Foraging mode switching: the importance of prey distribution and foraging currency

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Foraging methods are highly variable, but can be grouped into two modes: searching and ambush. While research has focused on the functioning of each mode, the question of how animals choose which to use has been largely neglected. Here we consider a forager that exploits prey that are patchily distributed in space and time. This forager can either sit and wait for prey to appear or search for prey, which is more likely to result in encounters with prey but costs more energy and/or exposes the forager to greater predation risk. The currency that natural selection appears to have optimized will be determined by the additional costs of searching and whether there is a risk of starvation. We therefore compare the predictions of models based on currencies that consider only energy and predation risk to state-dependent models in which energy reserves are used to trade off predation rate, starvation rate and investment in growth. The choice of currency qualitatively affects how mode should change when prey abundance and prey patchiness increase. We show how differing prey distributions can explain variation in effects of experimentally increasing prey abundance. Our work has several implications for the study of foraging mode, population dynamics and the methods used to assess population size.

Food is usually spatially and temporally clumped, and effective foraging strategies must take this heterogeneous distribution into account. Foraging strategies can usefully be divided into two broad types. The first is to search actively for prey. Optimal foraging theory (Stephens & Krebs, 1986) has provided great insights into how foragers should choose among different prey (Krebs, Erichsen, Webber, & Charnov, 1977), adjust their search trajectories in response to clumped hidden prey (Prins & van Langevelde, 2008) and stop searching in the current patch to travel to another (Stephens, 2007). The second main foraging method, which can only be used when consuming mobile prey, is to sit and wait for prey to approach ('ambush' predation). Many foragers use this method (Cooper, Vitt, Caldwell, & Fox, 2001; Huey & Pianka, 1981; Johansson, 1991; Killen, Brown, & Gamperl, 2007; Scharf, Lubin, & Ovadia, 2011), which is more likely to be successful if a location can be found where prey arrive frequently, such as spiders waiting on flowers that attract pollinating insects (Morse, 2000). Research

on this mode of foraging has concentrated on understanding how sit-and-wait foragers choose foraging sites (Scharf et al., 2011), how they choose when to move between sites (Huey & Pianka, 1981) and the physiological correlates of sit-and-wait foraging as an obligate life history strategy (Lourdais, Gartner, & Brischoux, 2014).

Some animals are highly adapted for one of these two modes of foraging (Lourdais et al., 2014 and references therein), but many species switch flexibly between them. Among the African felids, for example, the cheetah, *Acinonyx jubatus*, lion, *Panthera leo*, and leopard, *Panthera pardus*, all make use of both foraging modes, differing in their relative use of the two (Turner, 1997). The optimal exploitation of patchily distributed prey has some commonality with the flexible use of ambush versus searching, but there are important differences. While the extensive literature on patch departure decisions and area-restricted search can be viewed as exploring a choice between waiting and moving, such models assume that decisions are driven by the spatial structuring of prey into patches and restricted information about food availability in the current patch (Stephens, 2007). However, many animals can see their prey and so are fully informed about the profitability of the current patch, and many prey are not found in discrete patches. Scavengers are especially obvious examples of such animals, since

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they seek individual prey items which may appear while they are waiting, or they can actively search for them. Furthermore, the short timescales involved in the approaches described above do not account for the likelihood that while active searching might bring benefits in enhanced encounter rates with prey, it is likely to increase costs: both metabolic and in greater exposure to predators. The relative magnitudes of these costs and benefits will be influenced by both the state of the focal organism and aspects of its environment. To our knowledge, few theoretical approaches have attempted to include these effects on foraging behaviour (see Bednekoff, 2007 for an overview). Our understanding of how animals decide whether to search or wait is less advanced than for other aspects of foraging theory, and since foraging mode clearly affects the distribution and/or behaviour of other species (Huey & Pianka, 1981), this is an important gap in our understanding of species interactions.

Norberg (1977) showed that a forager that has the 'aim' of minimizing the foraging time to achieve a given gain should respond to an increase in prey abundance by switching to a more costly but more rewarding strategy. This tactic is intuitively appropriate for endotherms that must meet a given metabolic need to stay alive, and experimental tests on endotherms tend to support this prediction (Rudolph, 1982). Ectotherms may instead maintain a minimum prey encounter rate (Helfman, 1990), but experiments on ectotherms known to use both foraging modes reveal a mixture of responses when prey abundance increases: switching from search to ambush (Anthony, Formanowicz, & Brodie, 1992; Formanowicz, 1982; Inoue & Matsura, 1983; Johansson, 1991), switching from ambush to search (Hirvonen, 1999; Huey & Pianka, 1981) or maintaining ambush at all prey densities (Greeff & Whiting, 2000; Johansson, 1991), and in one case predators switched from ambush to searching as prey abundance increased and back to ambush at very high prey densities (Hirvonen, 1999). This variability may occur because different ectotherms will have faced different selective pressures on their foraging behaviour (Griffiths, 1980), such as whether searching requires increased energy use or entails a higher risk of predation. Furthermore, different studies have used different prey and have manipulated prey abundance in various ways. Predators should respond to the distribution of their food, in addition to its abundance, and since experimenters may inadvertently alter prey distribution when altering prey abundance, we might expect differences between experiments in predator responses.

To understand the variability in foraging mode we make three biologically motivated developments. (1) We relax the assumption that the forager knows where the other patches of prey are, and therefore deciding to move gives no guarantee of finding food. We assume instead that the food distribution exhibits both spatial and temporal autocorrelation, and any strategy must take this into account. That is, we assume that the prey temporal distribution is independent of the spatial distribution encountered by the forager, such as may occur if prey move in a different spatial plane from predators (e.g. small mammalian carnivores accessing birds that forage on the ground) or arrive randomly and are consumed (e.g. scavengers on benthic carrion, birds preying on bees at flowers). (2) We assume that the metabolic cost and predation risk while searching for prey can be greater than the metabolic cost and predation risk while waiting. This assumption is likely to be true very generally (Bautista, Tinbergen, & Kacelnik, 2001; Bautista, Tinbergen, Wiersma, & Kacelnik, 1998; Berger & Gotthard, 2008; Cooper & Sherbrooke, 2013; Helfman & Winkelman, 1991; Lourdais et al., 2014; Williams & Yeates, 2004; Wood, Stillman, Wheeler, Groves, Hambly, et al., 2013). (3) Optimal foraging theory is based on the concept of natural selection as a fitness-maximizing algorithm, where fitness is assumed to depend on

the dominant costs and benefits associated with behavioural options. The combination of the dominant costs and benefits is known as the 'currency'. Because the types of foraging costs and the particular requirements of any animal determine the currency its behaviour will be selected to maximize, we explore how the predictions of foraging models depend on the currency that an optimal strategy maximizes. We find the optimal strategy, which may be state-dependent, given four critical characteristics of the environment: the abundance of prey items, the number of prey in the patches, the spatial clumpiness of the patches and the size of prey items. Given the variability in previously reported experimental results, we are especially concerned with how the foraging currency and prey distribution should affect whether an increase in prey abundance favours an increase or a decrease in the propensity to search actively. Our analysis enables us to explain the variation among experimental results, make predictions for future experimental tests and explain differences between species and environmental conditions in observed foraging behaviour.

MODELS AND RESULTS

General Overview

We assess behaviour in a generic system where at any one time a solitary forager is in one of two exclusive states: either in a patch of prey or not. We assume that the animal knows without error whether it is currently in a patch of prey. Patches of prey occur in a world consisting of an infinite one-dimensional series of interconnected potential patch locations, which contain a total of γ prey items at all times. That is, prey are replenished continuously and are eaten by other predators, and the focal forager has a negligible impact on overall prey abundance and distribution. This would apply in situations in which prey and predator populations are stable and prey are mobile, and so the per capita prey abundance and distribution experienced by individual predators are unchanging.

When in a patch of prey, the forager makes the binary decision θ whether to eat a prey item ($\theta = F$) or rest ($\theta = R$, if its reserves are sufficiently high). If the forager chooses to feed then it consumes a prey item and gains an amount of energy drawn stochastically from a symmetrical distribution with mean c. Owing to prey movement and competition from other predators, there is a probability ϕ per time step that a patch will become exhausted (i.e. be empty on the next time step) whether the forager eats or not. This implies that the number of prey in a patch is Poisson distributed (with the mean number of prey in a patch equal to $1/\phi$). We refer to ϕ as patch transience and $1/\phi$ as patch size. Thus, prey are clumped such that most locations are empty but patches of prey each consist of a variable number of food items. In Fig. A1 (Appendix 1) we show the distribution of the number of prey per location for some representative values of ϕ.

If there are currently no prey at its current location the forager decides whether to search for prey ($\delta = S$) or wait for prey to arrive ($\delta = W$). The consequences of this decision depend on the probability of finding prey under the chosen option, the energetic costs until the next decision time and the associated predation risk.

Assuming that the density of food in the environment is fixed at γ then every time a patch is exhausted prey must appear in another location. The proportion of locations that contain a prey patch depends on the size of patches and is $\gamma\phi$. Therefore $(1-\gamma\phi)$ of the possible locations do not contain prey at any given moment. Assuming that $\gamma \leq 0.5$ and time steps are sufficiently short that patches of prey cannot both appear and disappear from a location in the same time step, then if a forager waits at a location where there was no prey at the last time step, the probability that prey

arrives in the next time step is the product of the proportion of locations that contain a patch of prey ($\phi\gamma$) and the probability that any one becomes exhausted (ϕ), divided by the number of possible new locations ($1-\phi\gamma$):

$$P_W = \frac{\phi^2\gamma}{1-\phi\gamma} \qquad (1)$$

We also assume that patches of prey themselves may be clumped in space. Prey patches are spatially correlated according to the parameter ρ. In Fig. A2 (Appendix 1) we show the relationship between ϕ, ρ and the autocorrelation coefficient r as commonly used to measure spatial distribution in nature. For the baseline parameter values ($\phi = 0.25$, $\rho = 0.25$, $\gamma = 0.1$), there is a moderate positive autocorrelation ($r = 0.04$). We vary ρ from -1, representing strong negative clumping ($r = -0.35$ when ϕ is 0.9) to $+1$, representing strong positive clumping ($r = 0.35$ when ϕ is 0.9).

When searching, the forager moves in a straight line, searching the environment at a rate α. The probability it finds a patch containing prey in the next time step depends on γ, ϕ, ρ and α and is the probability that not all of the search locations are empty:

$$P_S = 1 - e^{-\alpha(1-\rho)\phi\gamma}, \qquad (2)$$

which decreases with ρ because the forager is currently located where there are no prey.

We assume that both metabolic costs (m) and exposure to predators (μ) depend on whether the animal is actively searching (m_S, μ_S), waiting (m_W, μ_W), feeding (m_F, μ_F) or resting (m_R, μ_R). We assume that being active is at least as energetically expensive and at least as dangerous as waiting, eating and resting, which we assume to be equally costly ($m_S \geq m_W = m_F = m_R$; $\mu_S \geq \mu_W = \mu_F = \mu_R$). If there is no added cost to searching rather than waiting ($m_S = m_W$, $\mu_S = \mu_W$) then the optimal strategy only depends on P_W and P_S. If $m_S > m_W$ and/or $\mu_S > \mu_W$ then the optimal choice depends on trade-offs between costs and the potential gains.

Foraging theory has typically been concerned with maximization of the net rate of energy gain (Stephens & Krebs, 1986) or the gain to mortality ratio (Werner & Gilliam, 1984). Neither currency can allow for the risk of starvation since they do not include energy reserves. If the threat of running out of reserves and starving is considered, then stochasticity in the food supply can play a crucial role in determining predictions. The magnitude of the threat of starvation changes with a choice of activity and so the strategy is state-dependent and can be found by stochastic dynamic programming techniques where the currency is the minimization of total mortality rate (through both starvation and predation). We can also use this methodology to combine the simple currencies mentioned above to allow for both growth and the risk of starvation. Here, we compare the predictions of these various currencies, comparing and contrasting the predictions that they make about how an animal will respond to an increase in the overall prey

Table 1
Parameters in the models and their default values

Parameter	Symbol	Value
Mean energy of prey items	c	10
Prey abundance	γ	0.1
Patch clumpiness	ρ	0.25
Patch transience	ϕ	0.25
Search rate	α	3
Energy use when searching	m_S	1
Energy use when not searching	m_W, m_F, m_R	0.25
Predation risk when searching	μ_S	0.0004
Predation risk when not searching	μ_W, μ_F, μ_R	0.0001

abundance of the environment and the distribution of prey. The parameters of all models and their default values are shown in Table 1. Parameter values were refined by a process of explorations of the model while considering predator behaviour and survival, choosing values that avoided floor or ceiling effects on choice of foraging mode and mortality, in order to maximize our ability to make predictions about effects of parameter values on the choice of foraging mode.

State-independent Foraging

First, we consider a forager that does not take into account its own level of energetic reserves in its decision making, which is likely to be realistic when the animal is not at risk of starvation. In such a case, we model a cycle of decision making that begins when a patch has just been exhausted and the animal acts to maximize some currency until the next exhaustion of a prey patch: this encompasses a phase in which the animal is either waiting for prey to appear in the current patch or searching for a new patch containing prey, plus the exploitation of the patch. For each situation we determine the combinations of parameter values under which we predict a switch between foraging modes as prey abundance changes. However, foraging mode decisions may be noisy, may differ between individuals and animals may show continuous responses (e.g. gradually increasing their allocation to searching behaviour), so we also predict the change in the relative value of searching.

Maximizing Probability of Encountering Prey

If $m_S = m_W$ and $\mu_S = \mu_W$ then the forager should search only if the chance of finding a new prey patch is greater than the chance that a patch of prey will arise at the current location ($P_S > P_W$); that is, if the relative benefit of searching,
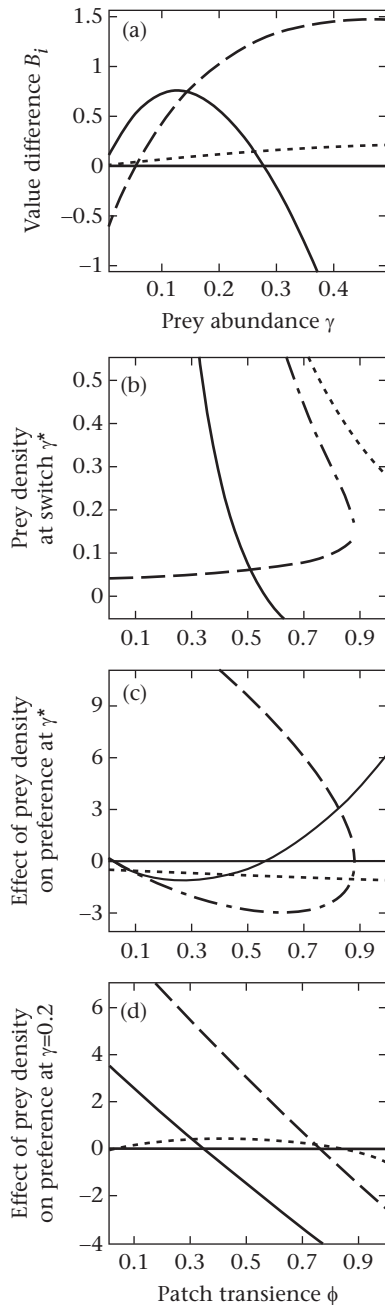
$$B_P = P_S - P_W, \qquad (3)$$

is positive. Substituting equations (1) and (2) into equation (3) gives

$$B_P = 1 - e^{-\alpha(1-\rho)\gamma\phi} - \frac{\phi^2\gamma}{1-\phi\gamma}. \qquad (4)$$

B_P is shown in Fig. 1a for some representative values. In Appendix 2 we explore the impact of the parameters and summarize the results in Table 2. We find that at the default parameter values (Table 1), increasing prey abundance and decreasing patch size both increase the benefit of searching (Table 2). If prey abundance is low then prey are hard to find; if prey patches are transient (i.e. high turnover of patches) then prey are likely to arrive at the current position. However, a switch of foraging mode ($B_P = 0$) only happens within the range of overall prey abundance ($0 < \gamma \leq 0.5$ if patch transience (ϕ) is large; Appendix 2, Fig. 1b); otherwise B_P increases with prey abundance, and the critical γ value for a behavioural switch, γ^*, is always at a high value (Fig. 1b). Furthermore, when a switch occurs (i.e. $\gamma^* > 0$) the switch is negative, indicating a switch to waiting (Fig. 1c). For $\gamma = 0.2$, the relative benefit of searching qualitatively depends on ϕ (Fig. 1d): if prey patches are small (γ is large) then increasing prey abundance decreases searching; otherwise increasing prey abundance increases searching. This conditionality occurs because if patches are large then they are very unlikely to appear if the forager waits, and increasing prey abundance has little effect because so many locations are empty and any given one is unlikely to receive a prey patch. It is therefore better to search.

Figure 1. Predictions of state-independent currencies: both predation risk and metabolic cost equal for searching and waiting (B_P, dotted lines), predation risk equal and metabolic cost larger for searching than waiting (B_R, $m_W = 0.25$, $m_S = 1$, dashed and dot-dash lines), metabolic cost equal and predation risk larger for searching than waiting (B_P, $\mu_W = 0.0001$, $\mu_S = 0.0004$, solid lines). (a) Relationship between prey abundance γ and B_i when $\phi = 0.4$. Effect of patch transience ϕ (x-axes) on: (b) value of γ at which the forager switches between modes ($B_i = 0$); (c) slope of B_i against γ at γ^*; (d) slope of B_i against γ at $\gamma = 0.2$. Note that unless ϕ is very large the switch from searching to waiting under probability maximization and rate maximization occurs at an impossibly high γ (i.e. >0.5). All parameter values are as shown in Table 1 except where otherwise stated.

Maximizing net rate of gain

If $m_S > m_W$ but $\mu_S = \mu_W$ then the forager may maximize the expected net rate of energy gain, given by

$$\frac{E(G) - E(k)}{E(t) + E(\tau)} \qquad (5)$$

Table 2
Summary of the direction of effects of the model parameters on the propensity to search actively, under each currency

Currency	γ	ϕ	ρ	α	c
No starvation					
Maximizing probability of encountering prey	+*	+*	−	+	
Maximizing net rate of gain	+	−	−	+	+*
Maximizing ratio of gross gain to mortality rate	−*	−	−	+	+*
Starvation					
Minimization of mortality rate	−*	−	+	−*	−
Maximization of investment in growth before death	−	−	+	−	−

γ: prey abundance; ϕ: patch transience; ρ: patch clumpiness; α: search rate; c: mean energy in prey. A plus or minus sign indicates that this propensity rises or falls, respectively, as the specified parameter value increases. All other parameter values are as shown in Table 1. * indicates that these directions may be reversed under some restricted conditions (usually if ϕ is large, i.e. $\lambda \geq 0.8$).

where G is the gain while in a patch of prey, k is the metabolic cost when feeding and before a prey patch is encountered (while either waiting or searching), t is the duration of a prey patch and τ is the time until the prey patch is encountered. This gives (see Appendix 2) the advantage of searching over waiting as

$$B_R = \frac{s\left(\frac{1}{\phi}\right) - m_S \frac{1}{\left(1 - \frac{1}{1 + \alpha(1-\rho)\gamma\phi}\right)} - m_W \frac{1}{\phi}}{\frac{1}{\left(1 - \frac{1}{1 + \alpha(1-\rho)\gamma\phi}\right)} + \frac{1}{\lambda}} - \frac{s\left(\frac{1}{\phi}\right) - m_W \frac{1-\phi\gamma}{\phi^2\gamma} - m_W \frac{1}{\phi}}{\frac{1-\phi\gamma}{\phi^2\gamma} + \frac{1}{\phi}}.$$

$$(6)$$

As we show in Appendix 2, the foraging mode switch ($B_R = 0$) is from waiting to searching (as in Norberg, 1977; Fig. 1a) with some rare conditions (high ϕ) causing a switch back from searching to waiting at high γ (Fig. 1b, c). Generally, the benefit of searching increases as γ increases (Fig. 1d).

Maximizing ratio of gross gain to mortality rate

If $\mu_S > \gamma_W$ but $m_S = m_W$ then we can assume that metabolic costs are negligible (for growing animals; Tammaru & Esperk, 2007) and maximize the growth to mortality ratio (Werner & Gilliam, 1984). This gives (Appendix 2) the advantage of searching over waiting as

$$B_G = \frac{s\left(\frac{1}{\phi}\right)}{\mu_W \frac{1}{\phi} + \mu_S\left(1 - \frac{1}{1 + \alpha(1-\rho)\gamma\phi}\right)} - \frac{s\left(\frac{1}{\phi}\right)}{\mu_W \frac{1}{\phi} + \mu_W \frac{1-\phi\gamma}{\phi^2\gamma}}. \qquad (7)$$

Here, where there is a mode switch ($B_G = 0$), this switch is always from searching to waiting as prey abundance (γ) increases (Appendix 2, Fig. 1a, b, c). Indeed, searching always decreases as γ increases, unless γ and ϕ are low (Fig. 1d). As with maximization of net rate, increasing patch transience (ϕ) tends to reduce the benefit of searching since prey are more likely to be encountered if the forager avoids the costs of searching and waits instead.

For all state-independent currencies the benefit of searching always increases with search rate (α), because the predator is more likely to find a patch, and decreases with patch clumpiness (ρ), because if prey are clumped then they are harder to find as the forager is currently not among prey. When patches are large (ϕ is small) then searching increases with the size of food items (c) because the large benefit of finding a patch outweighs the additional costs of searching, but if patches are small (ϕ is large) then searching may decrease as c increases.

State-dependent Foraging

So far we have assumed that the forager cannot starve; however, for foragers that search for large but sparsely distributed food sources, starvation in the interval between encounters is often a nontrivial risk. Such animals use energy reserves to trade off the risk of starving against the risk of predation (Houston & McNamara, 2014). We characterize a forager by its level of energy reserves (x). We can assume either that the objective of the forager's strategy is only to avoid death or that it must also invest energy in growth. The latter therefore trades off growth against mortality (starvation plus
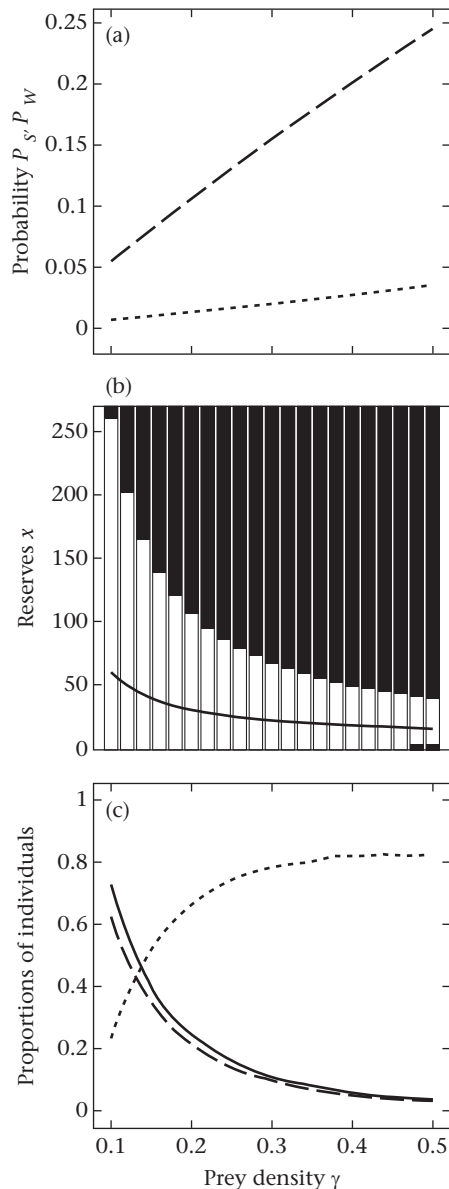
Figure 2. Effect of prey abundance γ (*x*-axes) on behaviour in a state-dependent growth model when both metabolic rate and predation risk are greater for searching than waiting ($m_S > m_W$, $\mu_S > \mu_W$). (a) Probability of finding food when waiting P_W (dotted lines) and searching P_S (dashed lines). (b) Optimal strategy showing levels of reserves where the forager searches (white) and waits (black); solid line indicates reserves above which the animal should invest in growth. (c) Proportion of individuals searching (means of 10 replicates of 1000 individuals) out of the total number of individuals (dashed lines) and out of the number of individuals not in a prey patch (solid lines), and the proportion of individuals waiting out of the total number of individuals (dotted lines). Other parameter values as shown in Table 1.

predation), and is applicable where an animal has been selected to minimize total mortality while growing to a fixed size (e.g. at maturity; Werner & Gilliam, 1984). At each time step, the forager can decide whether to invest one unit of reserves in growth. This decision must take into account the probability that reserves will be exhausted, which would cause the death of the forager. Predation rate and metabolic rates are assumed to increase with reserves (energy previously collected but not lost to metabolism) due to the negative impact of increased weight on ability to evade predators and the greater cost of maintaining more mass. However, our results are not qualitatively altered by this assumption, although it greatly aids finding optimal strategies (reducing convergence time). We find the optimal strategy by state-dependent dynamic programming (Houston & McNamara, 1999). Given the optimal strategy, we can use standard techniques to find the stationary state of a large population of foragers, giving the proportion of foragers feeding, waiting and searching at any time. See Appendix 3 for full details of these procedures. In initial evaluations of the model we first explored the impact of search rate α on fitness. Fitness (survival or contributions to growth before death) is maximized at a high search rate. We therefore assume in what follows that search rate is constrained below the optimal ($\alpha = 3$ throughout), but the particular value does not qualitatively affect our predictions.

Effect of prey abundance

The form of the optimal strategy is similar for most parameter values: search at low reserves and wait at high reserves (Fig. 2b). The contributions to growth occur when at high reserves, because there is little risk of starving, and can occur during either foraging mode depending on the conditions. The proportion of individuals searching at any time (Fig. 2c) depends on the distribution of reserves across individuals and the optimal level of reserves at which they switch (Fig. 2b), which in turn depends on the probabilities of finding a prey patch in the two foraging modes (Fig. 2a). We first explore the impact of different costs on the relationship between prey abundance γ and the proportion of individuals searching (Fig. A5). First, we note that increasing prey abundance generally causes a decrease in the proportion of individuals that are searching at any time (Fig. A5g, h, i), as might be expected from our analysis above because the model balances growth against mortality. The exception to this occurs when predation rate is not greater for searching than waiting and γ is high (Fig. A5a, d, g). In this case, there is little risk of starving and so there is a negligible effective cost of the higher metabolic rate and the animal can keep its reserves low and be active at all times. When γ is lower, the animal switches to waiting at high reserves in order to maintain reserves at the high level. Thus, for a small range of γ the proportion of individuals searching actually increases as γ increases (Fig. A5g).

When searching carries a higher predation risk than waiting (Fig. A5b, e, h, c, f, i) the animal should always reduce activity when γ increases because the risk of starvation decreases. Interestingly, if searching is energetically more costly animals should search more (see Fig. A5h, i) to maintain a higher level of reserves (see Fig. A5e, f) to compensate for greater average energetic expenditure. Additional evaluations showed that when search costs get even higher then searching does decline (results not shown).

Effect of prey distribution

Next, we assess how the distribution of prey affects the proportion of individuals that are searching. As patch transience ϕ increases, and so patches become smaller, the probability of encountering prey patches increases when both searching and waiting (Fig. A6a). This reduces the risk of starvation, and so the animal should maintain a lower level of reserves (Fig. A6d) and so search less (Fig. A6g). As spatial clumpiness ρ increases P_S declines

(Fig. A6b) because when the forager is currently not around food, and the more clumped food is, the more difficult it is to find. This increases the risk of starvation as the animal is more likely to go for a long period without food, so it attempts to maintain a higher level of reserves (Fig. A6e) leading to the counterintuitive effect of increasing the proportion of animals searching. When ρ and φ increase simultaneously, such as if the food of the prey becomes more clustered and prey compete to maintain a foraging area, the effect of φ dominates the outcome and the level of reserves below which the animal should search decreases (Fig. A6f), at least until high ρ, when the optimal probability of searching also declines (Fig. A6c). However, increasing ρ and φ together decreases reserve levels so the proportion of searchers increases (Fig. A6i). Increasing search rate α has the counterintuitive effect (not shown) of reducing the proportion of individuals searching, because it takes less time to find the patches and so favours less time searching between feeding. Increasing the energetic value of prey items c reduces the proportion of individuals searching because it becomes easier to reach a level of reserves at which the risk of starvation is low and the animal can rest.

These effects are qualitatively unchanged if we assess the strategy for just avoiding mortality (i.e. no contributions to growth), but the animals are far less likely to search and so we often have floor effects where parameters appear to have no effect because animals never search. The effect of each parameter is summarized in Table 2. The effect of all parameters is the same for both state-dependent models, with the interesting exception that in the survival-only model, increasing either γ and α can cause an increase in searching if patches are small (φ is large). This occurs because if patches are numerous and small, the best way to survive is to maintain low reserves; but as searching success increases then the forager should switch to maintaining high reserves, which involves more searching. The effect of γ and φ on the tendency to search for the different costs of search, whether there is a risk of
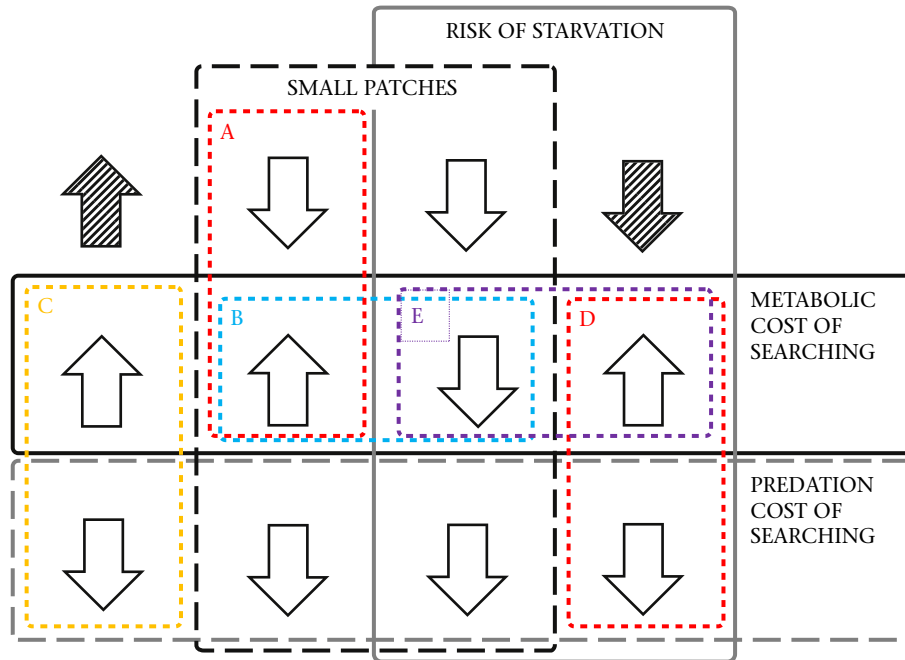
starvation and whether patches are small or large, is summarized in Fig. 3, in which we highlight some possibilities for testing our model.

*Causes of variation in experiments*

In manipulating prey abundance, experimenters studying the choice of foraging mode may inadvertently affect the distribution of prey. We explore how this affects predictions by altering patch clumpiness (ρ) and patch transience (φ) while doubling prey abundance (γ), and present in Fig. 4 the combined impact on the proportion of individuals searching. The solid line in Fig. 4b shows the negative effect of γ on searching for constant ρ and φ. As can be anticipated from Fig. A6, decreasing ρ and increasing φ (Fig. 4c and dashed lines in Fig. 4a, b) strengthens this negative effect. Decreasing both φ and ρ results in an inverted U-shaped relationship in the amount of searching (dotted line in Fig. 4c) because the combination of low γ, positive ρ and large φ leads to no searching. Increasing ρ or decreasing φ separately tends to result in a U-shaped relationship as the two effects are strongest when γ is high (e.g. solid line in Fig. 4a). Most significantly, increasing both patch clumpiness and patch size (increasing ρ and decreasing φ) as γ increases leads to the opposite prediction: searching increases as prey abundance increases (dotted line in Fig. 4a).

DISCUSSION

We have provided, to our knowledge, the first assessment of strategies for switching between foraging modes that depend on both prey distribution and foraging currency. We have shown that how animals should forage and respond to changes in prey abundance depends qualitatively on the temporal and spatial distribution of prey in their environment. This has implications for what patterns of foraging we expect to observe across species and populations, and for understanding how experiments manipulate the

Figure 3. Summary of the effect of γ and φ on the tendency to search. We show where the tendency to search increases with γ (up-arrows) and decreases with γ (down-arrows) for whether patches are small or large, whether there is a risk of starvation, the additional costs of search. Searching increases with patch size (decreases with φ) in all cases except where hatched (increases with φ). Possible tests of the model are shown in coloured dashed boxes that encompass comparisons where opposite trends are predicted. The tests are as follows: (A) walking versus flying; (B) surviving versus growing, or winter versus summer; (C) cryptic versus aposematic ectotherms; (D) cryptic versus aposematic endotherms; (E) invulnerable predator foraging for gregarious or solitary prey.
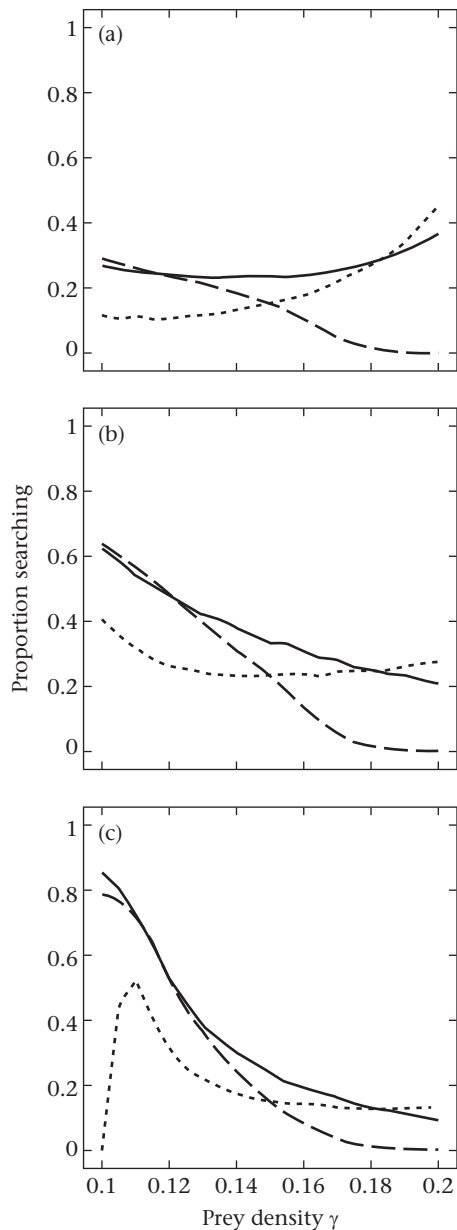
Figure 4. Effect of prey abundance on the proportion of all individuals searching (means of 10 replicates of 1000 individuals) when patch clumpiness ρ and/or patch transience ϕ change gradually as prey abundance γ increases. (a) ρ increases from −0.5 to 0.5, (b) ρ is held constant at 0.25, (c) ρ decreases from 0.5 to −0.5; (dashed lines) ϕ increases from 0.1 to 0.9, (solid lines) ϕ is held constant at 0.25, (dotted line) ϕ decreases from 0.9 to 0.1. Other parameter values as shown in Table 1. The usual negative effect of prey abundance γ on the proportions searching is reduced, and can even be reversed, by ϕ decreasing and ρ increasing (indicating larger, more clumped patches; dotted line in a).

environment that the subjects experience. We have considered the effect of maximization of various currencies on predicted behaviour. The expected currency depends on the costs of the foraging modes and the relative importance of the risk of starvation, and so enables us to predict how foraging ecology will influence the use of different foraging modes. Examples of comparisons between species or situations that are predicted to yield a qualitative difference in the relationship between prey density and searching are shown in Fig. 3. If prey group size and/or group distribution change when prey density increases, then Fig. 4 predicts the change in the incidence of searching behaviour. In Table 3 we offer a summary of explanations for the experimentally observed responses to increasing prey density highlighted above, giving the conditions under which the models predict each trend under different currencies, and when the distribution of prey changes as prey density is experimentally increased. Below, we discuss in detail some of the opportunities for testing our predictions.

Effect of Searching Costs

For animals for whom the stochastic nature of encounters with prey does not present a starvation risk, the strategy will be independent of the internal states of the animal. For state-independent currencies the direction of the switch in foraging mode depends on the relative importance (or magnitude) of the difference in metabolic costs and predation risk between the two foraging modes. When searching is not significantly more costly than waiting, such as for gliding birds (e.g. albatrosses and vultures) or benthic invertebrates that drift in lotic systems, animals should show a greater propensity to forage actively as the overall availability of food in the environment rises, as food becomes less concentrated into clumps and as the prey patches become more ephemeral. We note that gliding birds are famed for their extensive searching. The food may often be at low overall density but our results suggest that the key driver of extensive searching is likely to be that food is widely spaced and ephemeral (given competition with other consumers).

Where the predation costs of search dominate the metabolic costs, increasing food density should lead to reduced use of intensive searching, whereas when the dominant searching costs are metabolic the opposite pattern is predicted. Well-camouflaged individuals are very conspicuous when they move (Ioannou & Krause, 2009) so for them the predation risk should be more important. In this case, only when food is relatively scarce does enhancing encounter rate with food through movement compensate for the greater predation risk of searching; otherwise they should reduce movement when prey abundance increases. It seems likely that the metabolic cost will dominate only when there is negligible added predation cost to movement. This will be met by very well-defended organisms, such as by chemical defences for many invertebrates and very large size for some vertebrates (Ruxton, Sherratt, & Speed, 2004). Thus chemically or otherwise defended animals should forage more extensively in environments

Table 3
Explanations for observed responses to increasing prey density

Change in activity level	Source	Currency explanation	Distribution explanation (change as density increased)
Increase	Huey & Pianka, 1981	Metabolic but no predation cost of searching	Less evenly distributed, larger patches of prey
None	Johansson, 1991	No costs of searching	Less evenly distributed, unchanged patches of prey
Increase then decrease	Hirvonen, 1999	Predation but no metabolic cost of searching	More evenly distributed larger patches of prey
Decrease	Formanowicz, 1982	Predation but no metabolic cost of searching, high prey density	Smaller patches of prey (or no change in distribution)
Increase (endotherm)	Rudolph, 1982	Risk of starvation, metabolic but no predation cost of searching	Less evenly distributed, larger patches of prey

The table summarizes explanations for the experimentally observed responses to increasing prey density highlighted in the text, giving the conditions under which the models predict each trends under different currencies, and when the distribution of prey changes as prey density is experimentally increased.

with an abundance of food compared to more energy-poor environments, whereas the opposite pattern should be expected in undefended counterparts. In some conditions we even predict two switches as prey abundance increases: from ambush to search and then back to ambush, as has been observed (Hirvonen, 1999).

Effect of Risk of Starvation

When there is a real risk of starvation, the behaviour of the forager should take its internal state into account, since the reserves it carries will affect the risk of starvation. The more flexible state-dependent model that allows for starvation makes very consistent predictions for a broad range of parameter values: the forager should search expansively when its reserves are low and sit and wait for food when its reserves are high. An increase in the overall density of food generally causes a decrease in propensity to search. One exception to this rule is that if there is no increased predation risk associated with movement, increasing food density can encourage foragers to carry lower reserves and forage more actively. It is significant that the state-dependent models show a complete reversal of the effect of patch clumpiness (ρ), search rate (α), prey size (c) and prey abundance (γ, under some conditions) compared to the state-independent currencies. We can understand this by analogy with the established result that including stochasticity reverses our predictions of how changing food availability should affect the level of energetic reserves in simple models of survival (Houston & McNamara, 1993). In our present model, the difference in the response to prey size and prey abundance occurs because when the food supply is stochastic the forager should respond to a reduced risk of starvation by reducing the reserve level it maintains and thereby reduce its exposure to predation. The differing response to search rate and patch clumpiness occurs because the stochasticity allows us to separate out the decision from the time spent on activities, and when patches become hard to find the positive effect on time spent searching outweighs the reduction in the tendency to search. It is clear that optimizing simple currencies may lead us to make incorrect predictions due to ignoring starvation and stochasticity, both of which are known to have a significant effect on strategies for other types of foraging behaviour (Houston & McNamara, 1999). Care must be taken to ensure that simple currencies are valid in any particular circumstance.

Effect of Prey Distribution

An important implication relates to the experimental study of animal foraging strategies. When prey patches are small and quickly exhausted (ϕ is large), individuals maintain a lower level of reserves and search less. As the spatial aggregation of food ρ increases then animals attempt to retain higher levels of reserves and so search more extensively for food. An increase in prey abundance may increase the overall richness of patches, the spatial correlation of prey or both, depending on how it is altered. Hence, if we want to predict how a change in the food supply will affect the choice of foraging mode and how this will ultimately impact on life history (e.g. growth rates, risk of starvation, risk of predation), then we must carefully describe the food environment not just in terms of the overall density of food available throughout the environment but in terms of the turnover rate of individual food patches and in the spatial aggregation of food throughout the environment.

One important real-world implication relates to difficult-to-observe populations such as deep sea fish which scavenge on carrion that sink to the sea bed. The food source is highly patchily distributed, so fish may go for months without eating and their foraging strategies are likely to be heavily influenced by the risk of starvation. A low-energy environment (such as the deep sea) usually favours sit-and-wait foraging, but baited cameras observe high recruitment to baits, indicating that fish will move to find prey. Note that we are not implying that such fish wait for food to fall close to them, and they probably rely on scent, but scent only travels so far. If we assume that the fish detects new food items within, for example, a circle of 100 m radius, there remains the question of whether to stay still or to move such that this circle of perception moves around the ocean floor. Whatever the method of prey detection, using the rate of arrival of individuals at baited camera traps to assess population sizes is complicated because even if the overall fish population size remains unchanged between sampling periods or locations, very different arrival rates might be driven by differences in behaviour (as detailed in our work) rather than demographic changes. In the deep sea, prey (sinking corpses) are not abundant (γ is small), are spatially correlated because fish can die in single predation events (ρ is positive) and are large relative to foragers (ϕ is small). Our state-dependent models predict that under such conditions relatively more of the population are likely to find baits at baited cameras. If such methods are calibrated in easily observable environments with differing prey distributions, then there is a risk of overestimating population size. Furthermore, provision of baits may alter the perceived parameters of the system, causing an increase in patch size and patch clumping, thereby exacerbating the problem. Scientists therefore need to be mindful that increasing the density of camera traps in an attempt to gain more accurate data may run the risk of sufficiently altering the prevailing food environment in a way that alters the behaviour of the focal species.

Developing the Theory

We assumed that a forager can switch between waiting and searching, and that if a prey is encountered it will always be consumed. Thus, this applies to foragers with nonevasive prey or carrion-eaters. However, if the probability of subduing a prey item is the same in both foraging modes, this assumption does not limit the applicability of our results (as our preliminary explorations suggested). Our assumptions that patch sizes are Poisson distributed and that the forager has perfect knowledge of the number of prey items remaining means we avoided issues of patch-quitting strategies. This may mean that we underestimated the proportion of individuals searching (since they may quit patches before they are exhausted). Similarly, to make the modelling simpler we assumed that prey patches become exhausted even if the forager rests, which in some cases (e.g. where predators avoid one another) may be unrealistic. However, during model exploration we noted that very rarely is it optimal to rest when in a patch of prey, and then only at a level of reserves that are rarely reached. We assume that any predator has perfect knowledge of the distribution of prey in its environment. This may be a reasonable assumption where prey distributions are consistent over evolutionary time, so that their predators have evolved behaviour that approaches our predicted strategies, or if distributions are sufficiently consistent that predators can learn about them and predators have rules for making foraging decisions that have been shaped over evolutionary time. Our modelling rests on the implicit assumption that the previous history of an individual focal predator does not influence the local prey density that it currently experiences. We feel this is a reasonable assumption for situations with mobile prey especially. However, there will be other systems in which the previous behaviour of a predator will affect the distribution of prey available to it. We do not expect this change to substantially alter our main conclusions, but exploration of such systems will need system-

specific, spatially explicit models of both prey demographics and predator behaviours.

All this being considered, it can be helpful to test models that are formulated and parameterized by observations on specific empirical systems (Evans et al., 2013) and so specific implementations of our basic approach, with environmental parameters estimated from observation, are likely to lead to general insights about the use of flexible foraging modes. More broadly, by predicting how environmental change in either the higher or the lower trophic level will affect a focal species that has the behavioural ability to switch between these two foraging modes, our work should provide a useful basis for understanding how this behavioural flexibility manifests and impacts on life history and ultimately the population parameters of the species of interest.

Acknowledgments

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## APPENDIX 1. EFFECT OF PARAMETERS ON PREY DISTRIBUTIONS

Here, we present the effect of patch transience ϕ on the distribution of the number of prey per location (Fig. A1) and the relationship between patch clumpiness ρ and the correlation coefficient r (Fig. A2).

APPENDIX 2. SOLUTIONS FOR STATE-INDEPENDENT MODELS

Calculating the probabilities

Assuming that the density of food in the environment is fixed at γ then every time a patch is exhausted prey must appear in another location. The proportion of locations that contain a patch of prey depends on the patch transience and is therefore $\phi\gamma$, so that the greater the probability of a patch ending the more patches there are. Therefore $(1-\phi\gamma)$ of the possible locations do not contain prey at any given moment. Assuming that $\gamma \leq 0.5$ and time steps are sufficiently short that patches of prey cannot both appear and disappear from a location in the same time step, then if there was no prey at the forager's location in the last time step, the probability of a prey patch appearing in that location is the product of: the number of prey patches, the probability each patch is exhausted and the reciprocal of the number of empty locations. That is,

$$P_W = \phi \cdot \phi\gamma \cdot \frac{1}{1-\phi\gamma} = \frac{\phi^2\gamma}{1-\phi\gamma} \tag{A2.1}$$
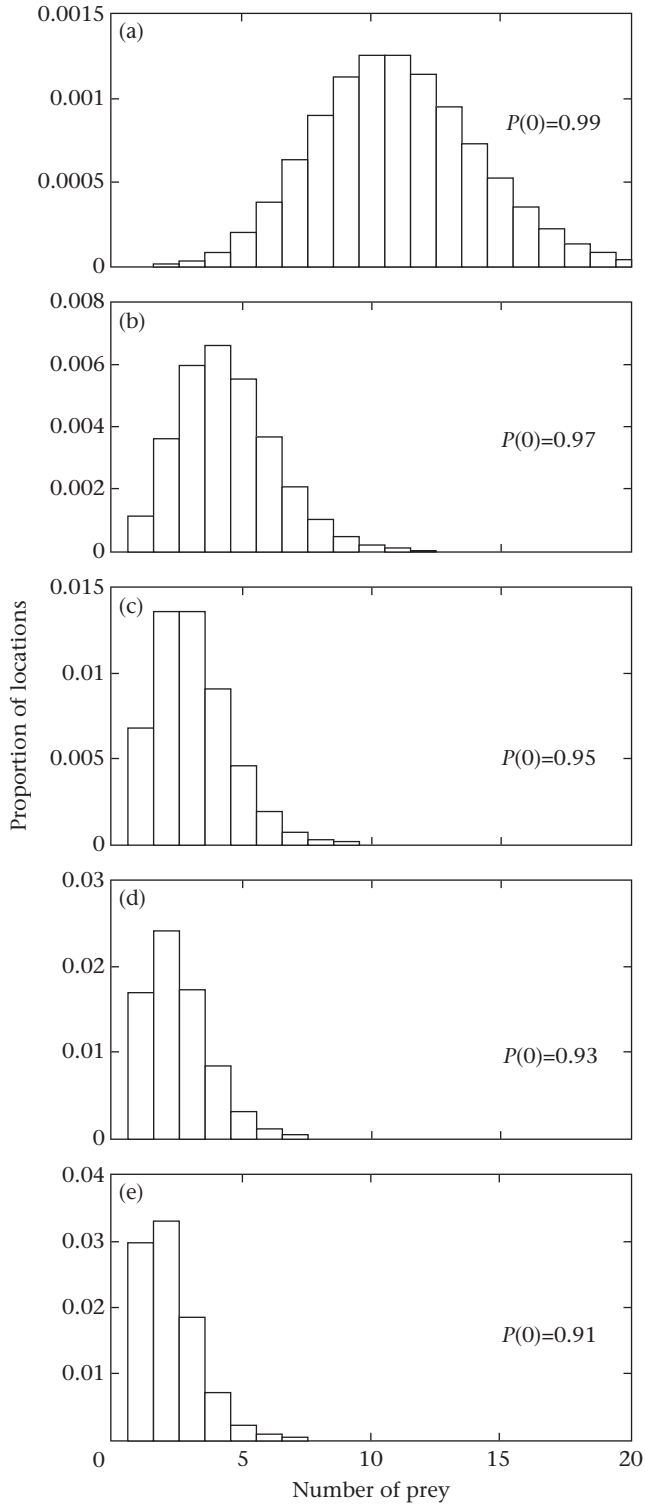
Figure A1. Distribution of numbers of prey per patch for five values of ϕ when $\gamma = 0.1$. (a) $\phi = 0.1$; (b) $\phi = 0.3$; (c) $\phi = 0.5$; (d) $\phi = 0.7$; (e) $\phi = 0.9$. We also indicate in the figure the proportion of locations where there are no prey $P(0)$.
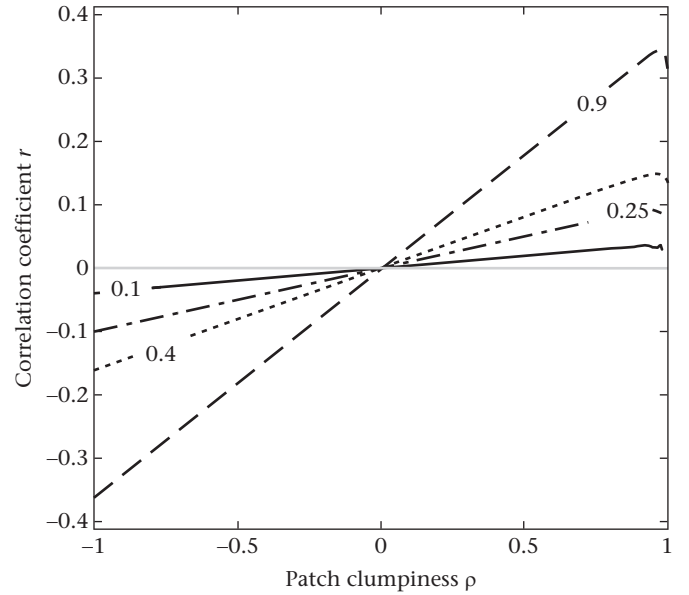
Figure A2. Autocorrelation coefficient r in the location of patches of prey as a function of patch clumpiness ρ (x-axis) and patch transience ϕ (shown on lines) for $\gamma = 0.1$. When ρ is zero, the correlation is zero, and when ρ is positive the correlation is positive. Increasing ϕ increases the absolute magnitude of the correlation r. The grey line indicates $r = 0$.

When searching, the forager moves in a straight line, searching the environment at a rate α. If the animal decides to search for prey the probability of finding a prey patch depends on γ, ρ and α.

$$P_S = 1 - e^{-\alpha(1-\rho)\phi\gamma} \tag{A2.2}$$

which decreases with ρ because the forager is currently located where there are no prey.

Foraging not more costly than waiting

If $m_S = m_W$ and $\mu_S = \mu_W$ then the forager should search only if it has more chance of finding a prey patch than the chance that a patch of prey will arise at the current location ($P_S > P_W$). That is, if the relative benefit of searching,

$$B_P = P_S - P_W \tag{A2.3}$$

is positive. From equations (A2.1) and (A2.2) this can be written as

$$B_P = 1 - e^{-\alpha(1-\rho)\phi\gamma} - \frac{\phi^2\gamma}{1-\phi\gamma} \tag{A2.4}$$

Since we are interested in qualitative predictions, we can simplify presentation significantly by using the linear Taylor series approximation for small exponents:

$$e^{\alpha(1-\rho)\phi\gamma} \approx 1 + \alpha(1-\rho)\phi\gamma \tag{A2.5}$$

Substituting (A2.5) into (A2.4) gives

$$B_P = 1 - \frac{1}{1+\alpha(1-\rho)\phi\gamma} - \frac{\phi^2\gamma}{1-\phi\gamma} \tag{A2.6}$$

Given that the forager should search if B_P is positive, the critical value of γ below which the forager should search is

$$\gamma_P^* = \frac{1}{\phi(\phi+1)} - \frac{\phi}{\alpha(1-\rho)(\phi+1)} \tag{A2.7}$$

There will be an observable switch between searching and waiting if γ^*_P is within the range of possible values of γ. $\gamma^*_P > 0$ if $\phi < \alpha(1-\rho)$ and $\gamma^*_P < 0.5$ if

$$\phi > \frac{-1 + \sqrt{\left(\frac{3\alpha(1-\rho)}{2}\right)^2 + \alpha(1-\rho) + 1}}{\alpha(1-\rho)} - \frac{1}{2} \qquad (A2.8)$$

which is positive if

$$\rho > 1 + \frac{\lambda\left(2\gamma + \phi^2\gamma(4-\gamma) - 2\gamma^2\phi^3 - 1 - (\gamma+1)\sqrt{4\gamma^2\phi^3 + \gamma^2\phi^2 - 8\gamma\phi^2 - 2\phi\gamma + 1}\right)}{2\alpha\phi^2\gamma^3(2-\phi\gamma)}.$$

The effect of an increase in prey abundance γ on the benefit of searching is

$$\frac{dB_P}{d\gamma} = \frac{\phi^2}{\phi\gamma - 1} - \frac{\phi^3\gamma}{(\phi\gamma - 1)^2} - \frac{\alpha\phi(\rho - 1)}{[\alpha\phi\gamma(\rho-1) - 1]^2} \qquad (A2.9)$$

$\frac{dB_P}{d\gamma} = 0$ if

$$\gamma = \frac{\pm[1 + \alpha(1-\rho)]}{[\alpha\phi(1-\rho) - 1]\sqrt{\alpha\phi(1-\rho)}} - \frac{(\phi+1)}{\phi[\alpha\phi(1-\rho) - 1]} \qquad (A2.10)$$

The negative root always lies outside the range [0,1] so is of no biological relevance. Within the range, $\frac{dB_P}{d\gamma}$ is negative if

$$\gamma > \frac{[1 + \alpha(1-\rho)]}{[\alpha\phi(1-\rho) - 1]\sqrt{\alpha\phi(1-\rho)}} - \frac{(\phi+1)}{\phi[\alpha\phi(1-\rho) - 1]} \qquad (A2.11)$$

At γ^* this condition reduces to $\phi < \alpha(1-\rho)$, which is the same condition as above, so whenever a switch occurs (i.e. $\gamma^* > 0$) $\frac{dB_P}{d\gamma}$ is negative, indicating a switch to waiting as prey abundance γ increases.

Next, we explore the effect of other parameters on the relative benefit of searching. The effect of α on B_P is

$$\frac{dB_P}{d\alpha} = \frac{\phi\gamma(1-\rho)}{[\alpha\phi\gamma(1-\rho) + 1]^2}. \qquad (A2.12)$$

This is positive if $\rho < 1$, which by our assumptions is always true, and so increasing search rate α always increases the benefit of searching.

The effect of ρ on B_P is

$$\frac{dB_P}{d\rho} = \frac{-\alpha\phi\gamma}{[\alpha\phi\gamma(1-\rho) + 1]^2} \qquad (A2.13)$$

This is positive if $\alpha\phi\gamma < 0$, which by our assumptions is never true, and so increasing patch clumpiness ρ always causes a decrease in the benefit of searching.

The effect of ϕ on B_P is

$$\frac{dB_P}{d\phi} = \frac{\alpha\gamma(1-\rho)}{[\alpha\phi\gamma(1-\rho) + 1]^2} - \frac{2\phi\gamma}{1-\phi\gamma} - \frac{\gamma^2\phi^2}{[1-\phi\gamma]^2}, \qquad (A2.14)$$

This holds only if ϕ is small. Hence, $\frac{dB_P}{d\phi} > 0$ when prey patches are large (ϕ is small) and $\frac{dB_P}{d\phi} < 0$ when prey patches are small (ϕ is large).

Maximizing net rate of gain

If $m_S > m_W$ but $\mu_S = \mu_W$ then the forager may maximize the expected net rate of gain, given by

$$\frac{E(G) - E(c)}{E(t) + E(\tau)} \qquad (A2.15)$$

where G is the gain once in a patch of prey, c is the metabolic cost when feeding and before a prey patch is encountered (either from waiting or searching), t is the duration of a prey patch and τ is the time until the prey patch is encountered.

For both decision options, $E(G)$ and $E(t)$ are the same and depend only how long prey patches last (ϕ). $E(\tau)$ for waiting and searching are simply the reciprocals of the probabilities P_W and P_S respectively. Equation (A2.15) becomes

$$R_W = \frac{s\left(\frac{1}{\phi}\right) - m_W\frac{1-\phi\gamma}{\phi^2\gamma} - m_W\frac{1}{\phi}}{\frac{1-\phi\gamma}{\phi^2\gamma} + \frac{1}{\phi}} \qquad (A2.16)$$

Similarly,

$$R_S = \frac{s\left(\frac{1}{\phi}\right) - m_S\left(1 - \frac{1}{1+\alpha(1-\rho)\gamma}\right)^{-1} - m_W\frac{1}{\phi}}{\left(1 - \frac{1}{1+\alpha(1-\rho)\gamma}\right)^{-1} + \frac{1}{\phi}} \qquad (A2.17)$$

Assuming that searching metabolic cost depends linearly on α we can rewrite (A2.17) as

$$R_S = \frac{s\left(\frac{1}{\phi}\right) - (1+\alpha)m_W\left(1 - \frac{1}{1+\alpha(1-\rho)\gamma}\right)^{-1} - m_W\frac{1}{\phi}}{\left(1 - \frac{1}{1+\alpha(1-\rho)\gamma}\right)^{-1} + \frac{1}{\phi}}, \qquad (A2.18)$$

and then solve $\frac{dR_S}{d\alpha} = 0$ for α to find the optimal search rate

$$\alpha^* = \frac{\pm\sqrt{c\phi\gamma m_W(1+\phi)(1-\rho) - m_W^2\phi} - m_W\phi}{\phi\gamma m_W(1+\phi)(1-\rho)} \qquad (A2.19)$$

Owing to c being an order of magnitude greater than all the other parameters, this is always large, and so we assume throughout this paper that $\alpha = 3$ and that α is constrained below the optimal search rate.

The relative benefit of searching when maximizing rate of gain is $B_R = R_S - R_W \cdot \frac{dB_R}{d\gamma} = 0$ if

$$\gamma = \frac{\alpha(1-\rho)(s+\phi - m_D\phi) - s\phi \pm \sqrt{K}}{2\phi s\alpha(1-\rho)(\phi+1)} \qquad (A2.20)$$

where $m_D = \frac{m_S}{m_W}$ and $K = \alpha^2(1-\rho)^2(s+\phi-m_D\phi)^2 + 2\alpha(1-\rho)\phi s[(\phi+1)(m_D-1)-s] + s^2\phi^2$. $\frac{d^2B_R}{d\gamma^2} < 0$ for all positive γ, and so B_R is a curve with a single maximum in real values.

Thus, B_R always has a maximum and crosses $B_R = 0$ at two (or no) values of γ. It can be seen from equation (A2.13) that if γ^* is real then it cannot be negative because $\sqrt{K}$ is positive if it is real, leaving the condition for $\gamma^* > 0$ dependent on

$$\phi > \frac{\alpha(1-\rho)s}{\alpha(1-\rho)(1-m_D) - s}. \qquad (A2.21)$$

Since $s > 0$ and $m_D \geq 1$, the right-hand side of inequality (A2.21) is also negative. Since the denominator is negative and $\phi > 0$, this condition therefore always holds.

The condition for $\gamma^* < 0.5$ (i.e. that a change will occur) is given by

$$\phi < \frac{2\alpha(1-\rho)(1-s-m_D) - 2s \pm \sqrt{L}}{2\alpha s(1-\rho)} \qquad (A2.22)$$

where $L = \alpha^2(1-\rho)^2(9s^2 + 4\{m^2 - 2m + sm + 1 - s\}) + 4\alpha(1-\rho)(s^2 + 2s\{1-m\}) + 4s^2$.

Numerical explorations of inequality (A2.22) revealed that the higher value of γ^* usually lies above 0.5. At the lower value of γ^* the value of $\frac{dB_R}{d\gamma}$ is always positive, so the forager should wait at low prey abundance and switch to searching at high density.

Next, we explore the effect of other parameters on the relative benefit of searching. The effect of α on B_R is

$$\frac{dB_R}{d\alpha} = \frac{-\gamma(1-\rho)(1-c-m_S)}{[1+\alpha\rho\gamma(1+\phi)]^2}. \qquad (A2.23)$$

This is positive if $c > 1 - m_D$, which by our assumptions is always true and hence increased search rate α always leads to more searching.

The effect of ρ on B_R is

$$\frac{dB_R}{d\rho} = \frac{-\alpha\gamma(c+m_S-1)}{[1+\alpha\rho\gamma(1+\phi)]^2}. \qquad (A2.24)$$

This is positive if $c < 1 - m_D$, which by our assumptions is never true and so increased patch clumping ρ always leads to less searching.

The effect of c on B_R is

$$\frac{dB_R}{dc} = -\frac{\gamma\alpha(1-\rho)(1 - \phi\gamma - \gamma\phi^2) - \phi\gamma}{-1 - (\alpha\gamma)(1-\rho)(1+\phi)}, \qquad (A2.25)$$

which is positive if

$$\phi < \frac{-1 - \alpha\gamma(1-\rho) \pm \sqrt{(1-\rho)^2(\alpha\gamma + 4\alpha + 2) + \rho(1+2\rho)}}{2\alpha\gamma(\rho-1)}. \qquad (A2.26)$$

For the default value of all parameters, this corresponds to $\phi < 1.145$. Numerical exploration revealed that under most conditions searching increases as prey size c increases. However, if ϕ and ρ are both large then prey are in small patches that are difficult to find, and so when prey size increases the predator should increasingly avoid the cost of searching.

The effect of ϕ on B_R is

$$\frac{dB_R}{d\phi} = \frac{-\gamma c - \alpha\gamma\left(\alpha(1-\rho)^2\left[c + m_D + 1 + c\gamma(\phi+1)^2\right] + 2c(\phi+1)(1-\rho)\right)}{[1+\alpha\gamma(1+\phi)(1-\rho)]^2} \qquad (A2.27)$$

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which is positive if

$$\phi < \frac{-1}{\alpha\gamma(1-\rho)} \pm \left(\frac{\sqrt{c\gamma^3(1-c-m_D)}}{c\gamma^3} - 1\right). \qquad (A2.28)$$

The right-hand-side of inequality (A2.28) only has real roots if $m_D + c < 1$, which by our assumptions never holds. Hence, searching always decreases as patch size decreases.

Maximizing gross gain to mortality rate

If $\mu_S > \mu_W$ but $m_S = m_W$ then we can assume that the forager maximizes the growth to mortality ratio, which for the two foraging modes is given by

$$G_W = \frac{s\left(\frac{1}{\phi}\right)}{\mu_W^{\frac{1}{\phi}} + \mu_W^{\frac{1-\phi\gamma}{\phi^2\gamma}}}, \qquad (A2.29)$$

and

$$G_S = \frac{s\left(\frac{1}{\phi}\right)}{\mu_W\frac{1}{\phi} + \mu_S\left(1 - \frac{1}{1+\alpha(1-\rho)\gamma}\right)^{-1}}. \tag{A2.30}$$

Optimal search rate is again large in almost all possible conditions:

$$\alpha^* = \frac{\pm 1}{\sqrt{\lambda\gamma(1-\rho)}}, \tag{A2.31}$$

as ϕ, ρ, γ are all ≤ 0.5, so we again assume search rate is constrained below the optimum. The relative benefit of searching when maximizing the growth to mortality ratio is $B_G = G_S - G_W$, which is zero when

$$\gamma_G^* = 0$$

or

$$\gamma_G^* = \frac{\alpha(1-\rho) - \phi\mu_D}{\phi\alpha(1-\rho)(1+\mu_D\phi)}, \tag{A2.32}$$

where $\mu_D = \frac{\mu_S}{\mu_W}$. γ_G^* is greater than zero when $\phi < \frac{\alpha(1-\rho)}{\mu_D}$, and less than 0.5 when

$$-\frac{2\mu_D + \alpha(1-\rho) + \sqrt{J}}{2\alpha(1-\rho)\mu_D} < \phi < \frac{\sqrt{J} - 2\mu_D - \alpha(1-\rho)}{2\alpha(1-\rho)\mu_D} \tag{A2.33}$$

where $J = \alpha^2(1-\rho)^2(1+8\mu_D) + 4\mu_D(1-\rho)\alpha + 4\mu_D^2$.

Since the lower limit is negative, which ϕ cannot be, we need only consider

$$\phi < \frac{\sqrt{J} - 2\mu_D - \alpha(1-\rho)}{2\alpha(1-\rho)\mu_D} \tag{A2.34}$$

By solving $\frac{dB_G}{d\gamma} = 0$ for γ we find that B_G has a maximum at

$$\overline{\gamma} = \frac{\sqrt{\mu_D\alpha\phi(1-\rho)} - \mu_D\phi}{\alpha\phi(\mu_D+1)(1-\rho)} \tag{A2.35}$$

so therefore the shift in foraging mode at γ^* is negative (i.e. a switch from searching to waiting with increasing γ) if $\overline{\gamma} < \gamma^*$. That is, $\sqrt{\mu_D\alpha\phi(1-\rho)} < \alpha(1-\rho)$, or equivalently $\phi < \frac{\alpha(1-\rho)}{\mu_D}$.

If this inequality does not hold then γ^* is negative. Thus, where there is a mode switch the switch is always from searching to waiting with increasing prey abundance.

Now we consider the other parameters. The effect of α on B_G is

$$\frac{dB_G}{d\alpha} = \frac{(1-\rho)c\gamma\mu_D}{[\alpha(1-\rho)\gamma\{1+\mu\phi\} + \mu_D]^2}. \tag{A2.36}$$

This is positive if $\rho < 1$, which by our assumptions is always true, and so increasing search rate always increases the benefit of searching.

The effect of ρ on B_G is

$$\frac{dB_G}{d\rho} = \frac{-\alpha c\gamma\mu_D}{[\alpha(1-\rho)\gamma\{1+\mu\phi\} + \mu_D]^2}, \tag{A2.37}$$

which is always negative because all the variables in the numerator are positive, and so increasing patch clumpiness always increases the benefit of searching.

The effect of c on B_G is

$$\frac{dB_G}{dc} = -\frac{\gamma[\alpha(1-\rho)(1-\phi\gamma) - \mu_D\lambda(1+\alpha(1-\rho)\gamma\phi)]}{\alpha(1-\rho)\gamma\{1+\mu_D\phi\} + \mu_D}. \tag{A2.38}$$

Hence, whether searching increases with c depends on the size of ϕ. Searching increases as c increases if

$$\phi < \frac{-\mu_S - \alpha\gamma(1-\rho) \pm \sqrt{[\gamma+4\mu_D]\alpha^2(1-\rho)^2\gamma + 2\alpha(1-\rho)\gamma\mu_D + \mu_D^2}}{2\alpha\gamma(1-\rho)\mu_S}, \tag{A2.39}$$

which for the default values of the parameters corresponds to $\phi < 0.43$. Numerical explorations revealed that the trends were the same as for net rate of gain.

The effect of ϕ on B_G is

$$\frac{dB_G}{d\phi} = \frac{-cs\gamma[\alpha^2\rho^2\gamma(\mu + \gamma + 2\mu\phi\gamma + \mu^2\phi^2\gamma) + 2\alpha\rho\mu\gamma(1+\mu\phi) + \mu^2]}{(\alpha\rho\gamma\{1+\mu\phi\} + \mu)^2} \tag{A2.40}$$

$\frac{dB_G}{d\phi} > 0$ only if

$$\phi > \frac{-\alpha\rho\gamma - \mu \pm \alpha\rho\sqrt{-\gamma\mu}}{\alpha\rho\mu\gamma}, \tag{A2.41}$$

which since $\gamma\mu > 0$ cannot be real, and so an increase in patch transience always decreases the benefit of searching.

APPENDIX 3. IMPLEMENTATION OF STATE-DEPENDENT MODEL

Here, we provide a complete description of the model implementation. Our optimization criterion follows that of McNamara (1990) and can be described as follows. At a decision epoch reserves are assumed to take values in the range $x = 0, 1, 2, \cdots, x_{max}$, and the animal is either in a patch of prey ($E = G$) or not ($E = B$). At each decision epoch the animal makes two decisions. The first decision is whether to invest in growth ($\beta = 1$) or not ($\beta = 0$), where investment in growth gives an immediate payoff of one unit and reduces reserves by one unit. The second decision is dependent on E: if the forager is in a patch of prey then it decides whether to feed ($\theta = F$) or rest ($\theta = R$); if the forager is not in a patch of prey then it decides whether to search ($\delta = S$) or wait ($\delta = W$). Both decisions are allowed to depend on reserve level (x). Long-term reproductive success is assumed to be maximized by the strategy that maximizes the expected total investment in growth before death occurs. In the case where we are interested in only minimizing mortality (ignoring growth), then the forager makes a single decision δ ($\beta = 0$ at all times).

We assume that the decision influences the metabolic rate of the forager and its exposure to predators, with the metabolic cost and predation rate when searching (m_S and μ_S, respectively) being at least as large as those associated with waiting (m_W, μ_W), eating (m_X, μ_X) and resting (m_R, μ_R), which are assumed to be equal in all model evaluations ($m_S \geq m_W = m_X = m_R$; $\mu_S \geq \mu_W = \mu_X = \mu_R$). We assume that carrying large reserves is costly in terms of increasing predation risk and/or increasing metabolic costs. The energy use and the probability of predation per time step are, respectively,

$$m = m_\delta\left(\frac{1}{2} + \frac{x}{x_{max}}\right) \tag{A3.1}$$

$$\mu = \mu_\delta\left(\frac{1}{2} + \frac{x}{x_{max}}\right) \tag{A3.2}$$

where $\delta \in \{W, S, F, R\}$. These assumptions of mass dependence are not critical for the insights we achieve, but do serve to reduce the time it takes for convergence of the decision array. It is never advantageous for the forager to search if it is currently in a patch of food, but if reserves are high it may be best to refuse to eat food that is available.

We assume that if the forager is in a patch of prey at time t, the probability of prey being present at the next time step is ϕ. That is, patches of prey persist for a Poisson-distributed number of time steps (with mean $1/\phi$), which is independent of the forager's decision to eat. If the decision between time t and $t+1$ is $\delta(x,B) = S$, i.e. to search, then the probability of being in a patch of food at $t+1$ is P_S. If the decision between time t and $t+1$ is $\delta(x,B) = W$, i.e. to wait, then the probability of being in a patch of food at $t+1$ is P_W.

Food items are of three types (type $j = 1, 2$ or 3) with relative abundance a_j ($\alpha_j = 1$), and provide a reward of energetic value r_j. Thus if the animal is in a patch of prey ($E = G$), has reserves x at time t and makes the decision $\theta = F$ (i.e. to eat) then its reserves at time $t+1$ are either $x + r_1 - m_X$, $x + r_2 - m_X$ or $x + r_3 - m_X$. If the new reserves would have been greater than the maximum value x_{max}, then reserves are taken to be x_{max}. Computations are based on the values $r_1 = c - 1$, $r_2 = c$, $r_3 = c + 1$ and $a_1 = 0.3$, $a_2 = 0.4$, $a_3 = 0.3$. If the animal is not in a patch of food then it cannot eat. If the change in reserves results in the new reserves being zero or below, the animal is assumed to have died of starvation. The changes in states given the decisions are summarized in Table A1.

Given these ingredients, the dynamic programming operator T^* can be expressed as follows. Let V be a function, $V(x,E)$, of energy reserves x and environmental conditions E satisfying $V(0,E) = 0$. Then VT^* is a new function of reserves and environmental conditions that satisfies $(VT^*)(0,E) = 0$ for all E and $(VT^*)(x,E) = \max_\delta H(x,E;\beta,\delta,\theta,V)$ for $x > 0$ and for $E \in \{G, B\}$. For the two current environments G and B, respectively

where $\theta = 1$ if $\theta = F$ and $\theta = 0$ if $\theta = R$.

$$H(x,B;\beta,\delta,\theta,V) = (1-\mu_\delta)\begin{bmatrix}(1-P_\delta)\cdot V(\max(x-\beta-m_\delta,0),B) \\ +P_\delta\cdot V(\max(x-\beta-m_\delta,0),G)\end{bmatrix}$$
(A3.3b)

To find the optimal strategy, we define a sequence of functions $V_0, V_1, V_2, \cdots$ iteratively as follows. Initially set $V_0(0,E) = 0$ for all E and $V_0(x,E) = 1$ for all $x > 0$ and all E. Given V_k, set $V_{k+1} = \frac{V_k T^*}{|V_k T^*|}$, where the norm, $|V|$, of a function V is given by $|V| = \max_{x,E}|V(x,E)|$. Then the sequence of functions converges pointwise to a limit $V^* = \lim_{k\to\infty} V_k$ (McNamara, 1990). Convergence was judged to have occurred when $|V_{k+1} - V_k| < 10^{-6}$, which typically happened within 500 iterations. Any strategy π^* satisfying

$$H(x,E;\beta_{\pi^*}(x,E),\delta_{\pi^*}(x,E),\theta_{\pi^*}(x,E),V^*)$$
$$= \max_{\beta,\delta} H(x,E;\beta,\delta,\theta,V^*) \text{ for all } x > 0 \text{ and all } E \qquad \text{(A3.4)}$$
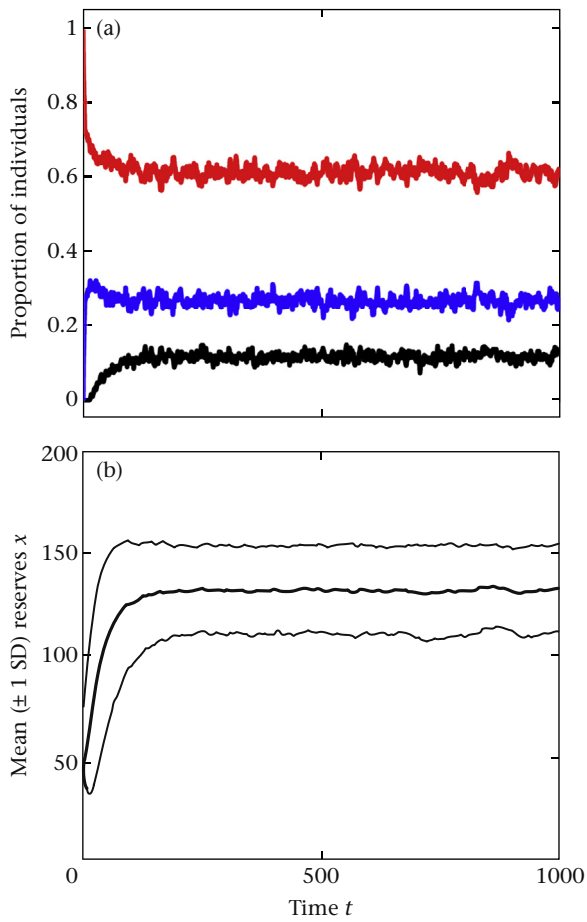
necessarily satisfies equation (A3.3a, A3.3b), and is hence optimal (McNamara, 1990).

To predict behaviour, we simulate 1000 individuals following the optimal strategy for 1000 time steps. The proportion of individuals making each decision (Fig. A3a) and the mean reserve level (Fig. A3b) quickly settle down. A typical distribution of reserves at the end of the simulations is shown in Fig. A4.
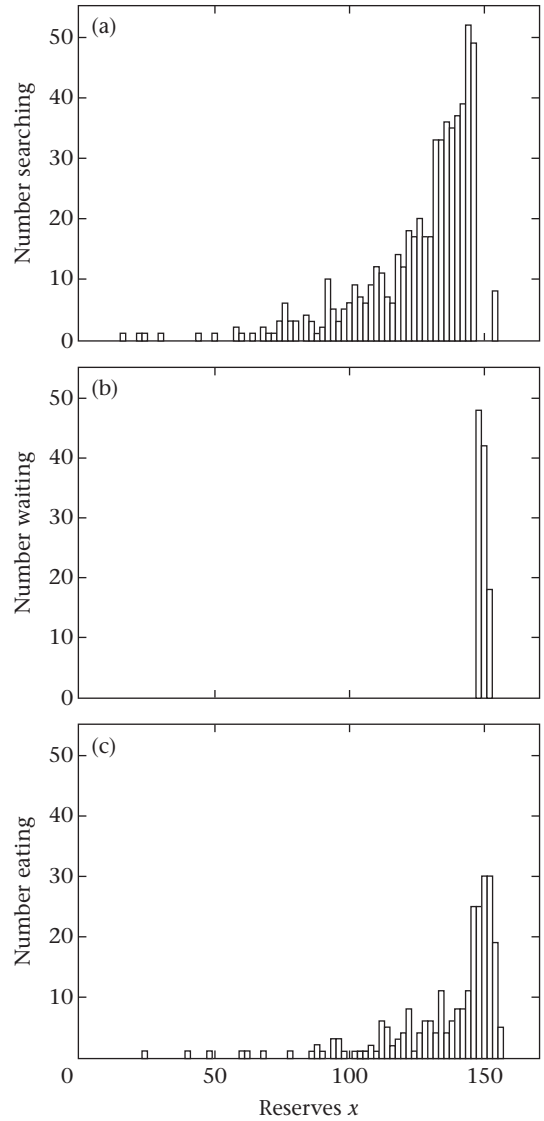
$$H(x,G;\beta,\delta,\theta,V) = (1-\mu_\delta)\begin{Bmatrix}(1-\phi)\sum_{j=1}^{3} a_j\cdot V(\min(\max(x-\beta-m_\delta+\theta r_j,0),x_{max}),G) \\ +\phi\sum_{j=1}^{3} a_j\cdot V(\min(\max(x-\beta-m_\delta+\theta r_j,0),x_{max}),B)\end{Bmatrix}$$
(A3.3a)

Figure A3. (a) Proportion of individuals over time searching (red line), feeding (blue line) and waiting (black line) and (b) the mean (±1 SD) reserve level for 1000 individuals for a typical simulation.


Figure A4. The final distribution of reserve levels for individuals (a) searching, (b) waiting or (c) eating. Note that the strategy here is to search when reserves are below 147 and wait otherwise.
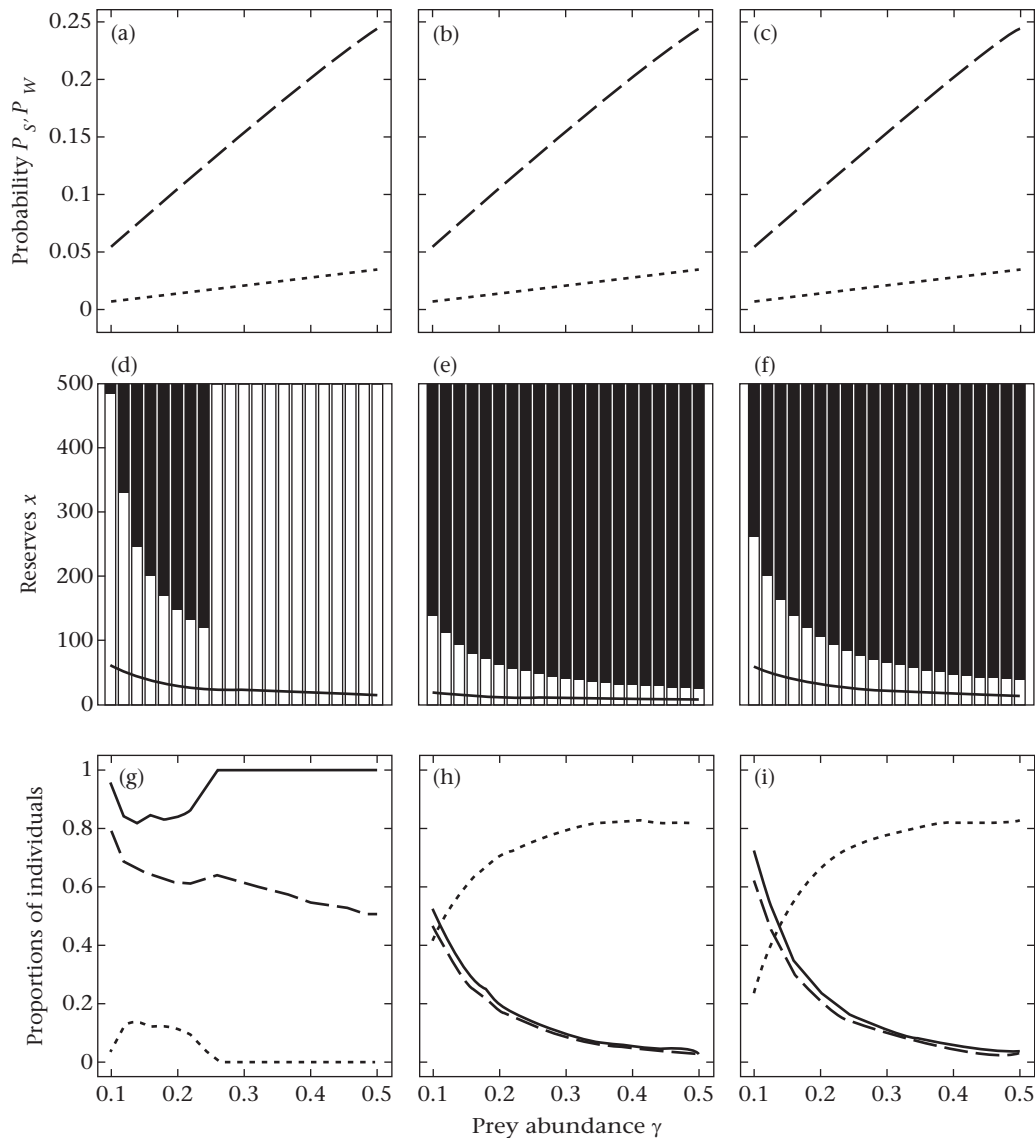
Figure A5. Effect of prey abundance γ (*x*-axes) on behaviour in a state-dependent growth model when (a, d, g) metabolic rate is greater for searching than waiting but predation risk is equal ($m_S > m_W$, $\mu_S = \mu_W$), (b, e, h) predation risk is greater for searching than waiting but metabolic rate is equal ($m_S = m_W$, $\mu_S > \mu_W$), (c, f, i) both metabolic rate and predation risk are greater for searching than waiting ($m_S > m_W$, $\mu_S > \mu_W$). (a–c) Probability of finding food when waiting P_W (dotted lines) and searching P_S (dashed lines). (d–f) Optimal strategy showing levels of reserves where the forager searches (white) and waits (black); solid line indicates reserves above which the animal should invest in growth. (g–i) Proportion of individuals searching (means of 10 replicates of 1000 individuals) out of the total number of individuals (dashed lines) and out of the number of individuals not in a prey patch (solid lines), and the proportion of individuals waiting out of the total number of individuals (dotted lines). Other parameter values as shown in Table 1.
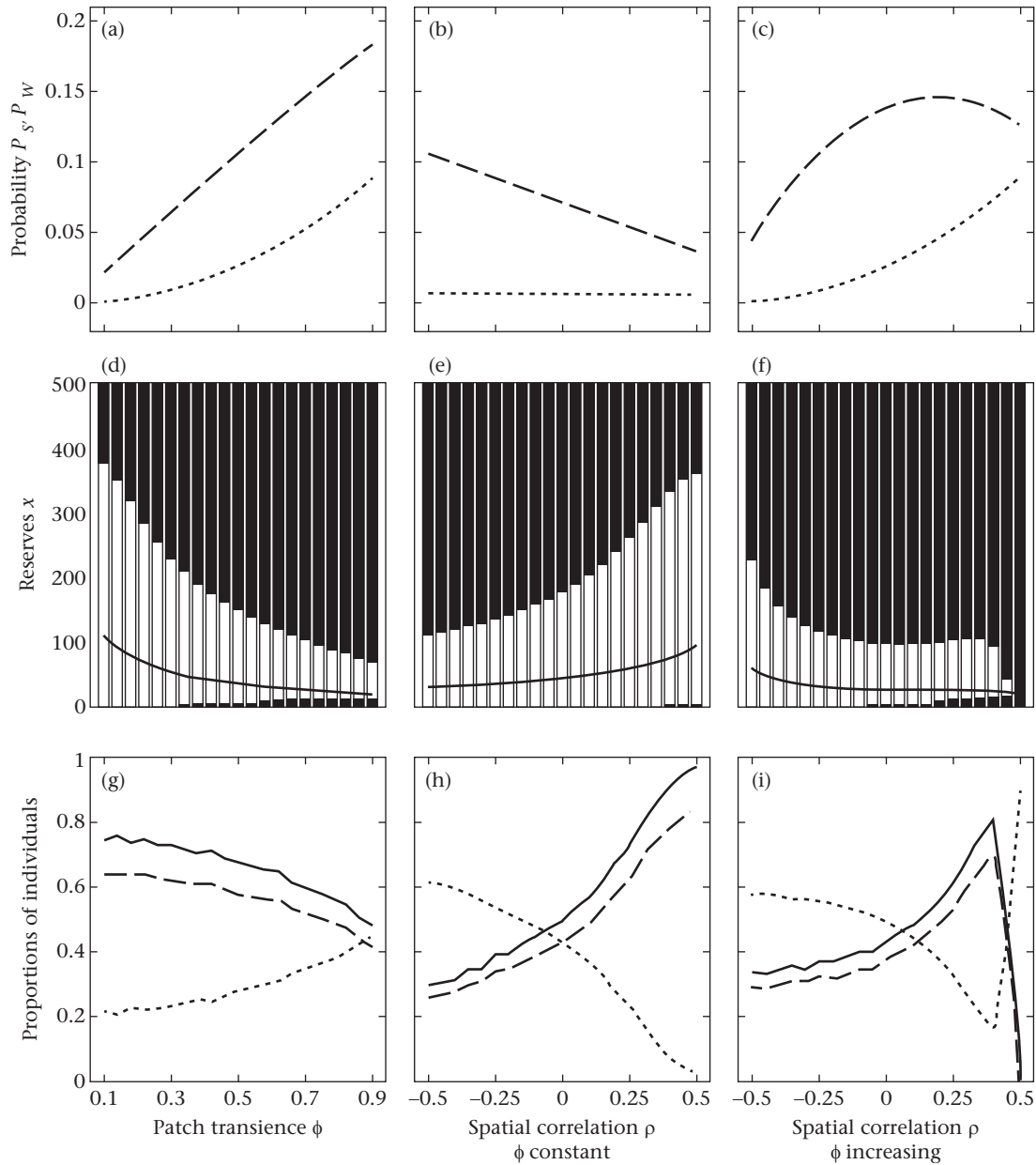
Figure A6. Effect of (a, d, g) increasing patch transience ϕ, (b, e, h) increasing spatial correlation ρ from negative to positive, (c, f, i) increasing both spatial correlation ρ and patch exhaustion probability ϕ. (a–c) Probability of finding food when waiting P_W (dotted lines) and searching P_S (dashed lines). (d–f) Optimal strategy showing levels of reserves where the forager searches (white) and waits (black); solid line indicates reserves above which the animal should invest in growth. (g–i) Proportion of individuals searching (means of 10 replicates of 1000 individuals) out of the total number of individuals (dashed lines) and out of the number of individuals not in a prey patch (solid lines), and the proportion of individuals waiting out of the total number of individuals (dotted lines). Other parameter values as shown in Table 1.

Table A1
Change in x and probabilities of transitions between environmental states depending on current state and decisions

State at t	Decision δ	x_{t+1}	$P(E_{t+1}=G)$	$P(E_{t+1}=B)$
x,G	F	$x-\beta-m_X+\theta r_i$	$1-\phi$	ϕ
x,G	R	$x-\beta-m_R$	$1-\phi$	ϕ
x,B	S	$x-\beta-m_S$	$P_S=1-e^{-[\alpha(1-\rho)\gamma\phi]}$	$1-P_S$
x,B	W	$x-\beta-m_W$	$P_W=\frac{\phi^2\gamma}{1-\phi\gamma}$	$1-P_W$