Learning to be different: acquired skills, social learning, frequency dependence, and environmental variation can cause behaviourally mediated foraging specializations

M. Tim Tinker[1], Marc Mangel[2] and James A. Estes[1,3]

[1] *US Geological Survey, Western Ecological Research Center, Long Marine Laboratory, Santa Cruz, California,* [2] *Center for Stock Assessment Research, Department of Applied Mathematics and Statistics, University of California at Santa Cruz, Santa Cruz, California and* [3] *Department of Ecology and Evolutionary Biology, University of California, Center for Ocean Health, Santa Cruz, California, USA*

ABSTRACT

Question: How does the ability to improve foraging skills by learning, and to transfer that learned knowledge, affect the development of intra-population foraging specializations?

Features of the model: We use both a state-dependent life-history model implemented by stochastic dynamic programming (SDPM) and an individual-based model (IBM) to capture the dynamic nature of behavioural preferences in feeding. Variables in the SDPM include energy reserves, skill levels, energy and handling time per single prey item, metabolic rate, the rates at which skills are learned and forgotten, the effect of skills on handling time, and the relationship between energy reserves and fitness. Additional variables in the IBM include the probability of successful weaning, the logistic dynamics of the prey species with stochastic recruitment, the intensity of top-down control of prey by predators, the mean and variance in skill levels of new recruits, and the extent to which learned information can be transmitted via matrilineal social learning.

Key range of variables: We explore the effects of approaching the time horizon in the SDPM, changing the extent to which skills can improve with experience, increasing the rates of learning or forgetting of skills, changing whether the learning curve is constant, accelerating ('J'-shaped) or decelerating ('r'-shaped), changing both mean and maximum possible energy reserves, changing metabolic costs of foraging, and changing the rate of encounter with prey.

Conclusions: The model results show that the following factors increase the degree of prey specialization observed in a predator population: (1) Experience handling a prey type can substantially improve foraging skills for that prey. (2) There is limited ability to retain complex learned skills for multiple prey types. (3) The learning curve for acquiring new foraging skills is accelerating, or J-shaped. (4) The metabolic costs of foraging are high relative to available energy reserves. (5) Offspring can learn foraging skills from their mothers (matrilineal social

learning). (6) Food abundance is limited, such that average individual energy reserves are low Additionally, the following factors increase the likelihood of alternative specializations co-occurring in a predator population: (1) The predator exerts effective top-down control of prey abundance, resulting in frequency-dependent dynamics. (2) There is stochastic variation in prey population dynamics, but this variation is neither too extreme in magnitude nor too 'slow' with respect to the time required for an individual forager to learn new foraging skills. For a given predator population, we deduce that the degree of specialization will be highest for those prey types requiring complex capture or handling skills, while prey species that are both profitable and easy to capture and handle will be included in the diet of all individuals. Frequency-dependent benefits of selecting alternative prey types, combined with the ability of foragers to improve their foraging skills by learning, and transmit learned skills to offspring, can result in behaviourally mediated foraging specialization, and also lead to the co-existence of alternative specializations. The extent of such specialization is predicted to be a variable trait, increasing in locations or years when intra-specific competition is high relative to inter-specific competition.

INTRODUCTION

Behavioural strategies (e.g. mate acquisition, parental care, foraging) are often described as fixed characteristics of animal species or populations, yet individuals within a population display some level of variability in almost any behavioural trait that can be measured. Even experimental confirmations of the predictions of optimality theory often show that individuals differ significantly with respect to the behaviour under study (e.g. Krebs *et al.*, 1977). Individual foraging specializations have been recognized for many years (Clark and Ehlinger, 1973; Heinrich, 1979; West, 1986; Werner and Sherry, 1987; Bridcut and Giller, 1995; Beauchamp *et al.*, 1997; Schindler *et al.*, 1997), as has the potential significance of foraging specializations from the perspective of both evolutionary ecology and community-level processes (Roughgarden, 1972; Chesson, 1984; Futuyma and Moreno, 1988; Sherratt and MacDougall, 1995). Bolnick *et al.* (2003) summarized many previously published examples of individual foraging specializations, making a strong case that such individual variation is likely a widespread and important phenomenon across species and ecosystems. Despite evidence for the ubiquity of individual foraging specialization and recognition of the need to incorporate such variation into broader ecological theory (e.g. Sherratt and MacDougall, 1995; Bolnick *et al.*, 2003; Estes *et al.*, 2003), quantitative models for understanding or predicting the dynamics of alternative specializations are mostly lacking (but see Svanbäck and Bolnick, 2005). Here we present a theoretical framework for exploring one class of foraging specializations, those associated with behaviourally plastic (rather than genetically fixed) polymorphisms.

Two recent case studies highlight the need for developing theory to examine factors responsible for behaviourally mediated foraging specializations. First, experimental manipulation of prey density in lakes demonstrated that foraging polymorphisms in three-spine stickleback (*Gasterosteus aculeatus*) were not fixed, but rather represented behavioural responses of individual fish to increased intra-specific competition (Svanbäck and Bolnick, 2007). The behaviourally driven shift from diet generalization to diet specialization in sticklebacks increased the correlation between diet and genetically based morphological differences. Svanbäck and Bolnick (2005) presented a model demonstrating that this scenario

– behaviourally mediated specialization superimposed over a genetically based poly-morphism – could be explained within the context of optimal foraging theory. The model of Svanbäck and Bolnick (2005) is built on the assumption that phenotypic differences between individuals are fixed; thus, while their model is broadly applicable to many systems exhibiting genetic polymorphisms, it is not directly applicable to species in which pheno-typic differences are dynamic and specialization is not necessarily associated with genetic variation (although many of their model predictions are likely valid for either circumstance).

In a second case study, increased individual specialization in diet and foraging behaviour of southern sea otters (*Enhydra lutris nereis*) was found to be driven by reduced food availability, although in this case the diversification into different specialist types was not associated with morphological or genetic differences between individuals (Tinker *et al.*, 2008). As with other taxa ranging from snails to whales (West, 1986; Werner and Sherry, 1987; Schindler *et al.*, 1997; Annett and Pierotti, 1999; Baird *et al.*, 2000; Sargeant *et al.*, 2005), diet specialization in sea otters appears to represent a plastic behavioural response of individuals to a particular set of ecological conditions. To explain such phenomena, we must therefore incorporate elements of optimal foraging theory, while accounting for the complex and dynamic feedbacks between individual foraging experience and phenotypic variation.

We start with the well-supported observation that specialists may experience an advantage over generalists in cases where specialization results in higher detection rates, capture success, improved handling efficiency, or improved digestive efficiency (e.g. Clark and Ehlinger, 1973; Heinrich, 1976; Partridge, 1976; Werner *et al.*, 1981; Partridge and Green, 1985; Werner and Sherry, 1987; Mangel and Clark, 1988; West, 1988; Dukas and Clark, 1995; Chittka and Thomson, 1997; Kandori and Ohsaki, 1998; Goulson, 1999; Golet *et al.*, 2000). One or more of these effects can occur as a result of a high degree of specificity of prey capture/handling skills (skills for one prey type cannot be transferred to other, dissimilar types) coupled with an inability to retain skills for multiple prey types (Hughes and O'Brien, 2001). When prey-specific foraging skills are dynamic rather than fixed – that is, they can be learned or improved through practice, but also be lost through lack of practice or interference – then the decision of an individual to specialize rather than generalize, or to switch from one specialization to another, becomes a function of the particular foraging history of that individual, mediated by species-specific characteristics of learning and memory (Partridge, 1976). Hughes (1979) demonstrated that the precise nature of the learning effect (i.e. the maximum possible improvement in foraging efficiency and the speed of learning and forgetting) could have important implications for the relative frequency of specialists and the likelihood of prey switching. However, because learning is inherently a dynamic process, in which individuals at any given time will behave according to their current state and past experience, a dynamic approach is needed to explore fully the effects of learning on foraging specializations (McNamara and Houston, 1985; Houston and McNamara, 1988; Mangel and Clark, 1988). Hughes' (1979) static model, which predicts equilibrium solutions but not temporal dynamics, is of limited use in this regard, and also fails to explain the co-occurrence of alternative foraging specializations within a population.

The existence of behavioural-based foraging polymorphisms implies not only that there are benefits of specializing, but also that there exists some mechanism for diversification and maintenance of alternative specializations within a population over ecological time-scales. A variety of selective and non-selective mechanisms have been proposed that may act alone or in concert to maintain alternative strategies, such as frequency-dependent benefits of rare strategies or ideal free distribution explanations (see Clark and Ehlinger, 1973; Houston and McNamara, 1985; Partridge and Green, 1985; Beauchamp *et al.*, 1997; Schmitz *et al.*, 1998). It has also been

suggested that the transmission of learned behavioural traits (including foraging skills or prey preferences) via social learning could contribute to the maintenance of alternative strategies in sea otters (Estes *et al.*, 2003) and perhaps in other species (Bonner, 1980; Partridge and Green, 1985; Laland and Hoppitt, 2003). It is increasingly recognized that many non-human species exhibit some form of social learning (Laland and Hoppitt, 2003), although there is considerable debate about whether or not the transmission of learned information constitutes culture (see Bonner, 1980; Boyd and Richerson, 1996). We restrict our consideration to the vertical transmission of learned foraging skills between a mother and her offspring, which can occur via active teaching or passive social learning, and we will refer to this process henceforth as 'matrilineal skill transmission'. Social transmission of prey specializations has been reported for a variety of taxa, including primates (Huffman and Quiatt, 1986; Lefebvre, 1995; Stoinski *et al.*, 2000), fish (Stanley *et al.*, 2008), cetaceans (Heimlich-Boran, 1988; Weinrich *et al.*, 1992; Rendell and Whitehead, 2001; Mann and Sargeant, 2003), sea birds (Norton-Griffiths, 1968; Annett and Pierotti, 1999), rodents (Terkel, 1996), and mustelids (Estes *et al.*, 2003). Aside from the individual examples mentioned above, however, little attention has been given to the potential role of matrilineal skill transmission as a driver of intra-specific variation in foraging behaviour.

Our goal is to develop a quantitative, conceptual framework that allows us to explore behavioural foraging specializations at two levels: first, at the individual level we seek to understand how and when the ability to modify skills through learning should affect an animal's decision to behave as a prey specialist or generalist; second, at the population level we seek to understand how particular behavioural and life-history characteristics of the forager and its prey populations will interact to mediate the co-occurrence of alternative foraging specializations. We use the sea otter example as a general guide in developing our model, both because of our familiarity with this system and because most of the phenomena of interest are exhibited by sea otters (Estes *et al.*, 2003; Tinker *et al.*, 2007, 2008). While this system specificity ensures that our model is grounded in biological reality, we are sensitive to the potential trade-off in generality and we therefore ensure that our methods and results are as broadly applicable as possible. We pose three general questions about variation in foraging specializations: (1) How does the ability to improve skills through learning affect a forager's propensity to specialize or generalize, and what other factors (including the temporal dynamics of the learning processes itself) are important in modifying this decision? (2) What characteristics of predator physiology, life history, behaviour, and predator–prey interactions are important for determining the co-existence and relative frequency of alternative specialists, and the temporal dynamics of specializations within a population? (3) To what extent can matrilineal skill transmission mediate the relative frequencies of alternative specializations, and temporal variation in these frequencies?

METHODS

General approach

We develop two complementary models with which to achieve our objectives: a stochastic dynamic programming model (SDPM) to investigate the dynamics of an individual's predicted decision to specialize or generalize, and an individual-based model (IBM) to examine the population-level dynamics of foraging specializations. Both of these models share the same basic assumptions about behavioural constraints, prey characteristics, and state variable dynamics. In developing these models, we define a large number of variables

Table 1. A summary of model parameters, their baseline values, and the range of values evaluated (where two sets of values are provided, the first applies to prey type 1 and the second to prey type 2)

Parameter	Definition and/or effect of parameter	Baseline	Range of values
T	Number of time intervals per model run	50	N.A.
λ_i	Average encounter rate for prey type i	0.3, 0.5	$0.1 \to 0.4, 0.6$
g_i	Energy gained by consuming one item of prey type i	7, 4	N.A.
H_i	Baseline handling time for prey type i	5, 3	N.A.
h_i	Realized handling time for prey type i	(see text, equation 1)	
E_M	Maximum level of individual energy reserves	20	N.A.
m	Metabolic rate	0.975	$0.95 \to 1$
S_M	Maximum skill level for prey type i	20	N.A.
l_i	Rate at which new skills are learned for prey type i	1	$0.3 \to 3$
f_i	Rate at which skills are forgotten for prey type i	1	$0 \to 3$
a	Effect of learned skills on handling time	0.6	$0.4 \to 0.8$
γ	Shape of learning curve (r-shaped, linear, J-shaped)	1	$0.67 \to 1.5$
θ	Slope of fitness function	$E_M/3$	$E_M/10 \to EM$
ϕ	Shape of fitness function	$E_M/10$	$E_M/20 \to E_M/2$
Z	Incidental mortality rate	0.001	$0.0002 \to 0.002$

Additional parameters for individual-based model

$v_i \omega_i \psi_i \delta_i$	Decision rule function parameters for prey type i	(unlimited range of values)	
W	Weaning success rate (calculated as a function of parent's total energy reserves at reproduction)	(see text, equation 3)	
K_i	Carrying capacity (in thousands) of prey population i	60, 80	N.A.
r_i	Mean per-capita recruitment rate of prey population i	0.15, 0.2	$0.1 \to 0.3, 0.4$
d_i	Maximum per-capita death rate for prey population i	r_i	N.A.
C_i	Number of prey species i consumed by predator	(outcome of simulation)	
p	Multiplier for C_i: controls potential for top-down effects of predation on prey population dynamics	0.5	$0 \to 1$
ε_i	Environmental stochastic variation in r_i (as std. dev.)	0.1	$0.01 \to 0.25$
κ_i	First-order temporal autocorrelation of r_i	0.5	$0.2 \to 0.7$
β	The proportion of parent's skills transferred to offspring via social learning (matrilineal skill transmission)	0	$0 \to 0.9$
μ	Mean skill level of new recruits, excluding effect of β	$S_M/3$	N.A.
σ^2	Variance in skill level of new recruits	$S_M/10$	$S_M/100 \to S_M$

and parameters, and to help the reader keep track we provide a summary key (Table 1) including definitions and ranges of values considered.

We begin with a simple prey selection model (Stephens and Krebs, 1986) composed of sequential encounters between a forager and $i = 1$ to n potential prey types, with mean encounter rates given by λ_i. At each time interval of searching ($t = 1, 2 \ldots T$), we assume that a forager might encounter no prey (in which case it will resume searching during the subsequent interval) or it might encounter a maximum of one prey item. The prey encounter dynamics in our model differ from a purely Poisson process (in which multiple items can be encountered at each time interval); rather, the predator is assumed to be searching among small, discrete patches, each requiring a single time interval to investigate and each of which

may turn out to be empty or may contain a single prey item. The likelihood of encountering no prey items in a single time interval is given by $1 - \Sigma\lambda_i$ (we require that $\Sigma\lambda_i \leq 1$, such that at maximum prey abundance, all patches are occupied), and if a prey item is encountered the likelihood that the item encountered belongs to prey type j is given by $\lambda_j/\Sigma\lambda_i$. When a prey item is encountered, the forager may capture, handle, and consume that prey item (which requires one or more additional time intervals) or resume searching for other prey. Each prey type is uniquely defined by its encounter probability (λ_i), the energy gained by consuming one item (g_i), and its baseline handling time (H_i). We distinguish between baseline handling time and realized handling time (h_i), which can vary with the past experience or current state of the forager as explained below.

The dynamic state variables of interest to us are the forager's energy reserves and the forager's skills associated with each potential prey type. The state dynamics of energy reserves (E) are based upon a well-established template (Clark and Mangel, 2000): E increases by g_i when the forager consumes an item of prey type i, up to a maximum of E_M, and decreases due to metabolic expenditures as a linear function of time (we assume a constant rate of metabolism, m, for all activity). If E declines to some critical level (0 in our model), the forager dies.

The state dynamics of foraging skills are less conventional and require more explanation. The skill level for each prey type i (S_i) can vary between 1 and some maximum, S_M. S_i is incremented by l_i after each capture and handling of prey type i ('learning') and decremented by f_i after each capture and handling of prey type j, where $j \neq i$. S_i remains unchanged if no prey is encountered or selected. Parameter f_i represents the effect of forgetting, or 'interference' – that is, the limited capacity of animals to master or retain complex handling skills for dissimilar prey types (Heinrich *et al.*, 1977; Goulson *et al.*, 1997). We evaluate the effect of varying both l_i and f_i.

Previous studies have shown that acquired experience with a single prey type can affect many aspects of forager physiology and behaviour (e.g. Werner *et al.*, 1981; Cunningham and Hughes, 1984; Partridge and Green, 1985; Croy and Hughes, 1991; Laverty, 1994; Kandori and Ohsaki, 1998; Reiriz *et al.*, 1998; Keasar *et al.*, 2002); here we consider only the effect of S_i on handling efficiency. Realized handling time, h_i, is modelled as a decreasing function of S_i:

$$h_i(S_i) = H_i\left(1 - \left(\frac{\alpha(S_i - 1)^\gamma}{(S_M - 1)^\gamma}\right)\right), \tag{1}$$

where $0 \leq \alpha < 1$ and $0 < \gamma < \infty$. The first parameter in equation (1), α, determines the magnitude of the learning effect. When $\alpha = 0$, h_i is fixed at H_i, resulting in no realized effect of acquired experience. As α approaches 1, learning has an increasingly strong effect on handling time, with h_i reaching its minimum value when $S_i = S_M$. The second parameter, γ, determines the temporal dynamics of the learning process. When $\gamma = 1$, h_i decreases linearly with S_i (this will be referred to hereafter as a linear learning curve). When $\gamma < 1$, h_i decreases rapidly with initial increments of S_i, but the rate of change decelerates and becomes asymptotic as S_i approaches S_M (this will be referred to hereafter as an 'r-shaped' learning curve). When $\gamma > 1$, h_i decreases slowly with initial increments of S_i, but the rate of change accelerates as S_i approaches S_M (this will be referred to hereafter as a 'J-shaped' learning curve).

For both the SDPM and the IBM models, we consider a simple system in which foragers have two potential prey types to choose from: prey type 1, characterized by high energy

content and long handling time, and prey type 2, characterized by lower energy content and shorter handling time (Table 1). With handling times set to their baseline values, the net energy return from prey type 1 (g_1/H_1) is higher than that from prey type 2 (g_2/H_2), making it the preferred prey in the absence of any learning effect. It is worth emphasizing that the effect of learning is fundamental to all results presented here: if $\alpha = 0$, our theoretical framework collapses to the simple optimal prey selection model (Schoener, 1971; Pulliam, 1974; Charnov, 1976; Stephens and Krebs, 1986) and a forager is predicted to ignore prey type 2 if:

$$\lambda_1 > \frac{g_2}{g_1}\left(\frac{1}{H_2 - H_1}\right),$$ (2)

otherwise the forager is expected to generalize (capture either prey type when encountered).

Stochastic dynamic programming model

The key feature of a SDPM is that each potential decision available to an individual at any time t can be evaluated in terms of its expected fitness consequences at time $t + 1$, and thus the expected behaviour depends on past experience, the current state and the probable future state of the forager (Mangel and Clark, 1988; Clark and Mangel, 2000). We equate fitness with reproductive success at time T, where reproductive success may be defined as the number and/or viability of offspring produced. The fitness of an individual at time t, $F(e, s_1, s_2, t)$, is the maximum expected reproductive success at T, assuming that the individual makes foraging decisions in such a way as to maximize its fitness and given that $E(t) = e$, $S_1(t) = s_1$, and $S_2(t) = s_2$. At time T, fitness is calculated as an increasing function of the individual's remaining energy reserves:

$$F(e, s_1, s_2, T) = \frac{\exp\left(\frac{e - \theta}{\phi}\right)}{1 + \exp\left(\frac{e - \theta}{\phi}\right)},$$ (3)

where θ and ϕ are parameters that together characterize the shape of the relationship between energy reserves and reproductive success (a *logit* function is used so that fitness varies between 0 and 1). This relationship could conceivably take a variety of forms: in sea otters, for instance, the probability of successfully rearing offspring is a logistic function of the mother's energy reserves (Monson *et al.*, 2000). We evaluate a range of potential values for θ and ϕ (Table 1), allowing for s-shaped, r-shaped, J-shaped, or linear relationships.

For times previous to T, fitness is calculated using the dynamic programming equation

$F(e, s_1, s_2, t) =$

    $[\lambda_1 \max\{F(e - m, s_1, s_2, t + 1), F(e + g_1 - m(1 + h_1(S_1)), s_1 + l_1, s_2 - f_2, t + 1 + h_1(S_1))\}$

    $+ \lambda_2 \max\{F(e - m, s_1, s_2, t + 1), F(e + g_2 - m(1 + h_2(S_2)), s_1 - f_1, s_2 + l_2, t + 1 + h_2(S_2))\}$

    $+ (1 - \sum_i \lambda_i)F(e - m, s_1, s_2, t + 1)]\exp(- Z),$ (4)

with the understanding that appropriate constraints apply to each state variable, as described above, and that realized handling times h_1 and h_2 are functions of S_1 and

S_2 (respectively) as described by equation (1). The last term accounts for the probability of incidental mortality (Z), defined as death due to causes other than depletion of energy reserves. The solution to the dynamic programming equation is calculated iteratively, moving backwards in time from $t = T - 1$ to $t = 1$ (see Appendix for a more detailed explanation of the solution to the dynamic programming equation). Solving the dynamic programming equation provides both the expected fitness and the predicted behaviour of a forager – to capture or ignore prey of type 1 or 2, when encountered – at each time, t, as a function of the current values of its state variables. The predicted behaviour is determined by evaluating the first two rows of equation (4) (row 1 corresponds to prey 1 and row 2 corresponds to prey 2). We solved the dynamic programming equation over a wide range of values for all parameters, to assess the effect of each parameter on the decision matrix, the multidimensional array of predicted 'best decisions' at all possible values of E, S_1, S_2, and t (Mangel and Clark, 1988; Clark and Mangel, 2000). Table 1 gives the baseline values of each parameter used for the SDPM, as well as the range of values evaluated.

Individual-based model

We next develop an IBM to conduct replicated simulations of forager populations. This allows us to explore population-level dynamics of foraging specializations in a simple world with two prey types, where the behaviour of each individual at any given time is determined by the current environmental conditions (i.e. prey population densities), the individual's own state, and its decision rules. One possible way of specifying the appropriate decision rules for individuals in an IBM is to use results from an SDPM to specify optimal behaviour under every possible set of conditions. However, the results of our SDPM (Table 2; Fig. 1) suggested that a much simpler function could be used to closely approximate the predictions of the decision matrices, thereby providing a simple set of 'rules of thumb'. Specifically, a forager that has encountered an item of prey type i will either capture it or keep searching based on the state of its skill level for the encountered prey (S_i), its skill level for alternative prey types included in its diet (S_j, $j \neq i$), and the current encounter rates for all prey types ($\lambda_1, \lambda_2 \ldots \lambda_n$). The SPDM results indicated that the abundance of energy reserves could also affect prey selection decisions (Table 2); however, initial trials suggested that adding a separate parameter for energy reserves made no qualitative difference to the population simulation results, probably because energy reserves were so strongly correlated with prey encounter rates. We therefore use a four-parameter function to define an appropriate decision cut-off value for each prey type: if the skill level for prey type i is below the cut-off value, the individual will reject it, otherwise it will accept it. Specifically, in the case of two possible prey types, an individual is predicted to ignore prey type 2 when encountered (and thus specialize on prey type 1) if:

$$S_2 < v_1(S_1 - \omega_1 S_1^2 + \psi_1) + \delta_1\left(\frac{\lambda_1}{\lambda_2}\sum_{i=1:n}\lambda_i\right). \tag{5}$$

Similarly, it is predicted to ignore prey type 1 (and thus specialize on type 2) if:

$$S_1 < v_2(S_2 - \omega_2 S_2^2 + \psi_2) + \delta_2\left(\frac{\lambda_2}{\lambda_1}\sum_{i=1:n}\lambda_i\right). \tag{6}$$

Table 2. Summary of the effects of the SDPM parameters

Change to model parameter	Effect of change on decision matrix	Figure 1
$t \to T$ (reproduction imminent)	Increased specialization, particularly on prey 1 (high-energy prey), and reduced region of generalization	1c, 2c
$\uparrow \alpha$, effect of learned skills on handling time	Increased region of specialization on both prey types	1c, 2c
$\downarrow \alpha$, effect of learned skills on handling time	Decreased region of specialization on 1, and no region of specialization on 2	1b
$\uparrow l_i$, rate of learning new skills	Increased region of generalization	1b, 2b
$\uparrow f_i$, rate of forgetting	Increased region of specialization on both prey types	1c, 2c
$\uparrow \gamma$: learning curve is 'J'-shaped	Increased region of specialization on both prey types	1c, 2c
$\downarrow \gamma$: learning curve is 'r'-shaped	Increased region of generalization	1b, 2b
$\downarrow e(t)$, state of energy reserves	Increased region of specialization on both prey types	1c, 2c
$\uparrow E_M$, maximum energy reserves	Increased region of generalization	1b, 2b
$\downarrow E_M$, maximum energy reserves	Increased region of specialization on both prey types	1c, 2c
$\downarrow m$, metabolic costs	Increased region of generalization	1b, 2b
$\uparrow m$, metabolic costs	Increased region of specialization on both prey types	1c, 2c
$\downarrow \lambda_1$, encounter rate for prey type 1	Increased region of specialization on 2, decreased region of specialization on 1	1b, 2c
$\downarrow \lambda_2$, encounter rate for prey type 2	Increased region of specialization on 1, decreased region of specialization on 2	1c, 2b

Note: The third column refers to the labelled lines in Fig. 1 that define the regions of specialization on each prey type.

The parameter v_j determines the magnitude of the effect of a forager's skill level for alternative prey type j, ω_j allows for non-linearity of the function with respect to skill, ψ_j is a constant, and δ_j determines the effect of prey abundance (i.e. the encounter rate of prey j relative to prey i, scaled to the encounter rate for all prey types). Depending on the values of v, ω, ψ, and δ, equations (5) and (6) can result in rules of thumb corresponding to a wide array of alternative strategies: always specialize on one prey type irrespective of prey encounter rates; always generalize; specialize on one prey type if that prey is very abundant; or anything in between. Our goal was to select appropriate parameter values, such that individuals would make foraging decisions so as to maximize their fitness, for each unique combination of model variables. An important feature of the IBM approach is that the dynamics of interest arise as emergent properties from the cumulative behaviour of many individuals, each following very simple decision rules (Railsback, 2001); moreover, the decision rules themselves may be among the emergent properties. Accordingly, we use simulations of natural selection to parameterize the decision rule function for each hypothetical scenario, as we explore the effect of model variables. Specifically, for each scenario we initialize a starting population with randomly assigned values for the decision rule parameters and treat each unique set of values as a 'genotype'. The algorithm for our natural selection simulations is identical to that described below except that we assume that the decision rules are heritable and exhibit additive genetic variation (e.g. Kolliker *et al.*, 2000), which we simulate by adding small, random deviations to the decision rule parameters inherited from parents by offspring (deviations are normally distributed with mean = 0). Genotypes can thus drift over generational time, with selection sorting out those combinations of values that
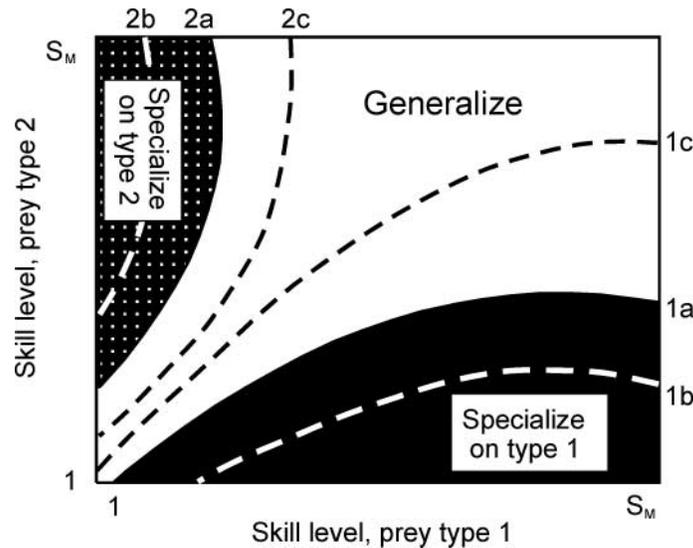
Fig. 1. Graphical representation of the decision matrix, showing the expected behaviour of a forager plotted as a function of its skill level for prey type 1 (horizontal axis) and skill level for prey type 2 (vertical axis) when all parameters are set to their baseline values. The unshaded area indicates combinations of skill levels where the predicted behaviour is to generalize (never reject prey when encountered), the solid-shaded area indicates combinations of skill levels where the predicted behaviour is to specialize on prey type 1 (ignore prey type 2 when encountered), and the stippled area indicates combinations of skill levels where the predicted behaviour is to specialize on prey type 2 (ignore prey type 1 when encountered). The dashed lines indicate alternative model outcomes, in which the areas of specialization change as model parameters are varied (see Table 2): lines 1b and 1c show changes in the region of specialization on prey type 1, and lines 2b and 2c show changes in the region of specialization on prey type 2 (1a and 2a correspond to the baseline regions of specialization). The decision rules of thumb used for the individual-based model (equations 5 and 6) produce a pattern identical to the one shown here.

produce non-viable strategies (e.g. specializing when generalizing would actually be more profitable, or vice versa). We allow a sufficiently long period of time (at least 2500 years per replication) for the surviving genotypes to converge to a stable distribution, and we conduct 10 replications of the selection process to ensure that results are repeatable and consistent. A random sub-set of 'optimal' genotypes is then selected from the final distribution, and used for further simulations to evaluate temporal dynamics.

The basic algorithm for IBM simulations is as follows: initialize the population (with starting values for state variables selected randomly) and, starting at time $t = 0$, allow all individuals to actively forage for T time units (T can be thought of as one year in the life of the forager). The sequence of prey encounters for each individual is entirely stochastic, and individuals accept or reject encountered prey items following the rules of thumb described above. The state variable dynamics are identical to those described for the SDPM. Individuals whose energy reserves dip to 0 are assumed to die; additionally, incidental sources of mortality (e.g. disease, predation) can strike any individual at any time during the year with probability Z. At the end of each year, those individuals still alive can reproduce;

for simplicity, we assume an all-female population. Some proportion of the parent's energy reserves (arbitrarily set to ¼) are transferred to the offspring, which survive to weaning with probability W, where W is given by equation (3) (offspring viability is thus a function of the parent's energy reserves at year-end). After the year-end reproduction period, all adults and surviving new recruits begin another year of foraging.

   We make a number of modifications to the basic algorithm to produce a life-history pattern typical of larger vertebrates (such as sea otters) for which both alternate foraging specializations and MST have been reported. The age of first reproduction is delayed until 2 years, and annual reproductive output consists of a single offspring. Incidental mortality of adults (Z) is low until 5 years, after which Z increases rapidly, thereby limiting maximum lifespan to approximately 10 years. We use these particular values because further increases to the age of reproductive maturity or the onset of senescence do not alter the simulation results, but do increase substantially the number of iterations required for natural selection simulations to equilibrate. These life-history traits result in a relatively low intrinsic growth rate for the population. To prevent forager populations from growing exponentially and indefinitely, we add density dependence such that Z increases with population size, resulting in a carrying capacity for the forager population of approximately 1000 individuals.

   Mean encounter rate for each prey type, λ_i, is re-calculated at the beginning of each year:

$$\lambda_{i,y} = \frac{N_{i,y}}{\sum_i K_i}, \tag{7}$$

where $N_{i,y}$ is the population size of prey species i at year y, and K_i is the carrying capacity of the ith prey species. The inclusion of the summed K_i term in the denominator of equation (7) ensures that $\Sigma \lambda_i \leq 1$, as required for our formulation of prey encounter probabilities (explained above). By re-calculating encounter rates only once per year, we assume that intra-annual variation in prey population size is insignificant relative to inter-annual variation. Given the large size of prey populations relative to the forager population, we believe this is a reasonable assumption. We further assume that prey population recruitment is discrete, annual, and occurs at the beginning of each year:

$$N_{i,y+1} = N_{i,y}\left(1 + r_{i,y} - d_i\left(\frac{N_{i,y}}{K_i}\right)\right) - p \cdot C_{i,y}, \tag{8}$$

where $r_{i,y}$ represents the per-capita recruitment of new individuals into prey population i during year y, and d_i represents the per-capita death rate (excluding mortality from the focal predator) at carrying capacity, and is equal to mean $r_{i,y}$. The final term, $p \cdot C_{i,y}$, accounts for the number of individuals of prey population i consumed by the focal predator population during year y. By using this modified logistic growth equation, we assume that recruitment is density-independent and stochastic, while non-predation mortality is density-dependent and deterministic. This is a reasonable representation of many recruitment-limited species (including most benthic invertebrates typically consumed by sea otters) in which recruitment is both highly variable from year to year and essentially decoupled from adult density. To model stochasticity in prey recruitment, a mean value for r_i is (arbitrarily) specified for each simulation, and annual deviations from the mean are modelled as correlated random deviates with mean of 0, standard deviation ε_i, and first-order temporal autocorrelation κ_i (following the methods of Doak and Morris, 2002). By adjusting parameters ε_i and κ_i,

we vary the magnitude and frequency of fluctuations in prey abundance, and thus evaluate how patterns of variation in prey populations affect the temporal dynamics of foraging specializations.

Equation (8) tracks the effect of predation on prey species i ($p \cdot C_{i,y}$) separately from other sources of mortality, thus facilitating the consideration of two alternative scenarios of predator–prey interaction. Under the first scenario, $p = 1$ and the predator population has the potential to limit prey populations because the number of prey consumed by the predator (C_i) translates directly into reductions in prey abundance. This scenario, often referred to as 'top-down control' of prey by predators, can lead to feedback between the frequency of predators specializing on a particular prey species and the relative abundance of that prey species. Under the second scenario, $p = 0$ in equation (8) and the dynamics of the prey population are decoupled from depletion effects by the focal predator population, so that there is no opportunity for top-down control. These two scenarios represent extreme cases along a continuum, thus we modelled intermediate levels of top-down control by varying p between 0 and 1.

We evaluate the temporal dynamics of foraging behaviour both with and without the social transmission of foraging skills. We consider only matrilineal skill transmission, whereby a mother transfers some of her acquired skills to her offspring. Specifically, the skill at handling prey type i for a new forager k recruited to the adult population is:

$$S_{k,i} = \beta(Y_{k,i}) + \chi_{\mu,\sigma}, \tag{9}$$

where $Y_{k,i}$ is the skill level of k's mother for prey type i, β is the fraction of $Y_{k,i}$ inherited by the offspring and thus represents the effect of matrilineal skill transmission, and $\chi_{\mu,\sigma}$ is a normal random deviate with mean μ and variance σ^2, representing the effect of random variation in innate foraging skills. We assess the effect of phenotypic variation by comparing low and high variation in innate foraging skills (Table 1). We evaluate the effect of social learning on the temporal dynamics of foraging specialization by varying β from 0 (no matrilineal skill transmission) to 0.9 (extensive matrilineal skill transmission).

For each combination of parameters (Table 1), having first arrived at appropriate distributions for decision rule parameter values using simulations of natural selection, we ran 100 replications of 100 years to evaluate the temporal dynamics of foraging behaviour in the population. We quantified the tendency of individuals to be foraging specialists by tracking I, the annual index of specialization. We calculated I as the population average of I_k, the diet overlap between individual forager k and the population:

$$I_k = \sum_i \min\left(\frac{n_{i,k}}{\sum_i n_{i,k}}, \frac{\sum_k n_{i,k}}{\sum_k \sum_i n_{i,k}}\right), \tag{10}$$

where $n_{i,k}$ is the number of items of prey type i consumed by individual forager k during the year (Bolnick *et al.*, 2002). For individuals that specialize on a single prey type, I_k takes on the value q_i, where q_i is the proportion of the population's diet composed of the ith prey type. In contrast, I_k is equal to 1 for generalists that consume resources in direct proportion to the population as a whole. Small values of I thus reflect a high prevalence of specialization in the population. In addition to tracking I, we also recorded L, the likelihood

of co-occurrence of alternative specialists in each simulation. We calculated L as the proportion of years in which prey type-1 specialists and prey type-2 specialists each make up at least 10% of the forager population (we reasoned that co-occurrence implies that specialists of each type are sufficiently abundant to be both observable and biologically relevant, and individuals are considered to be specialists if their diet consists solely of one prey type). Finally, we tracked the between-year variation in the frequency of specialists of each type (measured as the coefficient of variation).

In total, we evaluated 100 unique combinations of IBM parameter values. We determined the sensitivity of the IBM results to model parameters using multiple regression analysis: specifically, we calculated the proportion of variance in two response variables – the index of specialization, I, and the likelihood of co-occurrence of alternative specialists, L – explained by each parameter, after accounting for variance due to all other parameters. Individual variance components were estimated by their partial coefficients of determination ($r^2_{y1\cdot2\ \dots\ n}$), following Neter *et al.* (1990), and a stepwise approach was used to exclude parameters that did not contribute significantly to variance in the response variable ($P > 0.05$) after accounting for the effects of other parameters. To account for uncertainty, we calculated 95% bootstrap confidence intervals for the $r^2_{y1\cdot2\ \dots\ n}$ estimates (DiCiccio and Efron, 1996).

Unless otherwise indicated, effects associated with variation in each parameter are reported assuming that all other parameters are held at their baseline values (Table 1). Error bars in figures and all ranges of values reported in the text (in parentheses) represent the 95% confidence intervals for the statistic in question.

RESULTS

Stochastic dynamic programming model

The results of the SDPM suggest that when acquired (learned) skills have a sufficiently large effect on prey handling times ($\alpha \geq 0.5$), and when learning of prey-specific handling skills is slow enough relative to the organism's life span, there will be certain conditions under which a forager will specialize on one prey type or the other. More specifically, the expected behaviour of a forager can be expressed as a function of its relative skill levels for each prey type (Fig. 1). The graphical representation of the decision matrix portrayed in Fig. 1 shows three main 'regions' of behaviour: generalization, specialization on prey type 1, and specialization on prey type 2. Diet generalization is expected when the skill levels for both prey types are equivalent, while specialization is expected when the handling skills for one prey type are high relative to handling skills for the alternative prey.

Varying the functional relationship between energy reserves and reproductive success (determined by parameters θ and ϕ) had no appreciable effect on the model predictions, causing only slight differences in expected behaviour as t approached T and as prey-specific skill levels (S_1 or S_2) approached their maximum (S_M). Consequently, for all further analyses we held θ and ϕ fixed at values that result in a s-shaped fitness function (Table 1); we chose these particular values because they approximate the functional relationship between energy reserves and reproductive success described for sea otters (Monson *et al.*, 2000). Varying other model parameters (Table 1) had the effect of changing the relative size of each of the three regions of the decision matrix (Fig. 1; Table 2). The extent to which learned skills impacted handling time (α) had the greatest impact on the decision matrix:

increasing α resulted in greater regions of specialization for both prey types, but when learning had little effect (α ≤ 0.4) there were no conditions under which an individual would specialize on prey type 2, the less-preferred prey type. The region of specialization on prey type 2 was generally smaller than that for prey type 1, except when the encounter rate for the preferred prey was low ($\lambda_1 < 0.15$). The regions of specialization for both prey types were greatest when the rate of learning was low ($l_i < 1$), the rate of forgetting was high ($f_i > 1.5$), the learning curve was J-shaped ($\gamma > 1$), and individual energy reserves were low ($e(t) < 10$).

Population dynamics

The population patterns of diet specialization predicted by the IBM were generally consistent with the individual responses predicted by the SDPM, as the prevalence of specialists in the population at any given time (measured by *I*) varied with the basic model parameters in the direction predicted by the results of Table 2. In particular, *I* decreased with the effect of learned skills on handling time (α), the shape of the learning curve (γ), and the rate of forgetting (f_i), but increased with the rate of learning (l_i; Fig. 2). The results of the IBM were most illuminating with respect to population-level dynamics that could not be evaluated using the SDPM. The degree of innate variation in the foraging skills of new recruits (equivalent to genetically controlled phenotypic variation) had a strong effect on both the prevalence of specialists and the likelihood of co-occurring alternative specializations: when all other parameters were held constant (and assuming no frequency dependence or matrilineal skill transmission), increasing σ^2 from the minimum to the
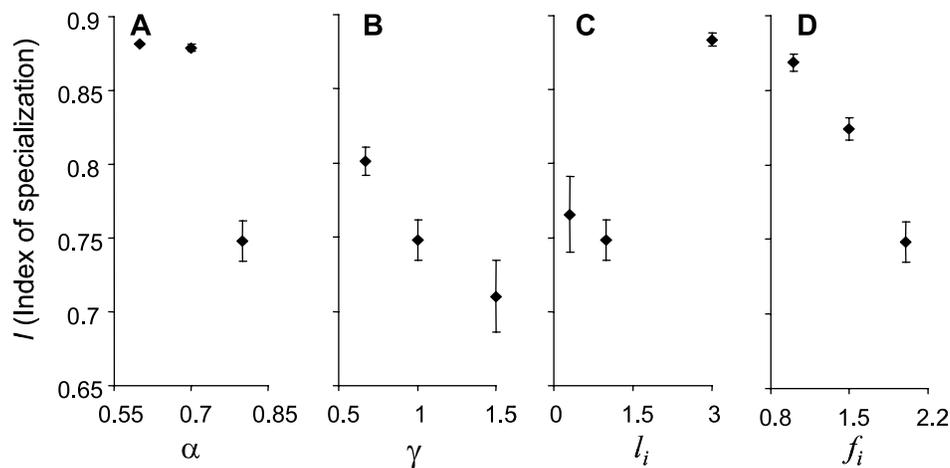

Fig. 2. The index of specialization (*I*) as a function of four model parameters: (A) the magnitude of the learning effect, α (higher values of α result in a greater decrease in handling time with experience); (B) the shape of the learning curve, γ ($\gamma > 1$ results in a J-shaped learning curve, $\gamma < 1$ results in a r-shaped learning curve); (C) the rate at which new skills can be learned, l_i; and (D) the rate at which prey-specific skills are lost by foraging on alternative prey types, f_i. Note that smaller values of *I* indicate a greater tendency of individuals to specialize rather than generalize, while higher values (approaching 1) occur when individual diets converge on the average diet of the population. Error bars represent 95% confidence intervals.

maximum allowed value (Table 1) caused a decrease in *I*, the index of specialization (from 0.75 ± 0.014 to 0.69 ± 0.012), and an increase in *L*, the likelihood of co-occurring alternative specialists (from 0.35 ± 0.091 to 0.65 ± 0.082). However, other factors that affected the temporal dynamics of specialization in the population – specifically, degree of top-down control, matrilineal skill transmission, and stochastic variation in prey species abundance – had the same qualitative effects irrespective of the magnitude of innate variation in foraging skills; therefore, we report all successive results for a single, intermediate level of variance ($\sigma^2 = S_M/10$).

The temporal dynamics of foraging specializations differed significantly between simulations in which the predator could exert top-down control of prey abundance ($p = 1$) and those with purely stochastic prey dynamics ($p = 0$). In the former case, frequency-dependent feedback between predation rate and prey abundance was associated with a greater degree of co-occurrence of alternative specializations (Fig. 3). To some extent, this trend appeared to reflect a decrease in the temporal variability of specializations, rather than simply an increase in the overall prevalence of specialists: using baseline values for all other parameters, the between-year variability in the frequency of type 1 specialists was greater for simulations without top-down effects [coefficient of variation (CV) $= 0.54 \pm 0.13$] than for simulations with top-down effects (CV $= 0.35 \pm 0.02$). The pattern was identical for type 2 specialists (CV $= 0.81 \pm 0.26$ for simulations without top-down effects vs. 0.44 ± 0.02 for simulations with top-down effects).

The ability of individual foragers to pass on learned skills to offspring, or matrilineal skill transmission, also affected the temporal dynamics of foraging specializations. Under certain conditions, a 30% increase in matrilineal skill transmission (from $\beta = 0.5$ to $\beta = 0.8$) resulted in a 100% increase in *L*, the likelihood of co-occurring alternative specializations (Fig. 3). The existence of frequency-dependent effects had a positive interaction with the effect of matrilineal skill transmission (Fig. 3A), and there were also interactions between β and other parameters such as the rate of forgetting (f_i) and the shape of the learning curve (γ). In simulations with an r-shaped learning curve, the introduction of matrilineal skill transmission resulted in a greater relative increase in co-occurring alternative specializations than did simulations with a linear or J-shaped learning curve (Fig. 3B). The effects of matrilineal skill transmission on the temporal dynamics of foraging specializations were explained in part by the optimal decision rules used by the foragers, which differed depending on whether matrilineal skill transmission was included in the natural selection simulations (Fig. 4).

The degree of stochastic variation in prey recruitment had some effect on the likelihood of co-occurring alternative specializations, although this effect was less striking than those of top-down control or matrilineal skill transmission. An increase in the magnitude of stochastic variation (ε_i) was associated with a decrease in the frequency of co-occurring alternative specialists (0.48 ± 0.08 when $\varepsilon_i = 0.01$ vs. 0.27 ± 0.07 when $\varepsilon_i = 0.25$). The relative speed of stochastic changes in prey populations also affected the frequency of co-occurrence, although this effect was only statistically significant in simulations with matrilineal skill transmission: increased temporal autocorrelation of prey abundance (κ_i) was associated with a lower frequency of co-occurring alternative specialists (0.57 ± 0.07 when $\kappa_i = 0.2$ vs. 0.48 ± 0.07 when $\kappa_i = 0.7$, and $\beta = 0.8$ in both cases). Low values of κ_i (resulting in rapid changes in prey abundance) were associated with less temporal variability in the frequency of type 1 specialists (CV $= 0.42 \pm 0.04$ when $\kappa_i = 0.2$ vs. 0.52 ± 0.04 when $\kappa_i = 0.7$).
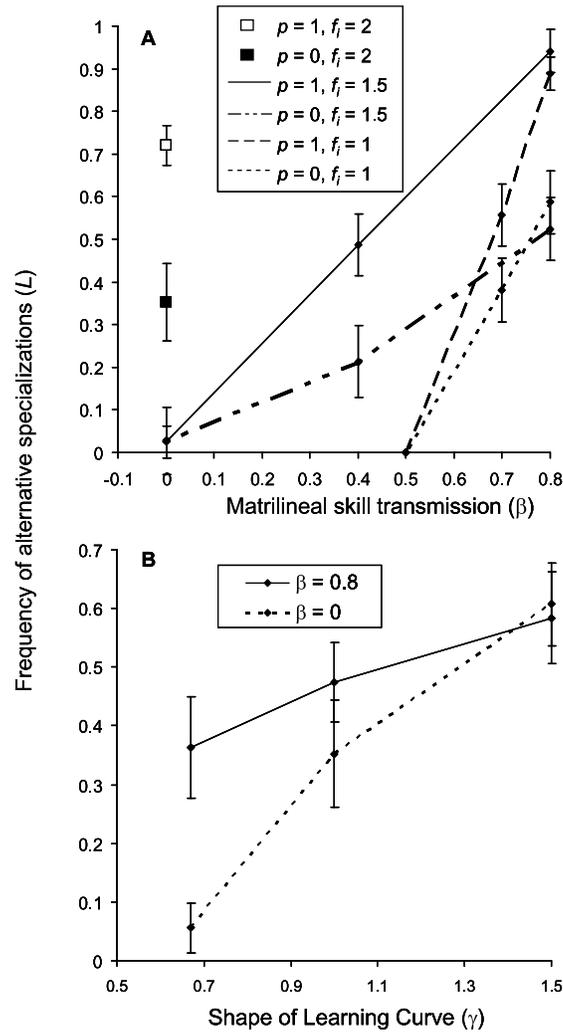
Fig. 3. The likelihood of co-occurring alternative specializations (L) plotted as a function of the degree of matrilineal skill transmission, β, and the shape of the learning curve, γ. (A) Square symbols show the difference between simulations where predators can limit prey (top-down effects, $p = 1$) and those with purely stochastic prey dynamics ($p = 0$) in the absence of matrilineal skill transmission ($\beta = 0$). Diamonds connected by lines summarize the interactions between top-down effects (p), β, and the rate of forgetting (f_i). (B) The effect of varying γ when $\beta = 0$ and when $\beta = 0.8$. Error bars represent 95% confidence intervals.

Multiple regression indicated that six of the model parameters (α, the effect of learning; β, the degree of matrilineal skill transmission; l_i, the rate of learning; f_i, the rate of forgetting; γ, the shape of the learning curve; and p, the potential for top-down control) explained 69.5% of the variance in the degree of specialization and 70.1% of the variance in the frequency of co-occurring alternative specializations. The model parameters with the
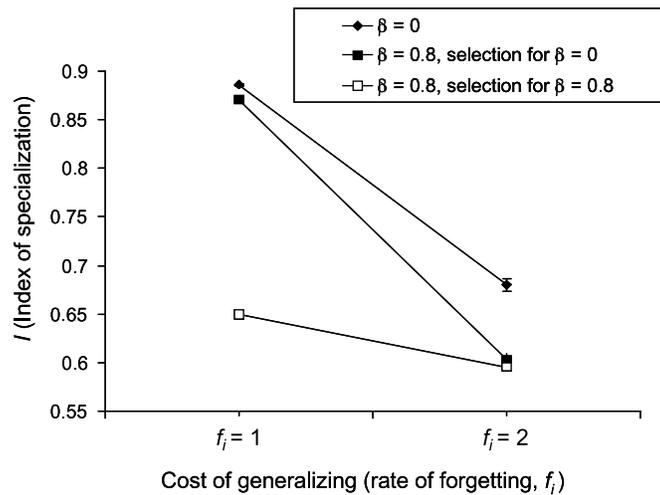
Fig. 4. The effect of matrilineal skill transmission (MST) on optimal decision rules, when $f_i = 1$ (slow rate of skill loss for generalists) and when $f_i = 2$ (fast rate of skill loss for generalists). Three sets of results are shown: (i) simulations with no MST ($\beta = 0$); (ii) simulations with a high degree of MST ($\beta = 0.8$) but where foragers were forced to use decision rules selected for without MST ($\beta = 0$); and (iii) simulations with a high degree of MST ($\beta = 0.8$) in which foragers used appropriately selected decision rules. Error bars indicate the 95% confidence bound around each point (all points shown are significantly different).

greatest impact on the IBM results were α, the intensity of the learning effect, and p, the potential for top-down control (Fig. 5).

DISCUSSION

The results of the stochastic dynamic programming model (SDPM) and the individual-based model (IBM) confirm the primary prediction of Hughes' (1979) model: the ability of animals to learn and improve foraging skills through experience leads to an increased tendency to specialize, and can also result in individual switching from one prey specialization to another. Given our results, we predict that the following behavioural, physiological, and/or life-history characteristics will be associated with increased levels of specialization:

1. Increased experience with one particular prey type has a strong effect on some component of foraging (e.g. handling time, capture success, digestion efficiency).
2. The rate at which new skills are acquired through experience is relatively slow.
3. There is limited ability to learn or retain complex learned skills for one prey type when many other prey types are included in the diet (i.e. skills are either forgotten through lack of use, or lost via interference with new skills).
4. The learning curve for new foraging skills is J-shaped, rather than linear or r-shaped.
5. The forager does not carry extensive energy reserves, or at least it cannot rely on such stores to supplement poor foraging performance over the time required to learn new skills.
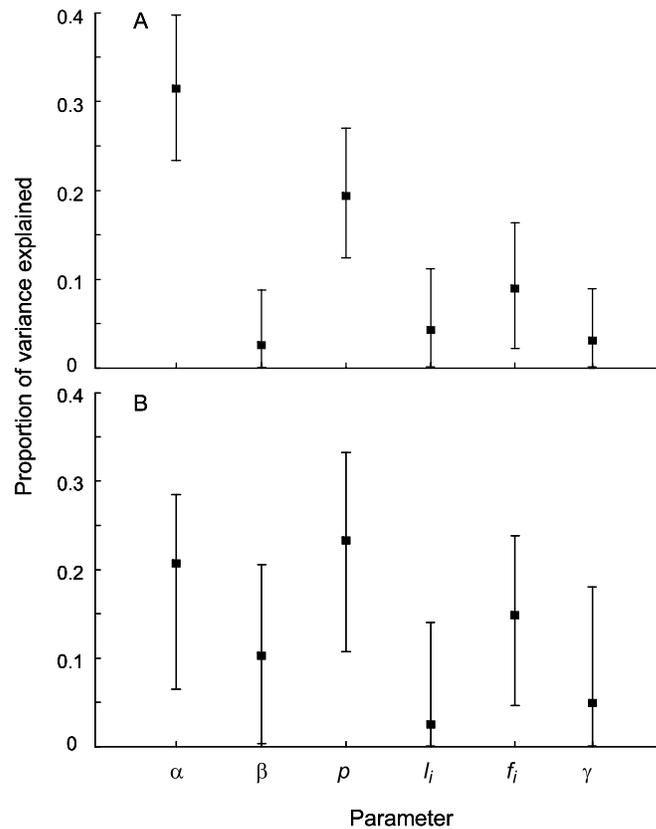
Fig. 5. The sensitivity of simulation results (measured as the proportion of variance explained) to six of the model parameters: the degree to which learning affects handling efficiency (α), the degree of matrilineal skill transmission (β), the potential for top-down control (p), the rate at which foraging skills are acquired by learning (l_i), the rate at which foraging skills are lost by forgetting (f_i), and the shape of the learning curve (γ). (A) The relative contribution of each model parameter to variation in I, the index of specialization; (B) the relative contribution of each model parameter to variation in L, the likelihood of co-occurring alternative specializations (see text for explanation). Error bars represent 95% confidence intervals.

6. The metabolic costs of foraging are high relative to energy reserves, or to the energy gained by each prey capture.
7. The forager is able to transfer learned skills to offspring, either actively (via teaching), passively [no direct teaching, but the offspring nonetheless learns skills through observation or mimicking of the parent (Stoinski *et al.*, 2001)] or through stimulus enhancement (e.g. Visalberghi and Addessi, 2001).

In addition to these characteristics of the forager, the following prey species characteristics are also predicted to result in an increased degree of specialization and/or likelihood of alternative specialists:

8. The encounter rate for all prey types is relatively high.
9. The population growth rates or abundances of the prey species are significantly

impacted by predation pressure by the forager, resulting in frequency-/density-dependent benefits of alternative specialist strategies (Partridge and Green, 1985; Estes *et al.*, 2003).

10. Stochastic variation in prey population dynamics (excluding variation due to predation by the forager) is neither too extreme in magnitude nor too 'slow' with respect to the time required for an individual forager to learn new foraging skills.

Some of these predictions – particularly predictions 1 and 2 – are immediate consequences of the fundamental assumptions of our model. Clearly, if there is little impact of learned skills on any of the components of foraging success, or if new skills can be acquired so quickly that there is little cost to doing so, then some (or all) of the potential benefits of specialization are negated. Some of the other predictions, however, are less intuitive, and bear closer examination. Prediction 3, that specialization is more likely when specific skills for one prey type are forgotten or lost when the forager switches to different prey, is essentially Darwin's interference hypothesis (Darwin, 1876; Heinrich *et al.*, 1977; Goulson *et al.*, 1997). Interference in handling skills for different prey types, resulting in reduced handling efficiency of generalists versus specialists, has been shown for diverse taxa (e.g. Cunningham and Hughes, 1984; Laverty and Plowright, 1988; Goulson *et al.*, 1997; Gegear and Laverty, 1998) and may be a common characteristic among predators with multiple, dissimilar prey types. In our current model, the interference effect was introduced using parameter f_i, although the precise nature and strength of an interference effect is likely to vary widely from system to system, and may by countered to some extent by the ability to transfer learned skills from established to novel prey types (Hughes and O'Brien, 2001). The results of the IBM were sensitive to this parameter (Fig. 5), suggesting that experimental quantification of the interference effect may provide a fruitful area for further research.

The results of both the SDPM and the IBM suggest that a J-shaped learning curve is more likely to result in specialization than an r-shaped curve, although the shape of the learning curve has a greater effect on the likelihood of co-occurring specializations than it does on the prevalence of specialization itself (Fig. 5). A J-shaped learning curve means that an individual's initial experiences with a novel prey type will have very little effect on its handling efficiency, and thus the relative cost of switching to a new prey type is greater than for an r-shaped curve. In those few cases where the learning dynamics for novel prey types have been accurately measured, the result has usually been an r-shaped learning curve (Cunningham and Hughes, 1984; Croy and Hughes, 1991; Hughes and O'Brien, 2001). However, the shape and slope of the learning curve will likely differ greatly between different prey types, even within the diet of a single predator species (Laverty, 1980, 1994). A slower, J-shaped learning curve may be more typical for apex predators such as sea otters (Estes *et al.*, 2003), which have a wide potential prey base that includes dissimilar taxa at multiple trophic levels, some requiring complex handling skills. At the extreme, foragers that utilize highly complex foraging techniques or use tools to manipulate prey may require years to become highly adept at a particular prey handling technique (Huffman and Quiatt, 1986; Guinet and Bouvier, 1995; Estes *et al.*, 2003). In tool-using foragers, the learning curve may be an exaggerated J-shape, or even a step function, with a long 'experimental period' resulting in virtually no increase in skill followed by a fairly rapid improvement as the tool is mastered (Huffman and Quiatt, 1986). A prolonged period of offspring dependency would be particularly adaptive in the case of strongly J-shaped learning curves, because the offspring can get past the initial slow-learning period and perfect its skills while still 'subsidized' by the parent.

A prolonged period of offspring dependency also allows for the possibility of transmission of skills from parent to offspring, or matrilineal skill transmission. Our model suggests that, under some sets of conditions, matrilineal skill transmission can promote the likelihood of alternative specializations developing within a population (Fig. 3). Vertical transmission of foraging skills, as we have modelled it, ensures that new recruits tend to start out their independent life with honed skills for one prey type but minimal skills for alternative prey, rather than intermediate skills for all prey. Such a tendency will result in increased specialization within the population; however, this only accounts for part of the observed effect. When we force identical decision rules for simulations run with and without matrilineal skill transmission, the difference in the degree of specialization is less pronounced than when we use appropriate decision rules for each simulation (and this is the case irrespective of the value of other model parameters; Fig. 4). This result demonstrates that selection will result in different optimal decision rules when matrilineal skill transmission occurs, likely because the inclusive fitness of individuals is no longer just a function of energy reserves transferred to offspring, but also a function of the skills that can be transferred. The potential of matrilineal skill transmission can therefore lead to a selective trade-off between competing rules of thumb. For example, although generalizing would be more likely to result in higher energy reserves at reproduction, continued specialization would be more likely to result in effective foraging skills to transfer to future offspring.

Transference of skills by social learning represents one solution to the problem posed by prey types whose relative profitability depends on complex, hard-to-master foraging skills. An alternative solution to the same problem is 'hard-wired' (i.e. genetically controlled) behavioural, morphological, or physiological adaptations to the specific requirements of a particular prey type. In the latter case, individual foragers are expected to specialize on the prey type appropriate to their particular phenotype (Werner *et al.*, 1981; Ehlinger, 1990), although the tendency to specialize at all may be behaviourally plastic (Svanbäck and Bolnick, 2007). This 'hard-wired' solution [or trophic polymorphism (*sensu* Robinson and Wilson, 1994; Smith and Skúlason, 1996)] has been documented for many taxa (e.g. Smith, 1990; Robinson and Wilson, 1995; Giorni Christopher *et al.*, 1996). In systems where the suite of potential prey is not sufficiently stable over time, however, there will be a trade-off between the foraging efficiency associated with genotypic specialization and the flexibility to switch to novel prey types. In such cases, genetic polymorphisms may be less adaptive than the behavioural plasticity conferred by individual learning ability and matrilineal skill transmission (Laland and Kendal, 2003).

In addition to increasing the prevalence of specialization, matrilineal skill transmission was associated with an increase in the co-occurrence of alternative specializations, likely due to an inter-generational lag effect created by transmission of skills from mother to offspring. As the relative abundance of different prey populations changes from year to year, the predicted 'optimal' behaviour for naive new recruits will also change (e.g. from specialization on prey type 1, to generalization, to specialization on prey type 2). In a population with no matrilineal skill transmission, the result of such changes is substantial annual variation in the prevalence of specialists, such that the population is often devoid of specialists of a given type. In contrast, when new recruits inherit prey-specific skills from their parents (such as through matrilineal skill transmission), it may remain profitable for them to specialize on one prey type even when its encounter rate decreases substantially. Matrilineal skill transmission can thus lead to the co-occurrence of alternative specializations, simply by delaying the time it takes for particular specializations to disappear from the population altogether. Our model predictions are consistent with empirical data from

guppies showing that foraging behaviours are indeed more stable across generations when social learning occurs (Stanley *et al.*, 2008).

The extent to which the dynamics of the prey populations were controlled by top-down predation pressure from the forager population was one of the key factors affecting our simulation results (Fig. 5). Strong top-down control can lead to greater depletion of the type of prey that is currently most preferred, with the result that the less-preferred prey will increase in relative abundance over time. This frequency-dependent feedback tends to result in regular, out-of-step oscillations in the relative abundance (and thus relative profitability) of alternative prey populations, and at the same time it tends to limit the absolute magnitude of such variation. When combined with the inter-generational lag created by matrilineal skill transmission, frequency dependence can act to prevent specializations from disappearing entirely from the population, thereby increasing the likelihood of observing alternative specializations within the population at any given time. The positive interaction between the effects of matrilineal skill transmission and top-down control (Fig. 3A) supports such a scenario. In the absence of frequency dependence, the degree of stochastic variation in prey population abundance can similarly affect the likelihood of observing alternative specializations within the population. Specifically, when the year-to-year changes in prey population abundance are low (corresponding to high temporal auto-correlation), individual learning is able to 'keep up' with variation in encounter rates, and thus the relative frequency of specialists essentially tracks prey variation. Conversely, in populations where the year-to-year changes in prey population abundance are high (corresponding to low temporal autocorrelation), individual learning cannot keep up with variation and there is a lag, similar to that associated with matrilineal skill transmission, which dampens variation in the abundance of specialists and increases the likelihood of observing alternative specializations within the population at any given time. However, when variation in prey abundance becomes too great in magnitude, any type of specialization can become risky – a prey type that is very profitable one year may be extremely rare the next – and so a 'risk-spreading' strategy of generalization becomes more prevalent.

The general patterns predicted by our model should be broadly applicable to many animal species. Nonetheless, we must highlight a number of qualifications. The most important caveat concerns the quantitative results reported, which (in contrast to the qualitative patterns highlighted above) depend entirely on the specific parameter values chosen for our simulations. For example, the co-occurrence of specialists for both prey types in the absence of frequency dependence or matrilineal skill transmission depended upon: (a) the range of prey-specific parameters being set so that either prey type could be 'preferred prey' under at least some realized combinations of prey abundance and skill levels; and (b) the existence of some variation in the initial skill levels of new recruits, corresponding to continuous phenotypic variation (Verbeek *et al.*, 1994). In the interest of generality, the underlying structure of our models also reflected some overly simplistic assumptions: for example, we assumed that energy was the sole limiting factor for our hypothetical forager, and that there were no other relevant constraints or decision criteria (e.g. no specific nutritional requirements, no elevated predation risks associated with one prey type). Incorporating more than two prey types, and including multiple constraints and decision criteria, would undoubtedly result in more complex dynamics. Future elaborations of this approach should also include some evaluation of the effect of the sensory and memory limitation of individuals, and thus the potential for errors in individual assessments of relative prey abundance (Hirvonen *et al.*, 1999).

Table 3. Suggested experiments or comparative studies to test the predictions of our models

Suggested experiment or comparison	Predictions
1. Manipulate individual energy reserves (e.g. decrease mean food abundance)	The degree of specialization will increase as mean abundance of food decreases
2. Manipulate top-down control of prey, or the degree to which predation intensity is coupled to prey population dynamics	There will be increased co-occurrence of alternative specializations in treatments due to frequency dependence
3. Manipulate variation in prey population (increase or decrease the magnitude or frequency of changes in prey abundance)	There will be increased co-occurrence of alternative specializations as prey populations become more temporally variable
	There will be decreased co-occurrence of alternative specializations when the rate of change is slow relative to the rate of learning
4. Manipulate metabolic costs of foraging (e.g. increase travel time between patches)	The degree of specialization will increase as metabolic costs increase
5. Compare the frequency of specialization in closely related taxa having different offspring dependency patterns	The degree of specialization will be higher in species having prolonged offspring dependency and known (or suspected) matrilineal skill transmission
6. Inter- or intra-specific comparisons of species that do effectively limit their prey populations with other species (or populations) that do not	There will be increased co-occurrence of alternative specializations in species with a greater potential for frequency dependence
7. Intra-specific comparisons of foraging behaviour among populations that utilize different suites of prey in different habitats	The degree of specialization will be lower in habitats where there is less individual variation in foraging efficiency (lower value of α) or where acquisition of prey-specific foraging skills is rapid (high value of l_i)
8. Intra-specific comparisons of specialization prevalence associated with particular prey types	The degree of specialization will be highest for those prey types requiring complex manipulation skills (i.e. slowest rate of learning or most J-shaped learning curve)
	Prey species not requiring complex skills (i.e. rapid rate of learning or r-shaped learning curves) will be ubiquitous in the diet of all individuals
9. Inter-population comparisons or multi-year studies of foraging behaviour incorporating differences in environmental conditions or population densities	The degree of specialization will be higher in locations or years when population density is high, food is scarce, and individuals have fewer energy reserves

Despite the caveats mentioned above, the general patterns observed allow us to suggest some explicit tests that could be used to either falsify or lend support to our model results (Table 3). The first four suggestions in Table 3 describe controlled experiments that could be performed in the laboratory or in highly tractable study systems conducive to manipulative field experiments [e.g. insect foragers (Gegear and Laverty, 1998)]. Many fish species lend themselves well to these types of manipulations because it is possible to manipulate foraging

conditions or food resources, and alternative specializations are already known to occur (Werner *et al.*, 1981; Wildhaber and Crowder, 1995). Indeed, the first suggested manipulation (decreasing food resources and measuring tendency to specialize) has already been tested by Werner *et al.* (1981), with results supportive of the patterns predicted here. Suggestions 5–9 in Table 3 describe possible field studies involving inter- or intra-specific comparisons. For example, comparisons of the degree of specialization on prey types having different learning curves (Table 3, #8) could be conducted with species such as bumble bees (*Bombus* sp.), where variable learning rates have already been described (Laverty, 1994). Multi-year studies of species such as the Cocos Island finch (*Pinaroloxias inornata*), for which alternative specializations have been reported (Werner and Sherry, 1987), would allow testing of the expected relationship between the degree of specialization and the abundance of energy reserves (Table 3, #9). Intra-specific comparisons of populations that utilize different suites of prey in different locations, and/or occur at differing population densities, can be used to test for correlations between specialization and prey-specific learning curves or inter-annual variance (Table 3, #7): sea otters (*Enhydra lutris*) provide an excellent study system for such comparisons, because different populations in Alaska and California utilize highly diverse prey assemblages (Riedman and Estes, 1990) and cover the full spectrum of possible population densities (Estes, 1990; Estes *et al.*, 1996).

The conceptual framework developed here suggests that frequency-dependent benefits of specialization, combined with the ability of foragers to improve their foraging skills by learning and potentially even transmit learned skills to offspring, can result in behaviourally mediated foraging specialization and lead to the co-existence of alternative specializations. While similar results have already been shown for polymorphisms associated with genetically based traits (Svanbäck and Bolnick, 2005), our model demonstrates how such patterns can occur even in the absence of genetic polymorphisms. We note that the ultimate driver of foraging specialization in both cases is intra-specific competition and the fitness trade-offs associated with alternative foraging strategies. Central to our results are the behavioural traits of the forager, including the dynamics of learning and inter-individual transfer of skills. The importance of individual learning and memory limitations on foraging behaviour has received some attention in the behavioural literature (e.g. Dukas, 1998; Shettleworth, 1998), but such considerations are rarely (if ever) considered at the level of community ecology, where diet selection patterns are considered to be features of populations or species, not individuals. Similarly, the significance of social learning has been explored from the perspectives of individual fitness and the evolution of culture (Boyd and Richerson, 1996; Laland and Hoppitt, 2003), but our results indicate that matrilineal skill transmission may also play an important role in maintaining generalist populations composed of individual specialists. This may in turn have important community-level implications: for example, the existence of alternative specializations may increase the robustness of a predator population to perturbations such as those caused by rapid, unpredictable variation in resource abundance. The existence of behaviourally mediated foraging specializations should therefore be viewed as more than a curiosity or a statistical nuisance by ecologists, but rather needs to be more realistically incorporated into our thinking about animal populations and community dynamics.

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APPENDIX

The programming algorithm for solving stochastic dynamic programming equations (SDPE) has been well documented in the literature: for example, a comprehensive explanation of the theory and description of the technique are provided by Clark and Mangel (2000), and we refer the reader to this reference for a full explanation of stochastic dynamic programming models. Here we explain in more detail the steps involved in the

solution of the SDPE used in this paper (see Methods, equation 4), for the benefit of those not familiar with this modelling technique.

The conceptual foundation of the SDPE is that the behaviour of an individual forager at any time, t, can be predicted on the basis of the current state of the forager. Specifically, we define the state of a forager in terms of its energy reserves ($E = e$), its skill level for prey type 1 ($S_1 = s_1$), and its skill level for prey type 2 ($S_2 = s_2$) (see the Methods section for a detailed description of state variable dynamics). What we wish to determine from the SDPE is the expected decision of a forager of a given state, and at a given point in time. By definition, the expected decision for a forager is that decision which confers the highest expected fitness; therefore, to determine the expected decision, we must first calculate the expected fitness value associated with each possible decision. The only tractable way to calculate the expected fitness associated with every possible decision, for a forager of any state, at any point in time, is to start at the final or 'terminal time' ($t = T$) and solve backwards in time to $t = 1$.

The fitness of a forager at the terminal time, T, is denoted by $F(e, s_1, s_2, T)$ and is assumed to be an increasing function of the forager's energy reserves (see Methods, equation 3). For every previous time step, $t < T$, we can calculate the fitness value associated with a particular decision, d, in terms of the expected future fitness of the forager should it adopt decision d. The possible foraging decisions available to the forager depend on which prey type (if any) it encounters at each time step. Should the forager encounter prey type 1 (which will happen with probability λ_1), it can choose to ignore the prey and keep searching (d_{1a}), or else attack and consume the prey (d_{1b}). In the case of the first decision, the expected future fitness is calculated as:

$$F(d_{1a}) = F(e - m, s_1, s_2, t + 1).   \tag{A1}$$

Equation (A1) reflects the fact that if the forager ignores the prey, its expected fitness is equal to the fitness of a forager 1 time unit in the future, having energy reserves equal to the current value of E decreased by the metabolic costs incurred by searching for 1 unit of time, and skill levels for both prey types unchanged from their current values. In the case of the second decision, the expected future fitness is calculated as:

$$F(d_{1b}) = F(e + g_1 - m(1 + h_i(S_i)), s_1 + l_1, s_2 - f_2, t + 1 + h_i(S_i))   \tag{A2}$$

Equation (A2) reflects the fact that if the forager decides to attack and consume the prey, its expected fitness is equal to the fitness of a forager $1 + h_1(S_1)$ time units in the future, having energy reserves equal to the current value of E incremented by the energy content of the prey minus the metabolic expenditure incurred by searching for 1 time unit and handling prey for $h_1(S_1)$ time units, skill level for prey type 1 equal to the current skill level incremented by l_1, and skill level for prey type 2 equal to the current skill level decremented by f_2. Note that the prey handling time, $h_1(S_1)$, is a function of the skill level of the forager for prey type 1 at time t (see Methods, equation 1). If the solution to equation (A2) is greater than the solution to (A1), the expected decision is to attack and consume the prey; otherwise, the expected decision is to ignore the prey. The expected fitness given an encounter with prey type 1 is therefore calculated as the maximum of equations (A1) and (A2):

$$F_1 = \max\{F(e - m, s_1, s_2, t + 1), F(e + g_1 - m(1 + h_1(S_1)), s_1 + l_1, s_2 - f_2, t + 1 + h_1(S_1))\}   \tag{A3}$$

Note that equation (A3) represents the first line of the SDPE.

Should the forager encounter prey type 2 (which happens with probability of λ_2), the decisions and their associated fitness values are calculated in an analogous manner to the steps described for prey type 1, with appropriate substitutions. As described above, these calculations give both the expected decision (in this case whether to accept or ignore prey type 2) as well as the maximum expected fitness given an encounter with prey type 2:

$$F_2 = \max\{F(e - m, s_1, s_2, t + 1), F(e + g_2 - m(1 + h_2(S_2)), s_1 - f_1, s_2 + l_2, t + 1 + h_2(S_2))\} \quad (A4)$$

Note that equation (A4) represents the second line of the SDPE.

Should the forager encounter no prey at time t (which happens with a probability of $1 - \Sigma\lambda_i$), the only decision available is to keep searching, and the expected fitness is given by:

$$F_0 = F(e - m, s_1, s_2, t + 1) \quad (A5)$$

The forager's expected fitness in this case is equal to the fitness of a forager 1 time unit in the future, having energy reserves equal to the current value of E decreased by the metabolic costs of searching for 1 unit of time, and skill levels for both prey types unchanged from their current values.

Finally, we sum equation (A3) (the expected fitness if prey 1 is encountered), equation (A4) (the expected fitness if prey 2 is encountered), and equation (A5) (the expected fitness if no prey is encountered), weighted by their associated probabilities and adjusted for the possibility of mortality occurring at time t, to arrive at the SDPE:

$$F(e, s_1, s_2, t) =$$
$$[\lambda_1 \max\{F(e - m, s_1, s_2, t + 1), F(e + g_1 - m(1 + h_1(S_1)), s_1 + l_1, s_2 - f_2, t + 1 + h_1(S_1))\}$$
$$+ \lambda_2 \max\{F(e - m, s_1, s_2, t + 1), F(e + g_2 - m(1 + h_2(S_2)), s_1 - f_1, s_2 + l_2, t + 1 + h_2(S_2))\}$$
$$+ (1 - \sum_i \lambda_i)F(e - m, s_1, s_2, t + 1)]\exp(-Z) \quad (A6)$$

Solving equation (A6) gives the fitness of a forager at time t having energy reserves $E = e$, skill level for prey type 1 $S_1 = s_1$, and skill level for prey type 2 $S_2 = s_2$. Equation (A6) is solved for all possible values of E, S_1, and S_2 at time t, thereby providing the expected decision matrix at time t, and also allowing the solution of equations (A1–A5) at time $t - 1$. The whole process is then iterated backwards in time until $t = 1$.