Research

Exploration or exploitation: life expectancy changes the value of learning in foraging strategies

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The acquisition of information is a fundamental part of individual foraging behaviour in heterogeneous and changing environments. We examine how foragers may benefit from utilizing a simple learning rule to update estimates of temporal changes in resource levels. In the model, initial expectation of resource conditions and rate of replacing past information by new experiences are genetically inherited traits. Patch-time allocation differs between learners and foragers that use a fixed patch-leaving threshold throughout the foraging season. It also deviates from foragers that obtain information about the environment at no cost. At the start of a foraging season, learners sample the environment by frequent movements between patches, sacrificing current resource intake for information acquisition. This is done to obtain more precise and accurate estimates of resource levels, resulting in increased intake rates later in season. Risk of mortality may alter the tradeoff between exploration and exploitation and thus change patch sampling effort. As lifetime expectancy decreases, learners invest less in information acquisition and show lower foraging performance when resource level changes through time.

Foragers that explore various prey types or resource patches may obtain information that can enhance future foraging performance. In such learning processes, foragers integrate pieces of information acquired through experience (Stephens 1993). Learners may adjust their behaviour to changing environments when fitness consequences of a given action vary within an individual's lifetime.

Information comes at a cost, however, as sampling often conflicts with other activities, such as resource exploitation (Stephens 1987, Krebs and Inman 1992). Traditional models of patch use (Charnov 1976) and forager distributions (Fretwell and Lucas 1970) commonly assume that animals have complete and free information about the spatial and temporal distribution of resources. When information has to be actively sampled and used, foraging behaviour often deviates from patterns predicted for such omniscient foragers (Abrahams 1986, Bernstein et al. 1988, Rodriguez-Gironés and Vásquez 1997).

When resource conditions vary temporally, new experiences become more valuable than older information, and a forager should bias its estimate towards recent information (McNamara and Houston 1985, 1987). However, with more weight given to each sample, estimates become more sensitive to natural variability and sampling errors (McNamara and Houston 1985, Hirvonen et al. 1999). In changing environments, this imposes a tradeoff between having a precise estimate on the one hand, and keeping the world-view up to date on the other.

Foraging models commonly consider only the ability of learners to reduce uncertainty in estimates of the environment (Mangel and Clark 1983, Dall et al. 2005). Information is, however, only valuable when knowledge can lead to changes in behaviour that have fitness consequences (Gould 1974, Stephens 1987, Dall et al. 2005). This perspective has important implications when studying foraging behaviour in heterogeneous environments. If foragers cannot change actions, or if behavioural shifts have small fitness consequences, then the value of information is low (Mangel 1990). In such cases, there is no need to accurately estimate environmental parameters or to learn from experience.

Information is thus a two-sided coin. On the one side, it does not exist separately from the environment,

but must be collected, often by altering behaviour. On the other side, the benefits are constrained by the fact that information is only valuable as long as it leads to more efficient foraging behaviour. The benefit of information must therefore be traded against investment in other activities, for instance when there is a conflict between harvesting information or resources (Clark and Mangel 1984). This does not necessarily mean that foraging and sampling are mutually exclusive behaviours. Commonly there is an interaction between the two (Cohen 1993), for example when information on patch quality is gained from resource encounters and search times (Oaten 1977, Iwasa et al. 1981, McNamara 1982, Green 1984, Olsson and Holmgren 1998). Foragers that explore several patches would gain a better estimate of the general resource level in the habitat, but frequent patch shifts could interfere with resource exploitation and the assessment made in each patch (Stephens 1987, Valone 1989, Mangel 1990). The investment to improve future foraging performance thus manifests itself as reduced intake rates during intensive sampling periods.

Evolutionarily adaptive foraging strategies should balance present and future foraging benefits, and make the best of both spatial and temporal heterogeneities. The precise nature of such adaptive strategies is far from obvious (Clark and Mangel 1986). Behaviours commonly range from those that are unaffected by specific experiences to those that wholly depend on them (Arak and Enquist 1993, Papaj 1993, Dukas 1998). Hence, to predict the way optimal learning strategies change with environmental characteristics, we need to understand the tradeoffs in behaviour and life-history that foragers face.

We study adaptive foraging behaviour that is partly specified by genetically inherited traits and partly updated with knowledge acquired during the forager's lifetime. The acquisition of information is treated as an integral part of the foraging behaviour, which emphasizes the tradeoff between investment in exploration (harvesting information by frequently changing patches) and exploitation (immediate foraging reward by exploiting each patch optimally). Costs and benefits of learning are dynamic properties that depend on local patch assessment, the updating mechanism, and characteristics of the resource environment. We illustrate how there is a separation in time between when learners pay for information and when they reap the benefit, which affects the value of information and modifies behaviour and foraging efficiency. Further, we study how ecological factors, including mortality risk, may alter the tradeoff between exploration and exploitation, and thus change patch sampling effort, learning rates, and eventually the quality of resource estimates.

Model description

We study foragers that explore a patchy and temporally changing habitat. Individuals search for discrete food items that are distributed in well-defined patches. By consuming resources, foragers deplete the patch, and intake rate drops. Foragers record the time between resource encounters and leave the patch when the search time exceeds a giving-up threshold. Harvesting information and harvesting resources are interlinked activities, as Learning foragers (also termed Learners) use their past experiences to estimate global resource conditions. The learning rule is simple, with a genetically determined learning factor that weights past information against present. To track temporal changes in average resource conditions, a learner may thus sample different resource patches in the habitat and update patch-leaving estimates from one patch to the next.

The costs and benefits of learning emerge from interactions between the foraging strategy and the environment. To quantify these costs and benefits, we compare behaviour and performance of Learning foragers to:

1. Informed foragers that have access to complete information about the global resource level. They receive the optimal giving-up threshold at no cost as they enter a new patch.
2. Fixed foragers that use a single genetically determined giving-up threshold throughout the foraging season, thereby ignoring information and avoiding the associated costs, but consequently also unresponsive to temporal changes in resource levels.

All three strategies have the same local assessment problem, and differ only in the way they access and utilize information about global resource conditions. We compare Learning foragers to Fixed foragers to determine the value of using environmental information (i.e., the value of learning), and to Informed foragers in order to evaluate the costs of imperfect information. We analyze the emergent costs and benefits of different learning rules to see how sampling is balanced against resource exploitation in different environments.

Resource encounters

The lifetime of a forager is divided into discrete time steps, in which the forager either searches for resources within a patch or moves between resource patches. Resource density in the habitat changes temporally with a constant factor g every time step:

$$R_t = R_0 + gt$$

R_0 is the initial resource density and t denotes the number of time steps since the start of a foraging season. We assume that a forager never returns to previously exploited patches and that there is no competition for resources within a patch. The number of food items remaining in the current patch at time t is therefore given by:

$$r_t = R_t - k$$

where k is the number of resources a forager has encountered in that patch. The forager searches randomly for food within the patch, and each time step the probability P_e that it will encounter a resource item depends on r_t and the search efficiency a:

$$P_e = 1 - e^{-ar_t}$$

Whenever a uniformly distributed random number [0,1] exceeds P_e the forager will hence encounter a resource. A forager can handle no more than one resource item each time step.

Patch assessment and the patch-departure rule

When a forager consumes resources, the patch is gradually depleted and the encounter rate drops. A forager uses time since last resource encounter to estimate the current quality of a patch. The encounter process is, however, stochastic in nature, and consequently this estimate is associated with uncertainty (Iwasa et al. 1981, Green 1984). The patch-departure rule is inspired by the Marginal Value Theorem (Charnov 1976) where a forager leaves a patch when resource intake rate falls below the environmental average. Hence, when time spent searching for the next resource exceeds a giving-up threshold, the forager will leave the patch to look for a new feeding location. To locate a new, randomly selected patch, the forager needs to travel for a fixed number of time steps d.

Learning

A Learning forager may update its estimate of the environment through experiences made in previously visited patches. Upon leaving a patch, the forager calculates the average time between resource encounters, including travel time d:

$$\bar{n}_p = \frac{d + \sum_{i=1}^{k} n_i}{k}$$

Here, n_i is the time searched before finding the i'th of the total k resources encountered in patch p. Learning is incorporated into the model by the use of a temporal

weighting rule, where the new giving-up threshold τ_{p+1} is a weighted average of the former threshold τ_p and experiences made in the last patch:

$$\tau_{p+1} = (1 - \gamma)\tau_p + \gamma\bar{n}_p$$

The learning factor γ determines the relative weighting of past information and the new patch quality sample. The learning rule is a linear operator (McNamara and Houston 1987, Mangel 1990) and like Bayesian updating rules it integrates prior estimates and new data. The initial giving-up threshold τ_0 and the learning factor γ can be regarded as genetically inherited traits. The learning factor does not change during the lifetime of the forager, but the giving-up threshold begins with a value of τ_0 and is updated by experience.

We evaluated the performance of the patch-leaving strategies by simulating individual foraging behaviour under different environmental conditions. The best parameter combinations of τ_0 and γ were found by exhaustive search: learning factors ranged from 0.0 to 1.0 (in steps of 0.001), and the initial giving-up thresholds could take any value between 1 and 50 in steps of 0.1. Mortality is a stochastic process in the model, and all individuals have an equal probability e^{-m} of surviving each time-step until the end of season T when all foragers die. Mortality rate does not change between years and we only consider within-year variation in resource levels. We assume that the fitness of a forager is proportional to the amount of resources accumulated during a foraging season.

Informed foragers and the cost of uncertainty

An Informed forager knows the best giving-up threshold to select when it enters a new patch. We used dynamic programming (Houston and McNamara, 1999, Clark and Mangel 2000) to calculate the optimal $\tau^*(t)$ that maximizes the expected future reproductive output for a forager entering a patch at time t. Computational details are presented in Appendix 1 along with dynamic programming equations.

Like Learners, Informed foragers 1) have to decide on a giving-up threshold when they enter a patch, 2) within each patch they rely on time between stochastic resource encounters to estimate the local patch quality, and 3) they update their giving-up threshold only as they shift between patches. As a consequence, the behavioural mechanisms of Learning and Informed forgers differ only in the way they obtain global knowledge.

To learn from experience imposes costs that have two major components in our model:

1. cost of sampling relates to lost foraging opportunities during periods when patch-sampling

frequency of Learners exceeds that of Informed foragers. Learners need to sample several patches to collect the information that Informed foragers have at no cost. As a consequence, Learners spend more time travelling between patches.

2. Cost of imperfect information represents the loss in resource accumulation due to time delays and sampling errors when Learners estimate giving-up thresholds from experience.

Both costs are emergent properties in our model and they partially depend on the inherited learning rule parameters (γ and τ_0).

Fixed foragers and the value of learning

A Fixed forager uses a single giving-up threshold throughout the foraging season, and hence ignores information on temporal changes in average resource conditions. It only responds to decreasing encounter frequencies caused by resource depletion in the current patch. We found the best giving-up threshold τ_F with highest average lifetime performance using dynamic programming (detailed in Appendix 1). The fitness difference between Learning and Fixed foragers represents the benefit of sampling environmental information and learning from patch experiences. Note that for $\gamma = 0$ the learning strategy is identical to a fixed-rule strategy with $\tau_F = \tau_0$.

For each strategy, we simulated the behaviour of 5000 individuals and compared average giving-up thresholds (strategies), patch-leaving frequencies (foraging behaviour), and resource intake (foraging performance, proportional to reproductive output) at different times within the foraging season. Individual foragers do not interact, meaning that resource levels are unaffected by the resource consumption of other foragers. We found learning factors and giving-up thresholds for different combinations of resource gain rates and mortality regimes (parameter ranges as in Table 1).

Results and discussion

Patch allocation strategies and sampling rates

Learners behave differently from both Fixed and Informed foragers. The giving-up threshold of Fixed foragers is constrained to stay constant the whole season. For strategies that utilize various degrees of information, on the other hand, the threshold varies as a response to changing resource levels (Fig. 1a). In an environment where resource conditions become increasingly better throughout the season, there are pronounced differences between the patch-leaving strategies of Learning and Informed foragers. Early in season, Learners sample the environment to adjust to resource conditions and track temporal resource fluctuations. This sampling activity has consequences at

Table 1. Variable and parameter definitions. Values are given for the standard model scenario with the range of parameter for which the model was tested given in parenthesis.

Variable or parameter	Description	Standard value (range)
t	Time since start of foraging season	
T	Time horizon (total number of time-steps)	2500 (1000–5000)
d	Travel time between patches	25 (5–100)
R_0	Initial resource level in patches	5 (0–60)
R_t	Resource level in environment (per patch) at time t	
r_t	Resource level in local patch	
g	Resource gain per time-step and patch	0.02 (−0.025–0.025)
a	Search efficiency of a forager	0.01
p	Patch number	
P_e	Encounter probability	
k	Total number of resources encountered in a patch	
i	Encounter number in patch	
n_i	Time since last resource encounter	
m	Mortality rate	0.000 (0.000–0.005)
γ	Learning factor	0.00–1.00
τ_0	Initial giving-up threshold of Learning foragers	1.0–50.0
τ_p	Giving-up threshold in patch p for Learning foragers	
τ_F	Giving-up threshold of Fixed foragers	
$\tau^*(t)$	Optimal giving-up threshold of Informed foragers at time t	
f	Reproductive value of one resource encounter	
F	Maximum expected reproductive output	
V	Reproductive value for Informed and Fixed foragers	
$I_{n_{i=\tau}}$	Patch-leaving indicator function	0 or 1

two levels. First, Learning foragers need to reside sufficiently long in each patch to estimate local patch quality. Second, they need to visit several patches to
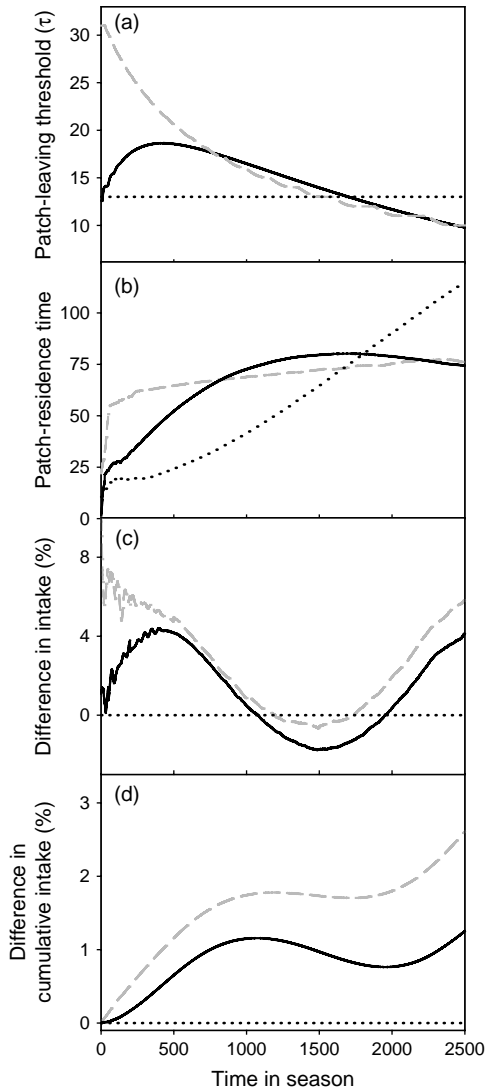

Fig. 1. Patch-leaving strategies, patch-allocation behaviour, and foraging performance as a function of time for a scenario where resource conditions progressively improve. Fixed foragers (black dotted) are restricted to use the same giving-up threshold throughout the season. Learning foragers (black solid) sample the resource environment and update their giving-up threshold based on experiences. Informed foragers (grey hatched) have free information on seasonal changes in resource levels and select the best giving-up threshold upon entering a new patch. (a) average giving-up thresholds τ, (b) average patch-residence times, (c) differences in resource intake rates, and d) cumulative resource gain of Informed and Learning foragers relative to Fixed foragers. ($g = 0.02$, $R_0 = 5$).

estimate the global resource conditions. As Learners harvest both resources and information, time allocated in each patch represents a tradeoff between resource exploitation and information gathering. The genetically determined initial giving-up threshold is therefore relatively low, which ensures that individuals make frequent movements and thereby sample more patches. Under poor environmental conditions, Learning foragers will continue to encounter patches with relatively few resources. Giving-up thresholds then increase and approach that of Informed foragers (Fig. 1a). Later in season giving-up thresholds of Learners will commonly lag somewhat behind that of Informed foragers. This is because Learners need to make experiences before they update their strategy.

Differences in giving-up thresholds are reflected in patch residence times (Fig. 1b). Early in the foraging season, Learners have short patch residence times and change patches more frequently than Informed foragers. After an initial exploration phase, Learners generally reside somewhat longer in each patch. When resource conditions improve during the season, giving-up thresholds decrease and Informed foragers leave patches of increasingly higher quality. As a result, patch residence times of Informed foragers change only slightly during the foraging season.

The value of learning

Since reproductive output is proportional to lifetime resource accumulation in our model, the difference in resource intake between Learning and Fixed foragers represents the value of learning. The relative performance of each strategy changes throughout the season as the Learning and Fixed forager strategies take turns in being closest to the Informed strategy (Fig. 1). The value of each strategy therefore has to be averaged over the entire season, discounting for the probability that the forager will die before the potential foraging benefit is realized. There will be a benefit of learning as long as the value of having an updated resource estimate outweighs the costs of sampling (Fig. 1c–d). Informed foragers experience the highest benefits of adjusting their patch-leaving threshold, whereas Learners reap approximately half the benefit in this particular example (Fig. 1d).

All foragers have to choose a giving-up threshold when they enter a new patch. At any time in season, both the populations of Learning and Informed foragers will span over individuals with different thresholds: Learning foragers because of differences in individual experiences, and Informed foragers because they entered patches and received their optimal giving-up threshold at different times. In contrast, Fixed foragers have a single giving-up threshold, and will be close to the

optimal strategy only for a short time period of the season (Fig. 1a). During this period, Fixed foragers have higher mean intake rates than the other strategies since all individuals in the Fixed forager population follow the optimal strategy (Fig. 1c). Variation among individuals represents a general cost for flexible strategies, and is most pronounced in Learners that acquire information from individual patch quality estimates.

Cost of learning

Learning and Informed foragers have the same uncertainty when they assess the resource level within a patch. Informed foragers, however, have complete information about changes in global resource levels – the property that Learners aim at estimating. Resource intake rates of Learners are therefore constantly below that of Informed foragers (Fig. 1c). This difference represents the cost that Learning foragers pay for not having a priori or complete information. First, Learners pay a time cost of frequent travelling as they sample more patches. This leads to a relatively low intake rate early in the season (Fig. 1c). Later, Learners still have to sample the environment, but now learning costs are more related to imperfect information. Due to the stochastic nature of the resource encounter process, foragers make sampling errors. This introduces uncertainty in estimates of giving-up thresholds and results in suboptimal patch residence times.

It is important to note that differences in strategy or patch allocation behaviour do not translate directly into differences in fitness. Extensive sampling behaviour has limited consequences on intake rates early in season, since resource conditions are relatively poor for the progressively improving environment in this case. Towards the end of the season, Learners get steadily better at estimating the optimal giving-up threshold, but the divergence in intake rates stays relatively constant since resource conditions continuously improve. It will be advantageous to prepare for this late and prosperous period whenever foragers have long life expectancies. This is in contrast to the situation where resource conditions deteriorate during the season. Then, the Learning strategy has to pay costs when resource conditions are at the most profitable, while the benefits of enhanced exploitation only can take place when resource conditions are poor.

Foraging strategies change with life expectancy

The costs and benefits of learning are to some extent separated in time. What can be considered an evolutionarily adaptive patch-leaving strategy therefore depends on survival prospects. When mortality rates increase, early resource harvest becomes more impor-

tant and foragers discount future foraging opportunities. As a consequence, Informed foragers change their strategies towards slightly higher giving-up thresholds (Fig. 2a). For Learning foragers, however, the strategy changes much more. First, the initial learning phase is compressed and patch sampling frequency drops (Fig. 2b). This is achieved by a higher initial giving-up threshold that more quickly approaches the informed strategy (Fig. 3a). Next, adaptive learning strategies have higher learning factors that bias estimates towards recent experiences. This potentially increases the rate at which Learners may adjust their giving-up thresholds (Fig. 3b).

Evolutionarily adaptive learning behaviour depends on the rate of change in environmental conditions (Fig. 3). When resource conditions are relatively stable (gain rates close to zero), a fixed strategy is beneficial with a giving-up threshold similar to that of the informed strategy. Learning factors generally increase with environmental variation, as has been found also in previous model studies (McNamara and Houston 1985, 1987). The effect is, however, more pronounced in high mortality regimes. When life-time expectancy decreases, fixed foraging strategies are advantageous even at moderate seasonal changes in resource levels (Fig. 3b). It is not a shorter life span itself that reduces the value of learning, but rather a shift in the potential costs and benefits of information acquisition (Dukas and Visscher 1994).

Learning never pays in environments where resource levels decrease through the season (Fig. 3b). Whenever patch sampling has to take place during the period of prosperous resource conditions early in season, the cost of exploration exceeds the benefit that can be attained by enhanced exploitation later on. As long as initial resource conditions do not change between foraging seasons, the model predicted a fixed threshold strategy which is tuned to exploiting the rich resource conditions early in life.

Investment in learning depends on future prospects

Life expectancy affects the behavioural tradeoff between resource exploitation and habitat exploration. When mortality increases, Learners invest more in present resource consumption at the expense of information harvesting. As a consequence, sampling costs decrease early in season (Fig. 2c). Less sampling, however, leads to less accurate estimation (Fig. 4) and reduces foraging performance of Learners later in season (Fig. 2c).

Three perspectives can provide a better view of the details and mechanisms that higher mortality incurs. First (motivation): the expected resource intake at any time in the season equals the intake rate achieved by a
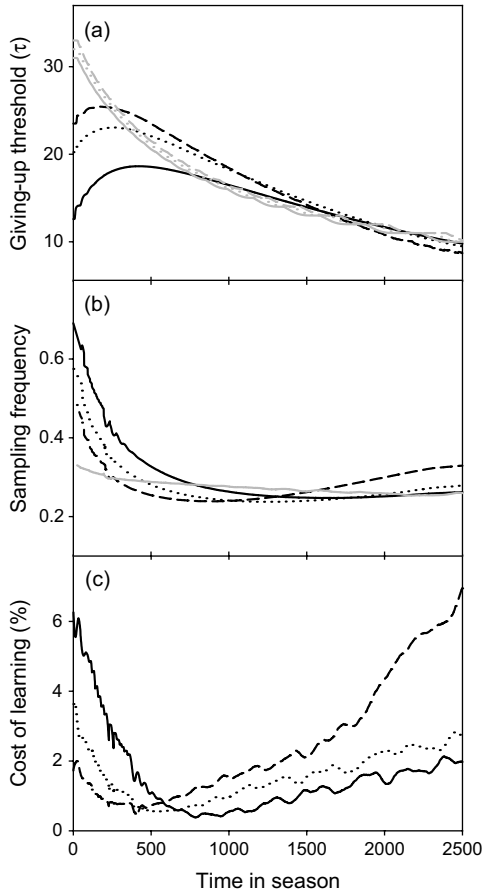
Fig. 2. Patch-leaving strategies, sampling frequencies and learning costs as a function of time in season. Learning (black lines) and Informed foragers (grey lines) are adapted to high (solid, m = 0.000), intermediate (dotted, m = 0.001), and low (hatched, m = 0.002) lifetime expectancies. (a) average giving-up thresholds τ in populations of Learning and Informed foragers. (b) number of foragers that enter a new patch, relative to the maximum number of patch shifts that foragers travelling for d = 25 time steps can potentially make. The relative frequency of patch shifts of Informed foragers is given as a reference (grey, m = 0.000). (c) relative differences in resource intake between Learning and Informed foragers represent the emergent costs of information acquisition. Costs are paid at different times for foragers adapted to various mortality regimes. During early sampling, learning costs are mainly associated with low patch-residence times, whereas imperfect information reduces foraging performance later in season. (Standard parameter values as listed in Table 1).

forager multiplied by the probability of survival up to that time. Consequently, sacrificing present foraging opportunities to improve performance later in season becomes less advantageous as life expectancy decreases. Second (mechanism): Learners attain higher initial giving-up thresholds when mortality rate increases, which reflects how they invest in early foraging. As
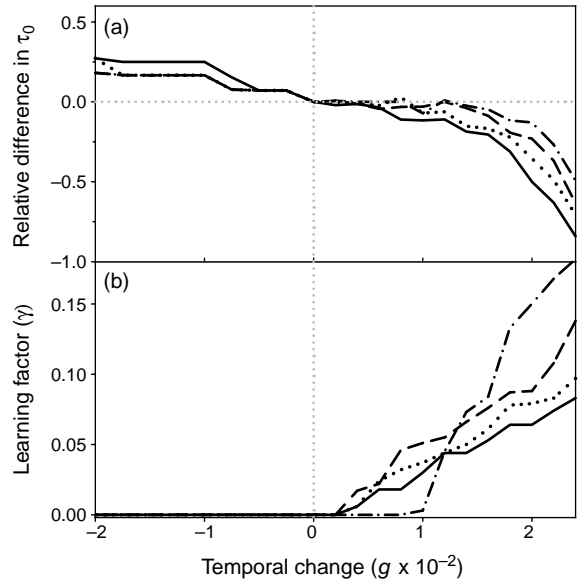

Fig. 3. Inherited traits (τ_0 and γ) of Learning foragers adapted to different mortality regimes (solid: m = 0.000, dotted: m = 0.001, hatched: m = 0.002, hatch-dotted: m = 0.004). The seasonal average resource level equals 30 resources per patch in all environments. Learning rule parameters vary with the rate of temporal change (g) in resource level. (a) the relative differences between the inherited giving-up thresholds τ_0 of Learning foragers and the corresponding initial threshold $\tau^*(1)$ of Informed foragers. (b) Learning factors γ of Learning foragers adapted to environments with different life-time expectancies.

the initial giving-up threshold of Learners approaches that of Informed foragers, the behaviour of the two strategies becomes more similar early in the season (Fig. 4a). Thus, Learners spend more time exploiting patches, which results in lower sampling activity and reduced information updating frequencies. To compensate, learning factors increase and consequently each individual patch experience is given more weight. Third (consequence): estimates of giving-up thresholds have lower precision and vary more among Learners when risk of mortality is high (Fig. 4b). Shorter lifetime expectancy selects for learning strategies that produce estimates with reduced accuracy and lower precision. The advantage is that this results in relatively high resource intake rates early in the season, when extensive sampling typically incurs high costs on foragers adapted to low mortality environments (Fig. 2c).

General discussion

Learners harvest both resources and information in this model, and both activities take place concurrently as information on resource conditions are gained while
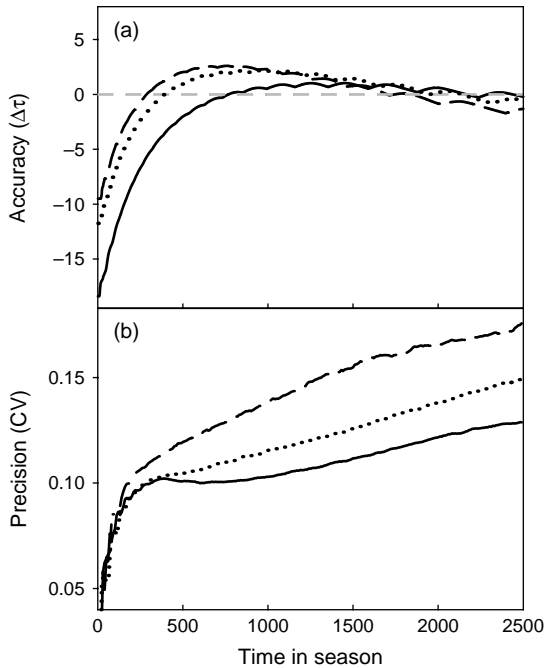
Fig. 4. Precision and accuracy in estimates of giving-up thresholds of Learning foragers adapted to different mortality regimes. Solid lines represent foragers adapted to environments with no mortality (m = 0.000); dotted lines represent intermediate life-time expectancies (m = 0.001); and dashed lines low survival prospects (m = 0.002). (a) deviations in giving-up threshold ($\Delta\tau$) between the Learning (black lines) and Informed foragers (grey dashed line) as a function of time in the foraging season. (b) coefficient of variation (CV) in estimates of giving-up threshold in a population of 10 000 Learning foragers adapted to different mortality regimes.

foraging. The Learning strategy hence reflects a tradeoff between exploration and sampling of different patches and exploitation of resources within each patch.

A period of habitat exploration commonly precedes a more intensive resource exploitation phase. During information harvesting, Learners are primarily motivated by the need to gain experience and canalize learning in right directions. Experimental studies of patch allocation and forager distributions have commonly omitted such early exploratory phases from analysis (but see e.g. Krebs et al. 1978, Shettleworth et al. 1988). Early models in behavioural and evolutionary ecology commonly assumed that gains derived from different strategies should be evaluated in immediate food intake rates (Emlen 1966, MacArthur and Pianka 1966). A general criticism of such models is that they ignore the benefit of acquiring information that may enhance future foraging or reproductive success.

Learning represents an investment that improves future foraging performance. It affects resource harvest directly, as individuals alter behaviour based on foraging experiences, and indirectly, as accuracy and precision of resource estimates influence behavioural decisions. The way that the behaviour of Learners deviates from predictions based on Informed or other types of omniscient foragers (Nonacs 2001), may therefore depend on 1) the period in which behaviour is observed, and 2) characteristics of the forager's natural environment. We demonstrate how survival prospects may alter the tradeoff between exploration and exploitation. Other ecological factors, such as seasonal variation in offspring survival and risk of starvation, may influence the value of information in similar ways. This illustrates how adaptive foraging strategies optimize rather than maximize the quality of resource estimates, and that the optimization criterion is not information precision but individual fitness. An additional aspect not addressed here, is the robustness of a strategy in obtaining basic requirements which becomes increasingly important in unpredictable and variable environments (Mangel 1990, Inglis et al. 2001, Dall and Johnstone 2002, Carmel and Ben-Haim 2005).

In parasitoids, patch-leaving behaviour ranges from that mainly based on innate rules to that which is mostly learned from experience (Vos et al. 1998, Wajnberg et al. 2000, Boivin et al. 2004). Egg-positing females may use one behavioural strategy or adjust their strategy depending on host type. For instance, the generalist parasitoid Cotesia glomerata alters its behaviour based on recent patch experiences when feeding on a highly aggregated host species (Vos et al. 1998). When feeding on a more uniformly distributed host, however, the females used a non-responsive fixed strategy.

The foraging performance of learners depends both on local patch quality estimates and their ability to track temporal changes in average resource conditions. The simple giving-up time rule used in local assessment may arrive at sub-optimal patch leaving decisions in highly stochastic environments (Oaten 1977, Iwasa et al. 1981, Green 1984). Hence, foragers that integrate their experiences of resource encounters with additional sensory information could be provided with better patch quality estimates (Iwasa et al. 1981, Green 1984, Valone 1989, Persons and Uetz 1996, van Alphen et al. 2003, Olsson and Brown 2006). Simple rules of thumb may often work satisfactorily (as Green 1984, illustrated for the giving-up time rule) and require less computational effort than for instance Bayesian updating rules (Gigerenzer and Todd 1999). In addition, foragers are generally better at accurately estimating and discriminating between shorter time periods (Shettleworth 1998, Stephens 2002). Rules of thumb may therefore be more biologically realistic as they offer quick responses to environmental cues (Bernays 1998, Hutchinson and Gigerenzer 2005).

Under natural conditions, learning abilities are commonly biased towards certain experiences (Arak and Enquist 1998, Dukas 2002). Genetic predisposition and prior knowledge are, however, seldom considered in studies of foraging and memory (McNamara et al. 2006). Our results illustrate that ecological factors may influence inherited traits and the way prior expectations are updated based on new information. Instead of incorporating an inherited patch allocation strategy adapted to forage efficiently early in life, Learners were genetically predisposed to learn to behave efficiently. When information acquisition is considered in an ecological context, learned experiences become a function of the behavioural strategy itself. Prior expectations hence function to canalize information acquisition and not only to give the best possible estimate from the start. This emphasizes how animals are more likely to learn from situations that ancestors have been exposed to, simply because they attend to and can interpret relevant information (McNamara et al. 2006).

References

Abrahams, M. V. 1986. Patch choice under perceptual constraints: a cause for departures from an ideal free distribution. – Behav. Ecol. Sociobiol. 19: 409–415.

Arak, A. and Enquist, M. 1993. Hidden preferences and the evolution of signals. – Philos. Trans. R. Soc. Lond. B 340: 207–213.

Arak, A. and Enquist, M. 1998. Neural representation and the evolution of signal form. – In: Dukas, R. (ed.), Cognitive ecology: the evolutionary ecology of information processing and decision making. Univ. of Chicago Press, pp. 21–87.

Bernays, E. A. 1998. The value of being a resource specialist: Behavioral support for a neural hypothesis. – Am. Nat. 151: 451–464.

Bernstein, C. et al. 1988. Individual decisions and the distribution of predators in a patchy environment. – J. Anim. Ecol. 57: 1007–1026.

Boivin, G. et al. 2004. Optimal patch residence time in egg parasitoids: innate versus learned estimate of patch quality. – Oecologia 138: 640–647.

Carmel, Y. and Ben-Haim, Y. 2005. Info-gap robust-satisficing model of foraging behavior: do foragers optimize or satisfice? – Am. Nat. 166: 633–641.

Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. – Theor. Popul. Biol. 9: 129–136.

Clark, C. W. and Mangel, M. 1984. Foraging and flocking strategies: information in an uncertain environment. – Am. Nat. 123: 626–641.

Clark, C. W. and Mangel, M. 1986. The evolutionary advantages of group foraging. – Theor. Popul. Biol. 30: 35–75.

Clark, C. W. and Mangel, M. 2000. Dynamic state variable models in ecology. – Oxford Univ. Press.

Cohen, D. 1993. The equilibrium distribution of optimal search and sampling effort of foraging animals in patchy environments. – Lect. Notes Biomath. 98: 173–191.

Dall, S. R. X. and Johnstone, R. A. 2002. Managing uncertainty: information and insurance under the risk of starvation. – Philos. Trans. R. Soc. Lond. B 357: 1519–1526.

Dall, S. R. X. et al. 2005. Information and its use by animals in evolutionary ecology. – Trends Ecol. Evol. 20: 187–193.

Dukas, R. 1998. Evolutionary ecology of learning. – In: Dukas, R. (ed.), Cognitive ecology: the evolutionary ecology of information processing and decision making. Univ. of Chicago Press, pp. 129–174.

Dukas, R. 2002. Behavioural and ecological consequences of limited attention. – Philos. Trans. R. Soc. Lond. B 357: 1539–1547.

Dukas, R. and Visscher, P. K. 1994. Lifetime learning by foraging honey-bees. – Anim. Behav. 48: 1007–1012.

Emlen, J. M. 1966. Role of time and energy in food preference. – Am. Nat. 100: 611–617.

Fretwell, S. D. and Lucas, H. L. J. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. – Acta Biotheor. 19: 16–36.

Gigerenzer, G. and Todd, P. M. 1999. Fast and frugal heuristics: the adaptive toolbox. – In: Gigerenzer, G. and Todd, P. M. and the ABC research group (eds), Simple heuristics that make us smart. Oxford Univ. Press, pp. 3–34

Gould, J. P. 1974. Risk, stochastic preference, and the value of information. – J. Econ. Theory 8: 64–84.

Green, R. F. 1984. Stopping rules for optimal foragers. – Am. Nat. 123: 30–43.

Hirvonen, H. et al. 1999. Significance of memory properties in prey choice decisions. – Ecol. Model. 115: 177–189.

Houston, A. I. and McNamara, J. M. 1999. Models of adaptive behaviour – an approach based on state. – Cambridge Univ. Press.

Hutchinson, J. M. C. and Gigerenzer, G. 2005. Simple heuristics and rules of thumb: where psychologists and behavioural biologists might meet. – Behav. Process. 69: 97–124.

Inglis, I. R. et al. 2001. An information primacy model of exploratory and foraging behaviour. – Anim. Behav. 62: 543–557.

Iwasa, Y. et al. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. – Am. Nat. 117: 710–723.

Krebs, J. R. and Inman, A. J. 1992. Learning and foraging: Individuals, groups, and populations. – Am. Nat. 140: S63–S84.

Krebs, J. R. et al. 1978. Test of optimal sampling by foraging great tits. – Nature 275: 27–31.

MacArthur, R. H. and Pianka, E. R. 1966. On optimal use of a patchy environment. – Am. Nat. 100: 603–609.

Mangel, M. 1990. Dynamic information in uncertain and changing worlds. – J. Theor. Biol. 146: 317–332.

Mangel, M. and Clark, C. W. 1983. Uncertainty, search, and information in fisheries. – J. Conserv. Int. Explor. Mer 41: 93–103.

McNamara, J. M. 1982. Optimal patch use in a stochastic environment. – Theor. Popul. Biol. 21: 269–288.

McNamara, J. M. and Houston, A. I. 1985. Optimal foraging and learning. – J. Theor. Biol. 117: 231–249.

McNamara, J. M. and Houston, A. I. 1987. Memory and the efficient use of information. – J Theor. Biol. 125: 385–395.

McNamara, J. M. et al. 2006. Bayes' theorem and its applications in animal behaviour. – Oikos 112: 243–251.

Nonacs, P. 2001. State dependent behavior and the marginal value theorem. – Behav. Ecol. 12: 71–83.

Oaten, A. 1977. Optimal foraging in patches: A case for stochasticity. – Theor. Popul. Biol. 12: 263–285.

Olsson, O. and Holmgren, N. M. A. 1998. The survival-rate-maximizing policy for Bayesian foragers: wait for good news. – Behav. Ecol. 9: 345–353.

Olsson, O. and Brown, J. S. 2006. The foraging benefits of information and the penalty of ignorance. – Oikos 112: 260–273.

Papaj, D. R. 1993. Automatic behavior and the evolution of instinct: lesson from learning in parasitoids. – In: Papaj, D. R. and Lewis, A. C. (eds), Insect learning: ecological and evolutionary perspectives. Chapman & Hall, pp. 243–272.

Persons, M. H. and Uetz, G. W. 1996. The influence of sensory information on patch residence time in wolf spiders (*Araneae: Lycosidae*). – Anim. Behav. 51: 1285–1293.

Rodriguez-Gironés, M. A. and Vásquez, R. A. 1997. Density-dependent patch exploitation and acquisition of environmental information. – Theor. Popul. Biol. 52: 32–42.

Shettleworth, S. J. 1998. Cognition, evolution and behavior. – Oxford Univ. Press.

Shettleworth, S. J. et al. 1988. Tracking a fluctuating environment: a study of sampling. – Anim. Behav. 36: 87–105.

Stephens, D. W. 1987. On economically tracking a variable environment. – Theor. Popul. Biol. 32: 15–25.

Stephens, D. W. 1993. Learning and behavioral ecology: Incomplete information and environmental predictability. – In: Papaj, D. R. and Lewis, A. C. (eds), Insect learning: ecology and evolutionary perspectives. Chapman & Hall, pp. 195–218.

Stephens, D. W. 2002. Discrimination, discounting and impulsivity: a role for an informational constraint. – Philos. Trans. R. Soc. Lond. B 357: 1527–1537.

Valone, T. J. 1989. Group foraging, public information, and patch estimation. – Oikos 56: 357–363.

van Alphen, J. J. M. et al. 2003. Information acquisition and time allocation in insect parasitoids. – Trends Ecol. Evol. 18: 81–87.

Vos, M. et al. 1998. Patch exploitation by the parasitoids *Cotesia rubecula* and *Cotesia glomerata* in multi-patch environments with different host distributions. – J. Anim. Ecol. 67: 774–783.

Wajnberg, E. et al. 2000. Patch leaving decision rules and the marginal value theorem: an experimental analysis and a simulation model. – Behav. Ecol. 11: 577–586.

Appendix 1. Informed and Fixed foraging strategies

A forager's contribution to the next generation depends on resource intake rate and survival prospects at different times in a foraging season. Foragers continuously reproduce proportionally to their accumulated resources, and we assume that the value of a resource in terms of reproductive output is f. Foragers have two behavioural options: they may either stay in a patch and search for resources; or leave and travel to a new patch. Informed and Fixed foragers will leave a patch when time since last resource encounter n_i exceeds a giving-up threshold τ in the same way as Learners. Strategies only differ in the way they obtain their giving-up thresholds.

Informed foragers have complete global information at no cost and know the best giving-up threshold to use when they enter a new patch. Foragers update this information only as they shift between patches, in much the same way as Learning foragers update their estimates of τ_p upon leaving a patch. We seek the giving-up threshold that maximizes expected lifetime reproductive output for a forager that enterers a patch at a time t in a foraging season of length T:

$$F(t) = \max_{\tau} E\{\text{accumulated reproduction from t to T}\}$$

The expected reproductive output is maximized over all possible giving-up times τ that a forager may select when it enters a patch at time t. Foragers are restricted to use the same threshold during the entire patch visit, but may change giving-up threshold every time it enters a new foraging patch.

The value of staying in the patch depends on the expected fitness consequences of 1) encountering a resource in the next time step, and 2) the value of resource encounters from time $t+1$ until the end of season. The probability P_e that a forager will encounter a resource in the next time step will depend on the global resource level R_t and the number of resources consumed k so far in the patch ($r_t = R_t - k$). For a given time t in the season, the value of utilizing strategy τ, V_τ, is therefore given by:

$$V_\tau(t, k, n_i) = e^{-md}F(t + d)I_{n_i = \tau}$$
$$+ [P_e(r_t)\{f + e^{-m}V_\tau(t + 1, k + 1, 1)\}$$
$$+ (1 - P_e(r_t))e^{-m}V_\tau(t + 1, k, n_i + 1)]$$
$$\times (1 - I_{n_i = \tau})$$

For a given strategy τ, the indicator factor $I_{n_i = \tau}$ equals 1 if $n_i \geq \tau$ and is 0 otherwise. The first part represents the value of leaving the patch. The probability that the forager survives to enter a patch after d time steps of travelling is e^{-md}, where m is mortality rate. The Informed forager selects the optimal giving-up threshold when it enters a new patch, hence the expected future reproductive value from the time it enters the new patch and onwards is F(t+d). The second part of the equation gives the value of staying, which is the sum of 1) the probability that the forager encounters a resource when it searches a patch multiplied with the expected future reproductive value given that a new resource is consumed, and 2) the corresponding value if no resources are encountered in time-step t.

At the time horizon T the reproductive output is F(T) = 0. As long as $t + d > T$ a forager will not reach a new patch before the end of season, and the best option is to stay in the patch. Earlier in season, there is an optimal giving-up threshold $\tau^*(t)$ that maximizes future reproductive value for a forager that enters a patch at a given time-step t:

$$F(t) = \max_\tau \{V_{\tau_F}(t, 0, 1)\}$$

Starting at the time horizon T and working backwards, we may calculate the optimal giving-up threshold $\tau^*(t)$ for all time-steps in the season (Clark and Mangel 2000).

Fixed foragers use a single, genetically determined giving-up threshold during the whole foraging season. At any time t in the season the expected reproductive output is:

$$V_{\tau_F}(t, k, n_i) = e^{-md}V_{\tau_F}(t + d, 0, 1)I_{n_i = \tau_F}$$
$$+ [P_e(r_t)\{f + e^{-m}V_{\tau_F}(t + 1, k + 1, 1)\}$$
$$+ (1 - P_e(r_t))e^{-m}V_{\tau_F}(t + 1, k, n_i + 1)]$$
$$\times (1 - I_{n_i = \tau_F})$$

As for Informed forages, the first part gives the value of leaving a patch, and the second the value of staying. Note that the value of leaving is conditional on a fixed giving-up threshold, as opposed to Informed forgers that select the optimal giving-up threshold every time they enter a new foraging patch. We search for the fixed τ_F that had the best average performance and that maximized expected lifetime reproductive output. Starting from the time horizon T, where future reproductive value is zero, we can calculate the value of using different strategies at all times t in a season. We can hence find the τ_F that maximizes lifetime reproductive output over a season, that is: $\max_{\tau_F}\{V_{\tau_F}(0, 0, 1)\}$.