding food on option 2 is g . As p is constant and known, and the probability of finding food on option 2 can only be g or b , then i is a complete representation of the information on this system. Throughout, we again follow Stephens (1987) and assume that the probability of change is symmetric between the states of option 2 (i.e. $1 - \alpha = 1 - \beta$). Hence, if a long time has elapsed since option 2 was chosen, i will be close to 0.5, for all $\alpha = \beta$. Similarly, if option 2 is not chosen at time t , i will be closer to 0.5 by time $t + 1$ (the information updating functions are given in Appendix A).

Moreover, we set up the sampling problem to be similar economically to that in Stephens (1987): the mean energetic returns from option 1, $\mu_1 = pe_1$, are intermediate to the contrasting gains on option 2, $ge_2 > \mu_1 > be_2$. In addition, we maintain the long-term returns from option 2, $\mu_2 = [(g + b)e_2]/2$, such that $\mu_1 > \mu_2$, to ensure that ‘blind’ exploitation of option 2 is penalized, at least in terms of the long-term rate of energetic intake. Hence, if it pays to reduce uncertainty by gathering information, we expect to observe tracking of the varying option and

switching back to the constant alternative whenever option 2 is expected to be bad.

Given the above formalization, choosing option 2 provides an expected gain of $be_2(1 - i) + ge_2i$, while choosing option 1 always returns a gain of μ_1 . Regardless of which option the forager chooses, it will incur a metabolic cost C . Moreover, this cost increases with the energetic state of the forager x ; thus we set the cost to insurance against uncertainty, modelled as a common mass-dependent cost (Witter & Cuthill 1993). Specifically, we assume that

$$C(x) = e^{rx}, \quad (2.2)$$

where r is the rate at which the metabolic costs accrue with x . Throughout we set r so that finding and consuming food always results in a net increase in energetic state; in other words, so that $\partial x/\partial t > 0$ with probability p for option 1, and probability g, b for option 2. The resultant state dynamics are detailed in Appendix A.

We find the strategy that maximizes the animal’s fitness at T , specified by equation (2.1). A strategy is a rule for choosing between the actions available to the forager during a foraging bout based on its energetic state and its current information on the system. As the fitness consequences of an action depend on future actions, we solve for the optimal strategy numerically, using dynamic programming (Houston *et al.* 1988; Houston & McNamara 1988; Mangel & Clark 1988). The dynamic programming equations are also given in Appendix A.

3. RESULTS

In general, we find that the foragers in our model are only likely to attempt to reduce their uncertainty in foraging returns by sampling and exploiting option 2 when the danger of starving to death in a foraging bout is minimal, and there is sufficient opportunity to both track and exploit the varying option. Consider the optimal strategy for a representative subset of parameter space. Figure 2 illustrates the general result that it is never optimal to sample the varying option when the forager is in poor condition and there is little time left in the bout. Note that, because the forager knows the state of the varying arm

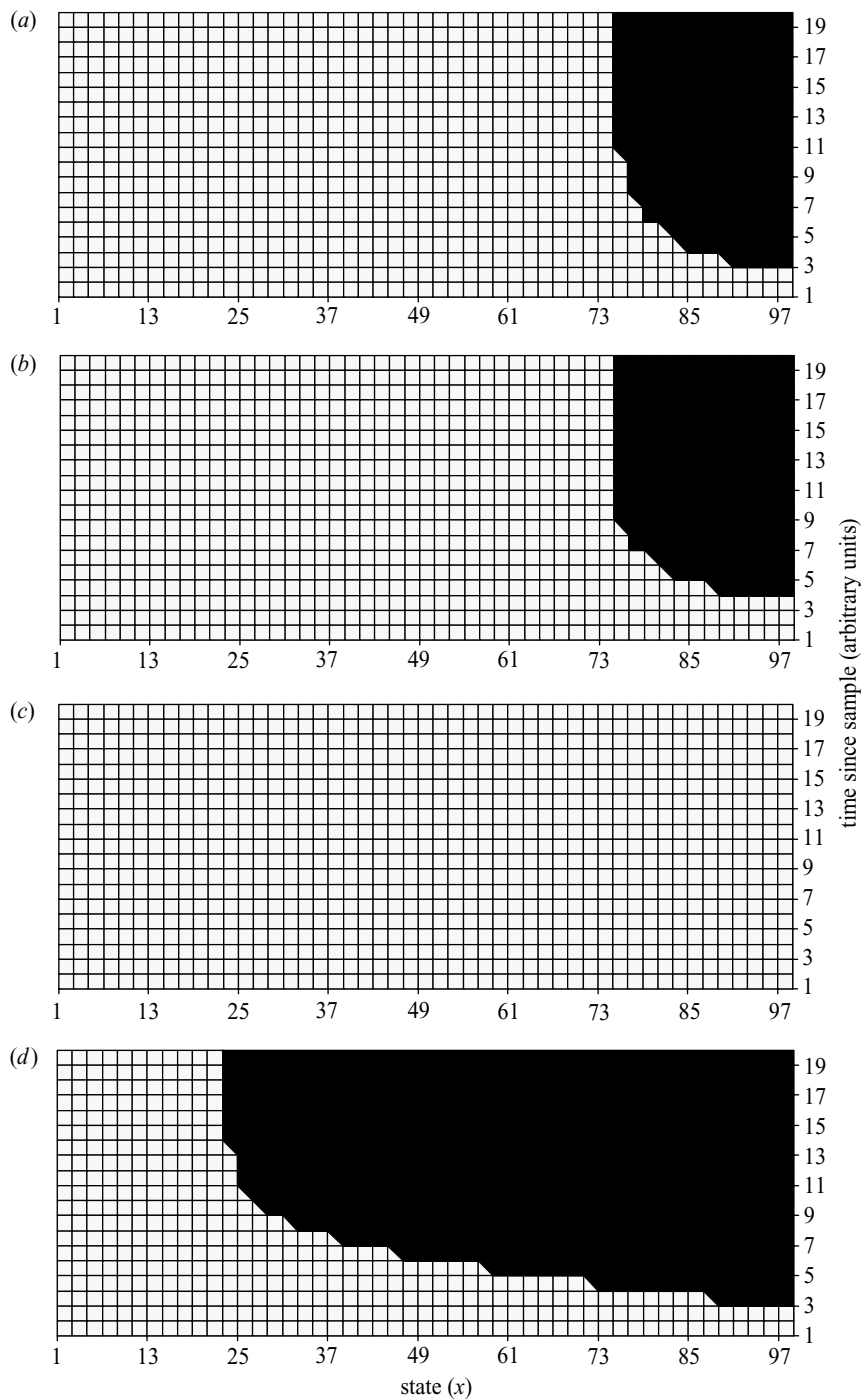


Figure 2. The optimal strategy for a representative subset of parameter space. The shaded areas of the decision matrices represent those energetic state values and times since the varying option was sampled when bad where it is optimal to choose option 2, the variable option. Parameter values: $e_1 = e_2 = 30$, $p = 0.5$ throughout; (a) $g = 0.6$, $b = 0.3$, $g/b = 2$ and $t = 56$; (b) $g = 0.6$, $b = 0.3$, $g/b = 2$ and $t = 57$; (c) $g = 0.6$, $b = 0.3$, $g/b = 2$ and $t = 58$; (d) $g = 0.7$, $b = 0.1$, $g/b = 7$ and $t = 58$. The values of the other parameters are given in table 1.

after it has been chosen, it should remain on it after it has experienced it as ‘good’ and leave if ‘bad’ (as $ge_2 > \mu_1 > be_2$). ‘Sampling behaviour’ can then be characterized by how long it is after option 2 has been experienced as bad before the forager should choose it again. In this way, figure 2 illustrates that, the closer it gets to the end of the foraging bout, the less willing the forager should be to return to (sample) the varying option (compare figure 2a–c). Moreover, the forager should never sample option 2 after it has been experienced as bad when in poor

condition, a result that holds regardless of the economic value of sampling to a rate maximizer (Stephens & Krebs 1986; Stephens 1987; McNamara 1996; Dall *et al.* 1999). This is illustrated by increasing g/b , while holding all other parameters equal (compare figure 2c,d), thereby increasing the value of learning to exploit the varying option, as the returns increase from following the strategy: forage on the varying option when it is in its good state and the constant option otherwise (the rate maximizing strategy with perfect information; McNamara 1996). At the same

time, however, the ratio of sampling error to overrun error costs (ε ; Stephens & Krebs 1986; Stephens 1987) is not changed substantially (figure 2*a-c*: $\varepsilon = 2$; figure 2*d*: $\varepsilon = 1.33$).

To understand the implications of these findings for expected behaviour, we determine the likelihood that foragers following the optimal strategy would be in a particular state, or subset of states (and hence behaving in a particular way), at each decision point in the foraging bout after specifying the initial states, X_{init} and I_{init} (Houston & McNamara 1999). We assume that foragers begin a foraging bout in relatively poor energetic condition $X_{\text{init}} = 5$ (e.g. small birds at dawn in winter; Houston *et al.* 1993) and with no information about the system $I_{\text{init}} = 0.5$.

In addition to the value of learning to exploit option 2 efficiently and the trade-off between the costs of sampling and overrun errors, the stability of the varying option, or the probability of it changing states, is known to influence rate-maximizing sampling behaviour (Stephens & Krebs 1986; Stephens 1987; Krebs & Inman 1992; Dall *et al.* 1999). Figure 3 illustrates the effect of varying $1 - \alpha = 1 - \beta$ on expected foraging behaviour and its consequences in our model; in other words, when stochasticity and the risk of starvation are also considered. By reducing the probability that option 2 changes states, it becomes easier to track its behaviour; any observation of the varying option's state will reduce uncertainty about the system in the future for longer as the probability of a change declines (Stephens 1987). This increases both the average proportion of time per t that foragers should spend exploiting option 2 (i.e. the proportion of time with relatively high expectation that it is good) and the amount of the foraging bout in which it pays to do so (figure 3*a*). Due to the fact that animals with more information about the foraging problem are in less danger of an energetic shortfall in our model system, less insurance against the risk of death by starvation is needed during the foraging bout; foragers can defend lower levels of energy reserves (Cuthill & Houston 1997). Instead, foragers can sacrifice energetic reserves, without risking death by starvation, in favour of sampling during the bout (which results in lower returns in the short run as $\mu_2 < \mu_1$), thus allowing efficient exploitation of the varying option (i.e. choosing it when it is good) to maximize fitness by improving condition markedly at the end of the bout (figure 3*b*). Note that there is no difference in the mortality rates of foragers following the optimal strategy under the different rates of change of option 2 in figure 3*c*.

Alternatively, the overall stochasticity in foraging returns, which it is not possible to reduce by collecting information about the system, should not influence rate maximizing sampling behaviour with perfect recognition of 'subtypes' (Stephens & Krebs 1986; Stephens 1987). Nevertheless, as the energetic state of a forager influences its optimal strategy significantly in our system (figure 2), the risk of energetic shortfall across options has consequences for expected behaviour. Figure 4 illustrates the consequences of changing the probabilities of finding food on the two options (p , g and b), along with the amount of food gained (e_1 , e_2), simultaneously, whilst holding all else constant (including μ_1 , μ_2 and g/b). Overall, as the risk of energetic shortfall increases, so the amount of foraging on option 2 declines (both in terms of the average

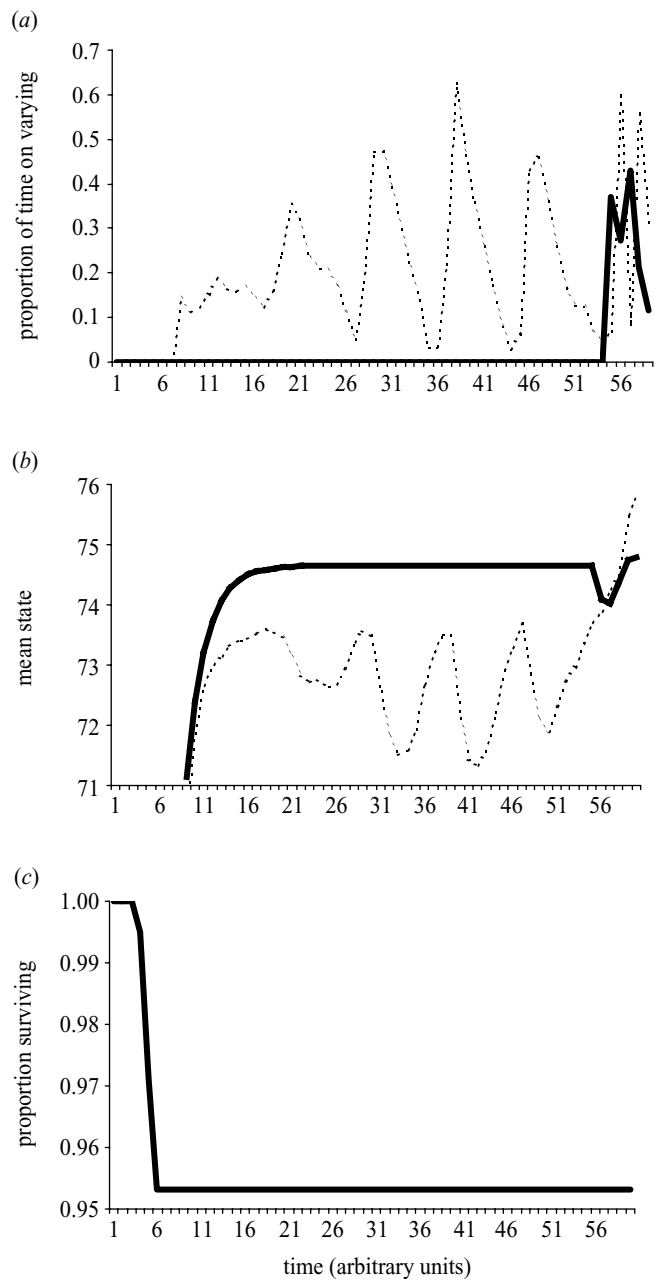


Figure 3. The influence of variability on expected behaviour. Each plot is a run of the model showing (a) the average proportion of time that foragers should spend on option 2; (b) foragers' mean energetic state; and (c) the proportion of foragers who survive, which varies over the foraging bout when following the optimal strategy. Parameter values: $e_1 = e_2 = 30$, $p = 0.5$, $g = 0.6$, $b = 0.3$ throughout. The thick solid lines represent $\alpha = \beta = 0.8$ (i.e. $p(\text{change}) = 0.2$), and the dashed lines represent $\alpha = \beta = 0.95$ (i.e. $p(\text{change}) = 0.05$). The values of the other parameters are given in table 1.

proportion of time spent and the amount of the foraging bout in which it pays; figure 4*a*). This is because increasing overall stochasticity decreases the level of reserves that it is possible to defend (figure 4*b*); to defend or increase reserves under increased energetic risk requires that more time be devoted to foraging (Houston *et al.* 1993), which is not possible in our model. However, as the risk of a shortfall increases, so does the need for a buffer against starvation (Cuthill & Houston 1997), and therefore the

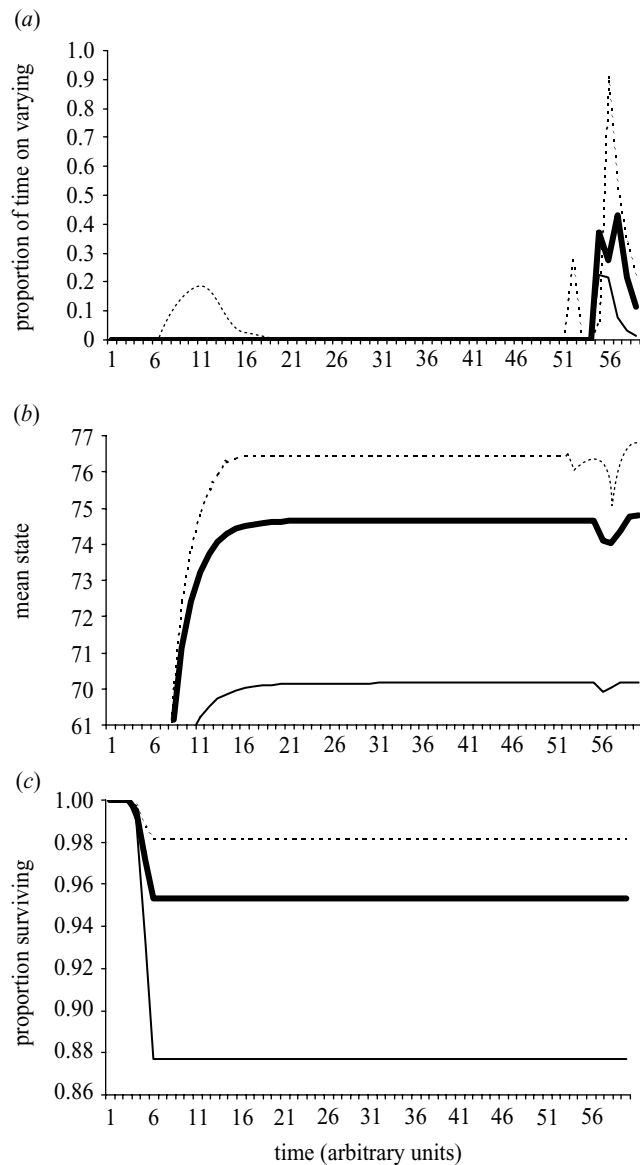


Figure 4. The influence of the risk of an energetic shortfall on expected behaviour. Each plot is a run of the model showing (a) the average proportion of time that foragers should spend on option 2; (b) foragers' mean energetic state; and (c) the proportion of foragers who survive, which varies over the foraging bout when following the optimal strategy. The thick solid lines represent moderate risk with $e_1 = e_2 = 30$, $p = 0.5$, $g = 0.6$ and $b = 0.3$; the dashed lines represent lower risk with $e_1 = e_2 = 25$, $p = 0.6$, $g = 0.72$ and $b = 0.36$; and the thin solid lines represent higher risk with $e_1 = e_2 = 40$, $p = 0.375$, $g = 0.45$ and $b = 0.225$. The values of the other parameters are given in table 1.

proportion of foragers surviving also declines (figure 4c). As minimizing the risk of dying of starvation is at a premium in our model (surviving in poor condition is better than a pay-off of 0), the extent to which energy reserves can be sacrificed in favour of sampling option 2 to reduce uncertainty and boost final state declines with overall stochasticity. Note that, in general, sampling can only be afforded after an initial period of foraging to build up reserves, even at low probabilities of change (seven time-steps: figure 3a) and low risks of an energetic shortfall (six time-steps: figure 4a).

4. DISCUSSION

To better understand the relative value of dealing with uncertainty by insuring against it versus attempting to reduce it by collecting information, we have extended previous analyses of economic sampling behaviour in behavioural ecology (Stephens & Krebs 1986; Stephens 1987) to include a risk of dying of starvation, and incorporating energetic state dynamics over finite foraging bouts. In doing so, we find that sampling activity on a variable food source (choosing it with low expectation that it will be good) should decline with lower energy reserves and late in the foraging bout (figure 2). This is driven by the fact that, in order to be able to reap the opportunities associated with exploiting a variable option effectively, foragers must be able to afford an initial increase in the risk of an energetic shortfall associated with choosing the option when it is bad. Therefore, it does not pay to sample with little or no reserves against the risk of finding no food, and little opportunity to forage effectively once a good estimate of when the varying option is likely to be good is attained. Consequently, exploitation of the varying option increases as it becomes less variable (figure 3) and when the overall risk of energetic shortfall is reduced (figure 4). In addition, little activity on the variable alternative is expected until reserves are built up early in a foraging bout (figures 3a and 4a). In this way, our first analysis of the problem indicates that gathering information is a luxury, while insurance is a necessity, when faced with uncertainty, at least in the context of foraging on stochastic and variable food.

As we limit our treatment here to simple variations on previous models of economic sampling in a variable environment (Stephens & Krebs 1986; Stephens 1987), we have glossed over a number of issues that may affect our conclusions. An additional consequence of considering stochasticity to foraging returns is that it will affect the tracking of variable resources when an animal must infer the state of a resource from its success on it (i.e. 'subtype' recognition is imperfect (Stephens & Krebs 1986)); decreasing the probability of finding food will reduce the information about the current state of an option generated by each sample as finding no food becomes more probable regardless of whether it is good or bad (McNamara 1996). Nevertheless, preliminary analyses of relaxing the assumption of perfect recognition in our model (i.e. setting information updating as in Dall *et al.* (1999)) indicate that it does not change the results presented here qualitatively. Moreover, relaxing the assumption of symmetric change between states on the variable option (i.e. when $\alpha \neq \beta$) also has little effect on our general findings about the relative value of information and insurance in this context (S. R. X. Dall and R. A. Johnstone, unpublished data).

Overall, then, our formal exploration of the advantages and disadvantages of coping with the problem of uncertainty in a foraging context indicates that 'insurance first and foremost, and information if affordable' is a robust adaptive response. We hope that, by highlighting the issues involved, further work on coping with uncertainty in other biological contexts will be forthcoming. One particularly productive extension of our current work may be to consider the state-dependent sampling problem in a social context, with competition and the availability of

public information (Valone & Templeton 2002). Indeed, current state-dependent foraging games indicate that pairwise interactions between foragers can create social roles by locking foragers into different subsets of energetic state space (S. A. Rands and R. A. Johnstone, unpublished data). If similar effects emerge in a state-dependent sampling game context then our results indicate the intriguing possibility of social-information-generating roles determined by condition; in effect a reverse ‘producer–scrounger’ situation, where individuals in good condition ‘produce’ while those in poor condition are forced to ‘scrounge’ (Barnard & Sibly 1981).

To conclude, it appears that, when faced with uncertainty in foraging returns and the possibility of starving to death, the best response only involves attempting to reduce uncertainty by collecting information when there are sufficient reserves to insure against the heightened risk of starvation that sampling entails, and there is sufficient opportunity to exploit the information gained. Only further work in other biological contexts will establish whether insurance is always a necessity, while information is a luxury, when managing the pervasive problem of uncertainty in biological systems.

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APPENDIX A: STATE-DEPENDENT SAMPLING MODEL

(a) Information updating functions

Suppose option 2 switches between the probability of encountering food ($p_2 = g$ and $p_2 = b$, where $g > b$, with switching parameters α and β (see § 2). The animal’s previous experience on option 2 can be characterized by how long ago it was sampled $L(t) = l$ ($0 \leq l \leq t$) and what state it was in when it was sampled $Q(t) = q$ ($q = 1 | p_2 = g$; $q = 0 | p_2 = b$), then the current probability that $p_2 = g$, or $I(t) = i$, can be calculated numerically as follows.

Let $i(0, q)$ be the posterior probability that $p_2 = g$ immediately after a trial on option 2, but before any possible change of p_2 . As the forager can recognize without error the current value of p_2 ,

$$i(0, q) = \begin{cases} 0, & q = 0 \\ 1, & q = 1 \end{cases} \quad (\text{A } 1)$$

Hence, for each $l = 1, \dots, t$ and $q = 0, 1$, allowing for the possible changes in p_2 , we have

$$i(l, q) = \alpha i(l-1, q) + (1 - \beta)(1 - i(l-1, q)). \quad (\text{A } 2)$$

(b) State transitions

Suppose an animal, characterized by the state of its energetic reserves, $X(t) = x$, how long ago it sampled option 2, l , and what state option 2 was in when sampled, q (see Appendix A(a)), can choose between two actions: $u_1 =$ ‘forage on option 1’ or $u_2 =$ ‘forage on option 2’. Note that $X_{\text{crit}} < x \leq X_{\text{max}}$ (table 1) and if $x \leq X_{\text{crit}}$ the forager starves.

(i) Option 1

If it chooses u_1 , it consumes food of expected energetic value e_1 with probability p and nothing with probability $1 - p$. Therefore, its potential state transitions are

$$x'_1 = x + e_1 - C(x) \quad (\text{A } 3a)$$

or

$$x''_1 = x - C(x), \quad (\text{A } 3b)$$

respectively, where $C(x)$ is the metabolic cost of foraging between t and $t + 1$ specified in equation (2.2). In addition,

$$l'_1 = l + 1 \quad (\text{A } 4)$$

and

$$q'_1 = q. \quad (\text{A } 5)$$

(ii) Option 2

Alternatively, if it chooses u_2 , it consumes food of expected energetic value e_2 with probability $r(i(l, q))$ and nothing otherwise. In addition,

$$r(i(l, q)) = (1 - i(l, q))b + i(l, q)g, \quad (\text{A } 6)$$

where $i(l, q)$ is specified in equation (A 2). Therefore, its potential state transitions are

$$x'_2 = x + e_2 - C(x) \quad (\text{A } 7a)$$

or

$$x''_2 = x - C(x), \quad (\text{A } 7b)$$

respectively, where $C(x)$ is the metabolic cost of foraging specified in equation (2.2). In addition,

$$l'_2 = 0 \quad (\text{A } 8)$$

and

$$q'_2 = 1 \quad (\text{A } 9a)$$

or

$$q''_2 = 0. \quad (\text{A } 9b)$$

(c) Dynamic programming equations

Let $F(x, l, q, T) \equiv F(x, T)$, defined in equation (2.1), be the fitness of the forager at T . Similarly, $F(x, l, q, t)$ is its fitness at $t = 1, \dots, T - 1$. Following equations (A 3)–(A 9), set

$$V_1(x, l, q, t) = pF(x'_1, l'_1, q'_1, t + 1) + (1 - p)F(x''_1, l'_1, q'_1, t + 1) \quad (\text{A } 10)$$

and

$$V_2(x, l, q, t) = r(i(l, q))F(x'_2, l'_2, q'_2, t + 1) + (1 - r(i(l, q)))F(x''_2, l'_2, q'_2, t + 1). \quad (\text{A } 11)$$

The optimal action $u^*(x, l, q, t)$ for the forager is then the value of j that maximizes $F(x, l, q, t; j)$, which is

$$F(x, l, q, t; u^*(x, l, q, t)) = \max_{j=1,2} V_j(x, l, q, t) \quad (\text{A } 12)$$

and

$$F(x, l, q, t) = \max_{j=1,2} V_j(x, l, q, t). \quad (\text{A } 13)$$

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