

Foraging ecology and learning

Adaptive behavioural strategies and the value of information

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Summary

All animals face the challenge of acquiring resources for growth, survival, and reproduction. In environments that vary in time and space, foragers need to make apparently complex foraging decisions on which prey to select, where to forage, and for how long. Animals gain information from sampling and exploring the environment, and in this ecological context information becomes valuable. Learning provides a way for foragers to track changes in environmental conditions, but it involves costs that may often offset this advantage. Animals pay for information by spending energy and time, forgoing opportunities to gain resources elsewhere. The value of acquiring information hence depends on the benefits an individual obtains from using that information and the costs of collecting it.

Early foraging models assumed that individuals had full information on resource levels and distribution patterns. Theoretical models predicted how individual foragers should allocate their time among resource patches, or how competing foragers should distribute to exploit the resource habitat most efficiently. These models emphasized the ultimate causes of behavior and did not consider the proximate mechanisms that foragers used to obtain information and to select the best behavioural option.

Asking the same basic questions, my thesis explores how limited information may affect distribution patterns and the evolution of foraging strategies. The thesis includes five models on how animals may allocate their foraging effort in time and space in response to experiences of local resource conditions, and in response to predators or competitors.

The presence of predators often causes prey to alter their behaviour. Confronted with several predator types such behavioural adjustments may cascade through several trophic levels. Prey susceptibility to one predator type (fish) may therefore depend on the abundance of another predator (zooplankton), as zooplankton prey manage their exposure to risk by moving vertically in the water column. This illustrates how the

inclusion of flexible behavioural responses alters predictions from classical population level models.

Behavioural decisions and flexible responses may also be important when considering dynamics of foraging groups. Social foragers may benefit from cooperative prey search or predator defence, but as groups increase in size resource competition intensifies. Foragers therefore often benefit from being in groups of intermediate size. Mobile individuals that sample the environment and collect information may aggregate in groups of preferred size. As the number of selective ‘learners’ increases in a population, groups become more similar and a simple sedentary ‘stayer’ strategy may prosper. The benefit of being selective hence depends on what the other foragers are doing, and such frequency dependence may facilitate coexistence between foraging strategies that differ in mobility and the way they sample information.

In natural systems, decision making incurs conflicting demands on the design of learning and memory systems. Under stable environmental conditions, information stored in inherited traits may suffice, whereas animals foraging in temporally changing environments often need to continuously collect information and learn from experience. The value of learning is tightly linked to both the temporal and spatial variability of the resource environment. When foragers are able to obtain accurate local information, they should rely on recent experiences and quickly adjust to temporal change. Short time memories are, however, susceptible to spatial variation as learners rely on some persistency in the information gained from different patch samples in order to track changes in resource conditions.

The trade-off between accuracy in estimates and ability to respond to temporal change varies also with ecological factors such as rate of predation. Learners generally take the costs of exploration early in life to enhance performance later on. When life time expectancy decreases, foragers should become less willing to invest in information acquisition. This thesis illustrates how low sampling activity enhances

resource harvest early in season, at the cost of lower precision and accuracy of environmental estimates as time progresses.

Changes in resource availability influence both the quality of information that a forager may obtain and the utility of this knowledge. Substituting assumptions of ideal omniscient individuals with more realistic and *less critical* assumptions of limited information and perceptual constraints yields different behavioural adaptations, which scale up to distribution patterns. This thesis illustrates how the action of individuals may themselves alter the quality of information, persistence of signals, and the value of exploring the habitat. As sampling and exploration alter resource and forager distributions, this affects the performance of learners, but may also alter fitness landscapes for other foraging strategies that interact within the same habitat.

Through the formulation of realistic behavioural strategies, it is possible to interpret *how* environmental and ecological factors affect competition between individuals and life-history trade-offs. The thesis provides a modelling framework in which to interpret the effects of ecological factors on the evolutionary process of phenotypic diversification.

List of papers

Paper 1

Fiksen, Ø, Eliassen, S & Titelman, J. (2005) Multiple predators in the pelagic: modelling behavioural cascades. – *Journal of Animal Ecology* **74**: 423-429.

Paper 2

Eliassen, S, Jørgensen, C & Giske, J. (2006) Co-existence of learners and stayers maintains the advantage of social foraging. – *Evolutionary Ecology Research* **8**: 1311-1324

Paper 3

Eliassen, S, Jørgensen, C & Giske, J. Exploration or exploitation: life expectancy changes the value of learning in foraging strategies. – *Manuscript conditionally accepted in Oikos*

Paper 4

Eliassen, S, Jørgensen, C & Giske, J. When to learn: the ecological basis for learning in a foraging context. - *Manuscript*

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The evolutionary ecology of foraging

A basic premise of Charles Darwin's theory of evolution by natural selection (Darwin, 1859) is that high production of offspring will inevitably lead to a struggle for existence. Darwin came to this realization after reading Thomas Malthus' pamphlet (Malthus, 1798) on the causes of human poverty. Hence, from the very beginning, foraging ecology has been a central theme in evolutionary biology.

Modern foraging ecology was founded with two papers printed back-to-back in a 1966 issue of the American Naturalist (Emlen, 1966; MacArthur & Pianka, 1966). Although the paper by MacArthur & Pianka has been most influential, Emlen stated what has been called the evolutionary premise of Optimal Foraging Theory (Emlen, 1966; p. 611):

"Let us assume that natural selection will favor the development (by whatever means — innate or learned) of feeding preferences that will, by their direction and intensity, and within the physical and nervous limitations of a species, maximize the net caloric intake per individual of that species per unit time."

Within this tradition, theoretical ecologists have studied how animals should allocate their feeding activity in space and time to maximize energy harvest rates (Schoener, 1987). Models of patch time allocation show a historical development from optimality models assuming rational and fully informed foragers towards more realistic assumptions considering how foragers may act under limited information. At the omniscient end is the Marginal Value Theorem (Charnov, 1976), which shows analytically and graphically how an organism should allocate its time between different resource patches. Of equal significance is the theoretical habitat selection models studied by Fretwell & Lucas (1970) that makes predictions about equilibrium spatial distribution of competing foragers (Ideal Free Distribution).

This thesis goes back to the crossroad between the Marginal Value Theorem and the Ideal Free Distribution, and studies how individual time budgets and population level patterns may be integrated within the same model framework. Even more important for the thesis is Emlen's neglected assumption, that evolution would favour behavioural *mechanisms* that would allow organisms to feed efficiently. Emlen (1966) indicated that optimal foraging behaviour must somehow be linked to sensory ecology ("*by whatever means — innate or learned*"). Forty years later, our understanding of how these means influence the organism's behaviour is still incomplete. Does it matter whether they are innate or learned, and what determines the way natural selection shapes decision rules and behavioural algorithms in different environments?

The gap between the Marginal Value Theorem and Ideal Free Distribution

Most environments are spatially structured with some part of the habitat containing more resources than others. A common model simplification is to assume that resources occur in discrete patches. This is a reasonable assumption in some natural settings: For insects feeding on nectar, each flower represents a distinct food patch, whereas for bison grazing on large meadows patches are not discrete units. Animals may, however, define their own patches by partitioning continuous environments in bins according to their productivity (Arditi & Dacorogna, 1988).

When searching for resources, foragers continuously decide whether to stay in the current patch or leave. A forager staying too long forgoes the chance to find a better resource location somewhere else, and an individual leaving too soon spends a lot of time travelling between patches (Figure 1).

The classical patch allocation model of Charnov (1976) predicts that a forager should leave a resource patch when the intake rate drops to the average rate for the habitat. The Marginal Value Theorem (MVT) predicts that a forager should spend more time on high quality patches, and that animals should remain longer on each patch when

travel time between patches increases (Charnov, 1976). In spatially heterogeneous environments, patches of different quality should therefore be reduced to the same resource level before leaving. These predictions have been qualitatively verified in a number of natural systems, but in most empirical studies the quantitative observations differ from predictions (reviewed in Nonacs, 2001). A consideration of the various assumptions of this model may provide good reasons for such deviations.



Figure 1: A female parasitoid wasp (*Lysiphlebus testaceipes*) searches for her preferred host, the aphid *Aphis gossypii*, in which to lay her eggs. Aphid larvae aggregate in colonies and from discrete resource patches distributed on different plants. The parasitoid has a large number of eggs to lay during her short life-time and consequently she needs to allocate her time between different aphid colonies

in an efficient way. The aphid population has a huge growth potential, hence resource quality may change rapidly within the habitat. How should a female parasitoid know what is a good patch, and how long should she stay before moving to another aphid colony? (Photo by Jean-Claude Malausa; printed with permission).

One of the most important assumptions of the Marginal Value Theorem is that animals are omniscient: they have complete and accurate information on the quality of all patches in the habitat and the time needed to reach them (Stephens & Krebs, 1986). Another key assumption is that prey capture is so frequent that it can be described as a continuous, deterministic process. In nature, however, a forager often has to cope with highly stochastic resource encounters, and typically needs to assess patch quality from experience (Oaten, 1977; Iwasa *et al.*, 1981; McNamara, 1982; Green, 1984; Olsson & Holmgren, 1998). Furthermore, the MVT model focuses on

optimal decisions of individual foragers and does not consider competition among foragers. Under natural conditions, competitors often affect foraging behaviour (Yamamura & Tsuji, 1987), especially if there is interference among individuals on a patch.

Another group of models descending from Fretwell & Lucas (1970) seminal Ideal Free Distribution (IFD) model has focused on distribution of competing foragers in spatially heterogeneous habitats (Rosenzweig, 1981; Kacelnik *et al.*, 1992; Tregenza, 1995; Giraldeau & Caraco, 2000). The classical IFD model assumes that equal competitors distribute freely among resource patches such that all foragers obtain the same intake rate. The intake rate of individual foragers decreases with increasing consumer densities; hence at equilibrium the number of foragers in a patch should exactly match the resource conditions at that location. Again, foragers are assumed to be omniscient, having full knowledge of the distribution of resources within the habitat, and relocate without time loss or metabolic costs.

Later studies have relaxed these assumptions and considered the distribution of individuals under limited information (e.g. Abrahams, 1986; Ranta *et al.*, 1999; Collins *et al.*, 2002; Hancock & Milner-Gulland, 2006). Such models often assume that foragers possess environmental information with some uncertainty or that they have complete local, but reduced global knowledge. The cost of information is therefore not an integrated part of the foraging strategy nor dependent on the environmental characteristics. Bernstein *et al.* (1988) considered the distribution of foragers utilizing a simple learning rule (see also descendants of this model: Bernstein *et al.*, 1991; Beauchamp *et al.*, 1997; Ward *et al.*, 2000). Here, foragers are assumed to possess full information of local patch quality, but need to integrate this information to estimate the general resource quality in the habitat. The actual learning strategies are, however, fixed. Hence, there is no way to adjust learning rate or memory properties to environmental conditions.

Generally, both theoretical and empirical studies assume that foragers are able to respond to temporal and spatial heterogeneities, but such flexibility is usually

associated with some costs (Dall *et al.*, 2004). Under what circumstances will inherited unconditional strategies be more profitable than strategies relying on information acquisition? Few studies have considered how animals form their expectation of resource distributions (or Bayesian priors; McNamara *et al.* 2006), whether they update these expectations and in case how they do so. There is also a need to understand how individuals collect foraging information and the frequency by which they update their environmental estimates (Giraldeau, 1997).

This thesis will address different, but interlinked, questions relating to distribution and time allocation of foragers in heterogeneous and changing resource habitats. I will switch between different focuses; addressing the effect of limited knowledge and information acquisition (**Paper 2**, **Paper 3**, **Paper 4 & Box 1**), the risk of predation on foraging behaviour (**Paper 1**, **Paper 3 & Box 1**), and density- and frequency dependent effects on the distribution of foragers (**Paper 2 & Box 1**).

The specific aims of my thesis are to:

- 1) investigate how information acquisition may alter foraging strategies, when information needs to be actively sampled and processed,
- 2) study how costs and benefits of learning change in different environments and how the value of information affects foraging strategies,
- 3) study how individual behavioural decisions scale up to population level patterns, in particular to predation rates and group-size distributions, and
- 4) explore the potential for foragers within the same population to utilize different information-harvesting strategies and study how such coexistence depends on life history trade-offs, predation risk, or other ecological factors.

In **Paper 1** and **Paper 2**, I focus on population level patterns emerging from individual behavioural responses to the physical and biotic environment. In **Paper 3** and **Paper 4** the focus is on individual behavioural strategies considering adaptive patch time allocation in variable resource environments. The synthesis will conclude

with a model approach that links several of the perspectives addressed in these papers (see **Box 1**). With this model, I explore strategies of learning and information harvesting in a frequency-dependent context, and include a feedback between ecological and evolutionary processes.

From individual behaviour to properties of the population

Interactions among species, including predation and competition, have traditionally been the domain of population and community ecology. In community ecology, mathematical theory is often used to formulate generalized models that describe inherent complexity of systems in a compact way (e.g. Yodzis, 1989). In the tradition of Lotka (1925) and Volterra (1926), populations are often represented as homogenous entities, ignoring the diversity and variation among individuals. Adaptive behavioural decisions may affect the amount of type of prey consumed, the level of interference among competitors, and the spatial distribution of foragers within a habitat. These are key elements in determining population dynamics, hence community models that incorporate behavioural detail produce different predictions both on system stability and on distribution of foragers and resources (Abrams, 1984; Ives & Dobson, 1987; Fryxell & Lundberg, 1997; Luttbeg & Schmitz, 2000). Scaling up from individual behaviour to population dynamics, however, remains a significant, but elusive objective of behavioural ecology (Fryxell & Lundberg, 1997; Giraldeau & Caraco, 2000).

Functional responses and spatial distributions of predators may determine the magnitude and stability of predator-prey interactions (Real, 1994). The behaviour of predators is, however, rarely considered in models of predator-prey interactions (Lima, 2002), nor is it common to include prey responses to multiple predators. In **Paper 1** we illustrate how prey susceptibility to one predator type (fish) may depend on the abundance of another predator (zooplankton). In the model, zooplankton prey manage their exposure to risk from functionally different types of predators by adopting dynamic habitat selection strategies. By moving vertically in the water column, they are able to trade predation risk against feeding opportunities and growth

potentials. The inclusion of flexible behavioural responses alters predictions from classical population level models, and illustrates how behavioural aspects are essential for key variables in population dynamics such as predation rates (**Paper 1 & Paper 2**).

In much the same way, social organization relies on individual movement, aggregation and dispersal (**Paper 2**). Forager distributions are influenced by the abundance of resources, but the action of foragers may also shape the environment to which they respond (Dieckmann & Ferrière, 2004; Nowak & Sigmund, 2004). The presence of others may enhance foraging performance due to vigilance or cooperation in prey search, but as group size increases so does resource competition. Among social foragers, fitness is therefore often a peaked function of group size (Giraldeau & Caraco, 2000). Individual foragers may benefit from locating groups of optimal size, but the performance of such a selective strategy will depend on its prevalence within the population. As illustrated in **Paper 2**, considering such frequency-dependent performance is crucial for the understanding of dynamic group size distributions among social foragers.

Idealized optimal behaviour or rules of thumb?

Predictions from models such as the Marginal Value Theorem or the Ideal Free Distribution tell us what animals should do in order to behave optimally (ultimate predictions), but they do not provide the behavioural strategy (proximate mechanism) an animal may use to arrive at this solution. The decision to stay in a patch or leave it requires knowledge of i) the current intake rate on the patch (local resource information) and ii) the maximal average rate of resource intake in the habitat (global resource information).

To a forager, resources are often discrete items turning up by chance. In these situations the underlying rate of resource intake is not directly observable. Foragers may then 1) rely on information from different sensory cues (e.g. van Alphen *et al.*, 2003), 2) make patch leaving decisions based on assessment of resource supply and

search time in a patch (Oaten, 1977; Iwasa *et al.*, 1981; McNamara, 1982; Green, 1984; Valone & Brown, 1989; Olsson & Holmgren, 1998), 3) observe the actions of other foragers in the habitat (Valone, 1989; Danchin *et al.*, 2004; Dall *et al.*, 2005), or 4) alternatively, make no assessment of the patch quality and allocate a fixed amount of time in all patches.

Under stable resource conditions, a forager may arrive at optimal patch residence times without being omniscient (Fig. 2). As long as proximate mechanisms are given sufficient time to adapt to the prevailing conditions, foragers may act as if they knew the resource level and distribution.

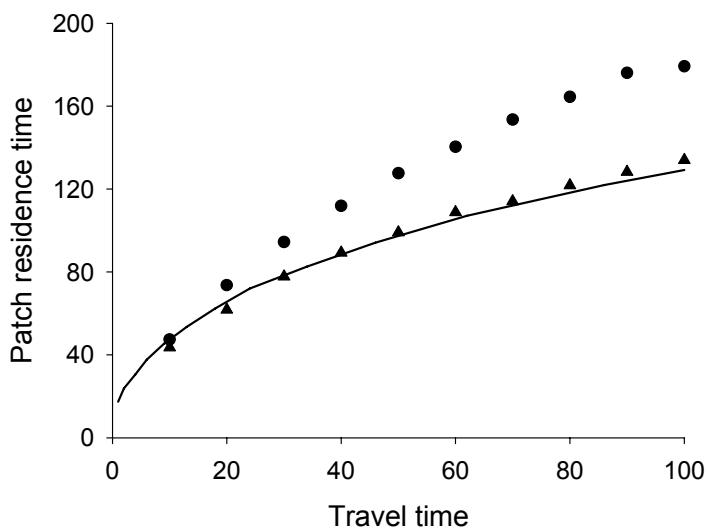


Figure 2: The Marginal Value Theorem (MVT) predicts that time spent on a patch should increase with travel time between patches (solid line). In a stable environment, foragers may arrive at a similar patch time allocation using a proximate patch-leaving strategy based on a simple giving-up time rule (symbols). The patch leaving thresholds are adapted to the prevailing environmental conditions using a genetic algorithm (details on decision rules and genetic algorithms in Appendix 1).

Relaxing the MVT assumption of no predation risk and infinite time horizons affects average residence times: foragers tend to reside longer in patches when mortality rate increases and the value of future foraging prospects decreases (see Wajnberg *et al.*, 2006). Each symbol indicates averages of 5 simulations with mortality rate equal to 0.01 (circle) and 0.0001 (triangle) per time step. All patches initially contain 20 resources, but the local resource level is reduced as the forager consumes resources.

A combination of empirical and theoretical studies may reveal how natural selection acts on behavioural mechanisms to control time allocation and habitat choice under different environmental conditions. For instance in parasitoids, the spatial distribution

of hosts may determine whether a host encounter will motivate a female for further search on a patch or increase her tendency to leave (van Alphen *et al.*, 2003). Whenever hosts are relatively uniformly distributed among patches, a host encounter should increase a female's tendency to leave the patch (Iwasa *et al.*, 1981), since it gives the forager information that the patch has been depleted. Whenever resources are highly aggregated, however, finding a resource suggests that this may be a profitable patch, motivating the female to stay (Iwasa *et al.*, 1981; van Alphen *et al.*, 2003). These mechanisms fit empirical results on different parasitoid wasps, illustrating how the effect of the same local information (a host encounter) may result in different behavioural outcomes (Driessen & Bernstein, 1999; van Alphen *et al.*, 2003; Wajnberg *et al.*, 2003).

Behaviour results from complex interactions between genetic information and the unique experiences of the individual that explores its environment (Arak & Enquist, 1998). Understanding complex behavioural traits at the genetic level may rarely be feasible; hence a focus on behavioural mechanisms and decision rules may offer a link between the underlying genetic traits and observed behaviours. In order to understand the principles that underlie these algorithms (Hutchinson & Gigerenzer, 2005), we need to incorporate the constraints that affect perception and manipulation of environmental information (Todd & Kacelnik, 1993; Bizo & White, 1997; Shettleworth, 1998; Hills & Adler, 2002; Stephens, 2002).

When resource environments change during a season or from one year to the next, foragers may often benefit from using information acquired during their lifetime (Shettleworth *et al.*, 1988; Cuthill *et al.*, 1990; Cuthill *et al.*, 1994; Wildhaber *et al.*, 1994; Fortin, 2003; Schilman & Roces, 2003; Outreman *et al.*, 2005; Tentelier *et al.*, 2006; Thiel & Hoffmeister, 2006). To track changes in resource distributions over time, foragers need some type of memory, time perception and learning ability. This is the focus of **Paper 3** and **Paper 4**, but also important aspect of the dynamic interaction among foraging strategies in **Paper 2** and **Box 1**.

Information in an ecological context

When an animal moves within its habitat, encounters a prey item, or searches for mates, it has no explicit information on the fitness consequences of different actions. However, it senses its internal states and its external environment, and through different types of sensory cues it can produce a wealth of information about correlation between events, about cause and effect and about the consequences of actions. Such cues are undoubtedly major sources of information about physical and biotic elements of the environment.

Learning from interaction is fundamental to nearly all theories of information use and intelligence (Sutton & Barto, 1998). In behavioural ecology, information acquisition, manipulation, and use are seldom considered explicitly, and as argued by (Dall, 2005) “*information is an integrative concept in biology that has yet to be integrated coherently*”.

The quality of information a forager obtains depends on both environmental characteristics and how it samples the habitat. Treating information in an ecological context alters predictions about individual behaviour and forager distributions (**Paper 2, Paper 3, Paper 4 & Box 1**), and emphasises that:

- 1) information needs to be actively sampled from the environment, which imposes time and energy costs (**Paper 2, 3, 4 & Box 1**)
- 2) information has no value unless it leads to behavioural changes that enhances individual fitness (**Paper 3 & Paper 4**),
- 3) costs and benefits of learning change with environmental characteristics (**Paper 3 & Paper 4**) and the frequency of alternative foraging strategies in the population (**Paper 2 & Box 1**),
- 4) the action of individuals themselves may alter the quality of information (**Paper 3**), persistence of signals (**Paper 2**) and the value of exploring the habitat (**Papers 2, 3, 4 & Box 1**), and

- 5) sampling and exploration alter resource and forager distributions. This feeds back on the performance of learners, but may also alter fitness landscapes for other foraging strategies that interact within the same habitat (**Paper 2 & Box 1**).

Learning: uncertainty reduction and utility

To forage efficiently in a changing environment, animals often need to acquire and integrate different sources of information. A fundamental question is therefore how new experiences are combined with information from the more distant past (McNamara & Houston, 1987; Krebs & Inman, 1992; Stephens, 1993). In rapidly changing environments, high rates of information updating are profitable since slowly updating estimates impose time lags (McNamara & Houston, 1985, 1987; Hirvonen *et al.*, 1999). As variation between patches increases, more samples are required for a reliable estimate, selecting for less weight given to each new sample. This introduces a behavioural trade-off between decreased information value and reliability of single samples versus rate of updating estimates concerning changing resource levels (**Paper 4**).

Foraging models have commonly considered how a forager may efficiently update its information on environmental characteristics (McNamara & Houston, 1985, 1987; Hirvonen *et al.*, 1999). However, the value of information ought to be understood in the context of individual fitness, not simply as reduction in environmental uncertainty (Dall *et al.*, 2005). The value of learning depends on the potential to alter behaviour in such a way that it enhances fitness (Gould, 1974; Stephens, 1989). A central question is therefore under what environmental conditions learning is expected to be advantageous?

Learners may adjust their behavioural responses to different environmental conditions, but this flexibility comes at the cost of being prone to make errors. The trade-off between having options to choose from and keeping track of these various sources of information could be understood as a generalist-specialist dilemma (Dall

& Cuthill, 1997). Temporal and spatial resource distributions influence whether foragers adopt a fixed or flexible strategy (**Paper 3 & Paper 4**), and the type of foraging strategy may also affect resource dynamics and facilitate coexistence between different forager types (Wilson *et al.*, 1999; Wilson & Richards, 2000)

Mobile strategies alter distribution patterns and affect resource intake rates of other foragers in the habitat. This may facilitate coexistence between foraging strategies that differ in the way they utilize environmental information. Patterns of coexistence between mobile “learners” and sedentary “stayers” in **Paper 2** were promoted by such frequency- and density-dependent performance. In **Box 1** similar behavioural strategies evolved from first principles as a result of emergent trade offs in behaviour and life-history. When adaptive processes at the individual level affect forager and resource distributions, it is possible to explore ways in which ecological factors interact with evolutionary processes.

Learners need to allocate their time between exploration and exploitation of the habitat. To obtain resources, they need to prefer actions found to be rewarding in the past. To discover such opportunities, learners need to explore new areas or test options they have not selected before. Neither exploration nor exploitation can be pursued exclusively without failing the task (Sutton & Barto, 1998), hence learners need to balance immediate and future resource harvest.

Paper 3 illustrates how ecological factors, such as risk of predation, may alter this behavioural trade-off. In this model, increased mortality risk reduces sampling efforts of adaptive foraging strategies, which again lead to higher intake rates early in season. This reduced exploration and information acquisition, however, lower precision and accuracy in environmental estimates later on. This illustrates how a forager may trade quality of the environmental estimate against other demands, and exemplifies the utility aspect of information in an ecological context.

Individual-based models

System level patterns, such as group size distributions (**Paper 2**) and patterns of coexistence between foraging strategies (**Paper 2** and **Box 1**), emerge from processes at the individual level. Linking interactions between foragers with adaptive behavioural strategies requires modelling tools that incorporate frequency- and density-dependent processes. Methodologies that are suited for these types of questions include individual-based models (Grimm & Railsback, 2005), in particular methodologies where population dynamics and evolution may take place concurrently (Huse *et al.*, 1999; Strand *et al.*, 2002; Giske *et al.*, 2003), and adaptive dynamics models (Dieckmann & Law, 1996; Meszéna *et al.*, 2001), where frequency dependence is more rigidly formalized. Individual-based models may be especially appropriate since individual characteristics, including behavioural and sensory mechanisms, can be incorporated and spatial and temporal dynamics can be modelled explicitly. Exploring such dynamic models may facilitate the study of how evolution of adaptive individual behaviors explains observable ecological patterns.

The flexibility of incorporating a variety of biologically realistic features, however, comes at a cost of generality in the result and complexity of the model analysis. Each simulation relates to a specific set of parameter values, and exhaustive search of every combination of values is usually not feasible. A number of interesting features may still emerge from using such modelling approaches, including cooperative strategies (Burtsev & Turchin, 2006), and divergence and speciation along environmental gradients (Doebeli & Dieckmann, 2003).

BOX 1: Coexistence of learners and fixed strategy foragers: linking ecological and evolutionary processes

In this section, I present a model on information harvesting and patch allocation behaviour in a population of interacting foragers (I refer to this model as Box 1 in the rest of the thesis). In the model I combine several perspectives from the approaches in **Papers 1-4** and integrate ecological forcing and evolutionary process within the same framework. The model is an individual-based simulation model, addressing the potential of coexistence between foraging strategies investing differently in information harvesting. In the model, competition leads to frequency-dependent selection facilitating exploration of new foraging strategies that differ in the way they respond to temporal change. Individual foragers use resource encounter frequencies to assess patch quality. They may also use patch experiences to track changes in average resource levels through a season. Each individual has three genetically inherited traits that determine their foraging strategy: The *learning factor* γ gives the rate of substituting old information with new experiences, and the *initial giving-up threshold* τ_0 determines the time between resource encounters at which a forager abandons the patch. *Time of hatching* ε determines the time in season at which the forager enters the resource habitat. A detailed model description is given in Appendix 1.

The model relates to optimal foraging models by considering adaptive strategies of individual foragers. It also bridges population ecology and game-theory models by including both competition among foragers and frequency-dependent selection. In addition, it incorporates the evolutionary perspective common in models of character displacement and sympatric speciation. By combining these different perspectives, the model departs from previous approaches in five important respects:

- 1) The behaviours of all individuals in the population are modelled explicitly, and the patch-leaving decisions of individual foragers affect resource consumption and patch depletion. This results in internally driven local and global variations in resource levels which depends on i) the rate of renewal of the resource (for each simulation this is a constant g), ii) the density of the forager population, iii) the foraging strategy of individuals in the population, and iv) the time at which foragers enter the resource habitat. The pattern of resource exploitation is a function of the common actions of all foragers in the population. The resulting temporal resource dynamics (Appendix 1) creates the potential for divergence in foraging strategies.
- 2) Patch time-allocation strategies and the way of integrating information are let to evolve under the selective forces of the model environment (see Appendix 1). The cost of learning emerges from the interaction between the individual strategies, the actions of other foragers (affecting both the spatial and temporal variance) and characteristics of the physical environment (season length, fragmentation of habitat, etc.).
- 3) The allocation of time on a patch is modelled explicitly for all individuals in the population, hence I need not rely on pre-determined distribution patterns such as an Ideal Free Distribution (Fretwell & Lucas, 1970) to be obtained. Here, the IFD becomes a potential outcome of the model, not a key assumption predetermined by the modeller. The distribution pattern that emerges however, depends on the behavioural strategies of individuals and the environmental constraints.
- 4) Similarly, instead of assuming a fixed competitive relationship, the relative performance of the different foraging strategies is an emergent property of the model system. The benefit of acquiring information is weighted against movement costs and sampling errors, hence the cost of flexibility is an emergent property of individual behavioural strategies and environmental constraints. As opposed to model approaches considering intrinsic growth

rates and carrying capacities (e.g. MacArthur & Levins, 1967; Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2000; Egas, 2004), this highlights the asymmetric relationship between costs and benefits, and how these properties change with biotic and physical feedbacks.

- 5) Individual behaviour is determined partly by inherited traits and partly by the experiences of each individual as it explores its environment. Commonly, models consider fixed behavioural outcomes or strategies that are not let to evolve under the frequency and density-dependent forces of the environment. The model thus couples hard-wired population genetics with environmental feedback and behavioural flexibility. The inclusion of a simple life-history trait (hatching time) allows individuals to trade life time expectancy against strength of resource consumption (see below).

In the remaining part of this section, I briefly outline some results from this modelling approach (further details in figure legends). It appears that competition leads to frequency-dependent selection and facilitates coexistence of foragers with different information harvesting strategies. Flexible learning strategies and fixed innate strategies, similar to those imposed in **Paper 2** (*Learners* and *Stayers*, respectively), emerge from first principles, where parameters of basic decision rules evolve under the selective forces of the biotic and physical environment.

The three genetically inherited traits determine the foraging strategy of each individual in the population. The evolutionary trajectories of strategy frequencies in two different simulations are illustrated in Fig. B1. The two scenarios differ in relative season length and the level of resource competition. In the upper panel strong resource competition and a long foraging season selects for individual differences in the time of hatching. This facilitates the evolution of both fixed innate strategies and flexible learning rules. In the lower panel, season is relatively short, resources are abundant, and all foragers

adopt a non-responsive innate strategy.

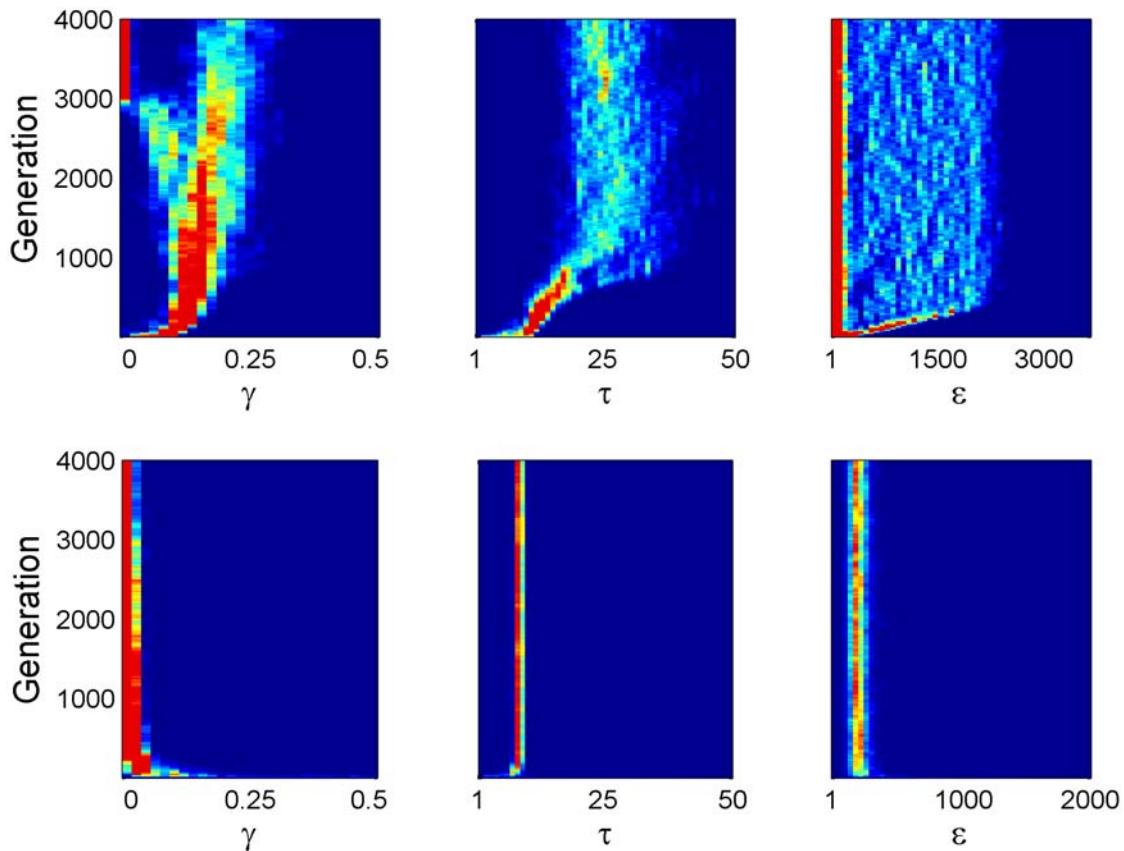


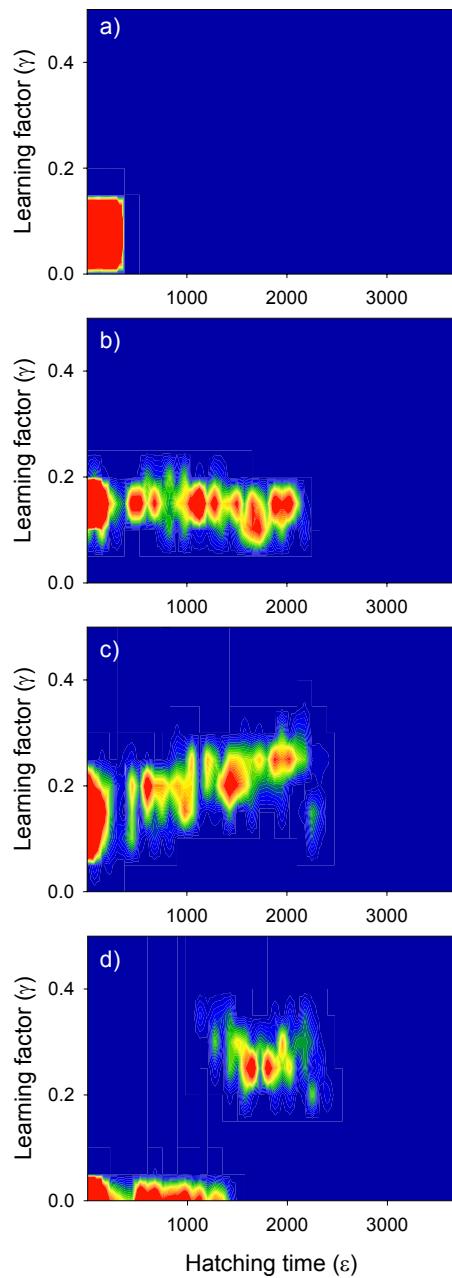
Figure B1. Artificial evolution of foraging traits: Typical trajectories of learning factors γ , initial giving-up thresholds τ and hatching times ε .

Upper panels. An initial diversification of the emergence time trait relaxes resource competition early in season. The learning factor and the initial giving-up threshold (τ) exhibit higher parameter values. Eventually, profitable τ_0 s evolve that facilitate the establishment of fixed threshold strategies. The learning factor γ splits in two distinct clusters; a fraction of the population adopts non-learning fixed rules whereas others obtain a flexible learning strategy. ($T = 3750$, $s = 0.025$, initiation range of $\gamma \sim 0.0\text{--}0.1$, $\tau \sim 1\text{--}10$, $\varepsilon \sim 1\text{--}375$). Each genetic trait space is divided into 50 categories where the number of individuals in a category increases from dark blue (none) to red (>300 individuals).

Lower panels. A population of non-learners evolves which utilises a fixed giving-up threshold throughout the season. The genetic trait has low variance within the population. Hatching only occurs early in season. The environment has a relatively short foraging season ($T = 2000$) and low offspring survival ($s = 0.01$), resulting in little resource competition among adult foragers.

Life-time expectancy of foragers decreases with time of hatching, since all foraging activity ceases at the end of the resource growth season. Foragers that emerges late in season, will have less time to exploit resource patches, selecting for an early time of emergence (low ε values). Directional selection on this trait is counteracted by frequency-dependent selection resulting from resource competition among foragers early in season.

Figure B2. Evolution of association between inherited foraging traits: Individual learning factors (γ) correlated with time of emergence (ε) in generation 1 (a), 400 (b), 2000 (c), and 5000 (d) of artificial evolution. In (b) we see how the population of strategies first evolves towards higher learning factors and more spread in time of hatching. Eventually in (c), higher learning factors become associated with late time of emergence. Last (d), the population splits in two distinct clusters of early non-learners and late-hatching learners. ($T = 3750$, $s = 0.025$, other parameter values as in Table A1). The association between the behavioural and life history traits may indicate an early step towards sympatric speciation (but note the low recombination rate used). The number of individuals increases from dark blue (none) to red (> 300 individuals)



Different foraging strategies proliferate during various parts of the season and facilitate coexistence of several patch allocation strategies (Fig. B2 & B3). As illustrated in **Paper 3** and **Paper 4**, strategies with fixed giving-up thresholds will prosper in periods with relatively stable population- and resource densities (Fig. B3). Only as resource levels fluctuate more, will the potential benefit of acquiring information outweigh the cost that learners pay for exploring the environment (**Paper 3** and **Paper 4**). Higher learning factors facilitating faster information updating are then beneficial (Fig. B2 & B3). Typically, an association between late hatching time and high learning factors gets established in the population as a result of larger resource fluctuations late in season (Fig. B2). The behavioural trade-off between flexibility and specialisation is hence a property tightly linked to both temporal and spatial resource dynamics and the emergent costs and benefits of information acquisition (see also **Paper 4**).

The adaptive foraging strategies reflect trade-offs in information updating processes (Fig. B4; see also **Paper 3** and **Paper 4**) and is linked to the life history trait (hatching time). Diversification in foraging traits is a result of temporal alteration of the competitive relationship among strategies. With increasing relative season length (related to adult survival probability and length of growth season of resource) and strength of foraging competition (population density of foragers), the potential for coexistence between learning and fixed-threshold strategies increases (Fig. B4).

In the model, risk of predation and distributions of competing foragers are important ecological factors affecting individual behaviour (see also **Paper 3**). Changes in these factors may alter behavioural or life-history trade-offs, potentially changing patterns of coexistence between learners and non-learners (Fig. B4). Differences in the ability to trade competitive ability against life history traits have been proposed as an explanation for the coexistence of competitors and the persistence of multi-species assemblages that exploit the same resource (Bonsall *et al.*, 2002; Bonsall, 2004).

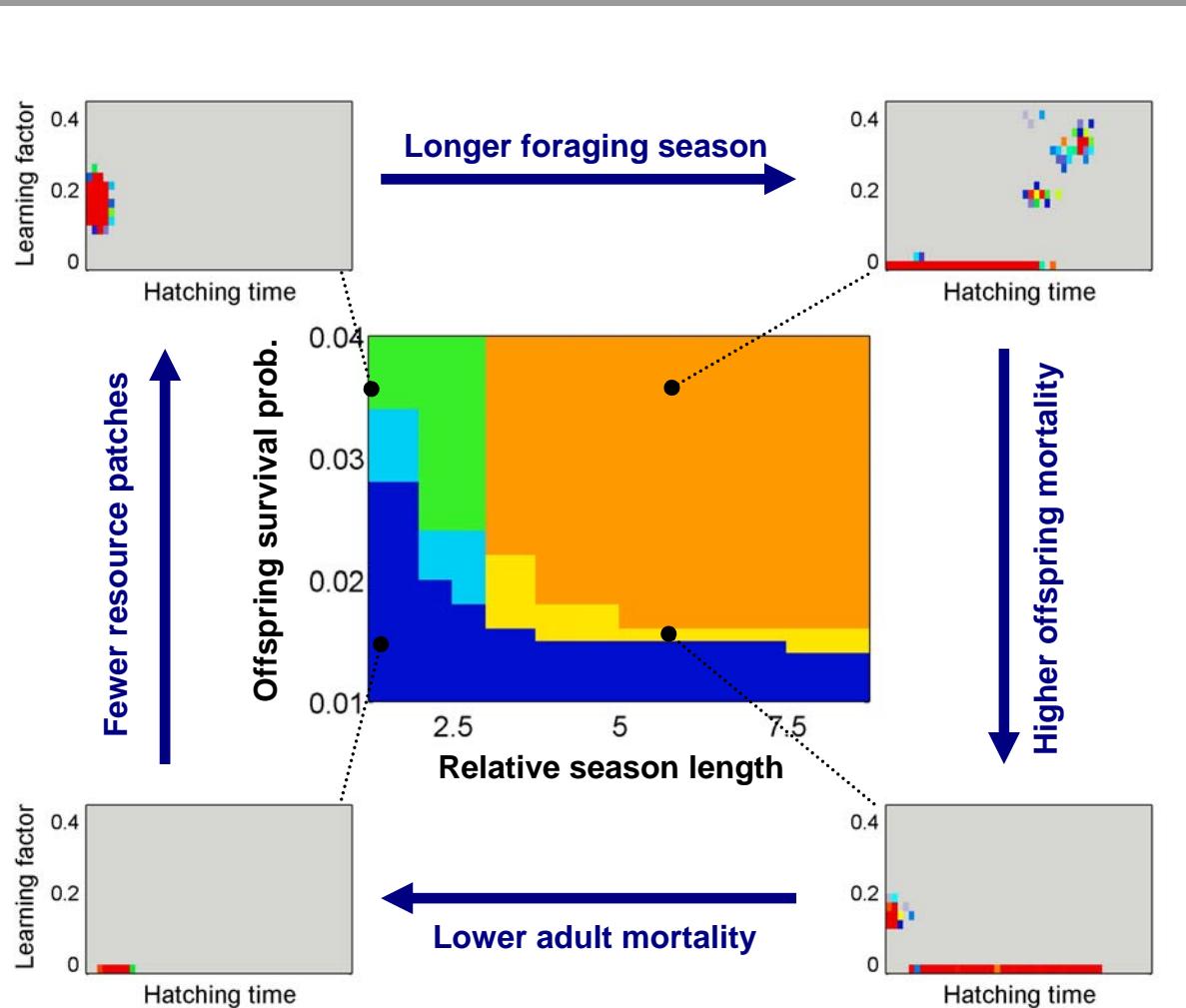


Figure B4. Coexistence and ecological trade-offs. The potential for coexistence between different foraging strategies as a function of the probability of offspring survival and relative season length (expected life-time of foragers relative to the length of season). Coexistence between learners and non-learners evolved for high levels of resource competition (high offspring survival) combined with large potential for temporal segregation (long seasons): The area of coexistence includes an area of early learners and later non-learners (yellow), and a more typical region of non-learning early hatchers with a smaller cluster of late-hatching learners (orange). Longer foraging seasons allow more variation in individual hatching time ε , which increases the potential for diversification in other foraging traits. In much the same way, decreasing life-time expectancy facilitates specialisation to short-term resource dynamics.

At low population densities (dark blue areas), fixed-threshold strategies are adaptive. With higher offspring survival rate, the population of adult foragers increases in density. This intensifies resource competition, and selects for flexible learning strategies. For relatively short foraging seasons, only learning strategies evolve in high-density populations (green area). Between these regions (light blue) the population contains both learners and non-learners after 5000 generations, with little or no segregation in hatching time (ε).

Through the formulation of realistic behavioural strategies, it is however possible to interpret *how* ecological factors such as rate of predation, season length, offspring survival and resource growth rate affect such trade-offs (Fig. B4). It is therefore possible to interpret the effects of ecological factors on the evolutionary process of phenotypic diversification.

(Figure B4. cont.)

Ecological factors alter life-history trade-offs and change patterns of coexistence (surrounding figures). The effect of increased predation rates may have multiple outcomes, depending on how it affects different life stages. Increased mortality on adult foragers facilitates phenotypic divergence, whereas reduced offspring survival relaxes the frequency-dependent selection pressure caused by forager competition. Through the alteration of behavioural or life history trade-offs, ecological forcing may hence aid or counteract the process of phenotypic divergence. (The number of individuals increases from blue to red).

Perspectives

The topic of my thesis is broad, yet I have only considered a tiny fraction of the aspects central to the evolutionary ecology of foraging. Decision rules, information acquisition and learning are central to several disciplines, including economics, behavioural ecology, psychology, and artificial life. Leaning against such huge pillars of research history, I see several intriguing paths ahead:

Evolution and learning

Of the four explanatory levels in biology that Niko Tinbergen (1963) proposed, behavioural ecologists have often emphasized the ultimate causes of animal behaviour. Despite the focus on evolutionary processes, the underlying genetic relationships between traits are seldom considered (Owens, 2006). Instead, it is commonly assumed that constraints on genetic architecture will not influence the evolution of behavioural traits and that the phenotype accurately reflects the genetic patterns (the ‘phenotypic gambit’ Grafen, 1984). These may be reasonable assumptions when behavioural traits are at long-term evolutionary equilibrium (Parker & Smith, 1990), but the link between phenotype and genotype may be crucial in other circumstances (Owens, 2006).

The models presented in this thesis assume a simple link between alteration in genetically inherited traits and learned solutions. For more complex learning tasks the solution to a problem may, however, be found with a few learning cycles, whereas it requires a large number of mutations to reach the same precision through genetic evolution (Nolfi, 1999). This is because learners are able to produce complex phenotypes from a limited number of genes by extracting some information from the environment (Nolfi & Parisi, 1996). In non-stationary systems, we need to consider the evolutionary dynamics of behaviour and it becomes important to focus on transient processes as well as optimal solutions (Todd, 1996; Nishimura, 1999).

Learners may prosper in periods when selection moves the strategy space towards a new peak in the fitness landscape, for instance when populations respond to novel situations, environmental disturbance, or rare catastrophic events. The rate at which a flexible strategy is replaced by a non-responsive innate rule (e.g. the Baldwin effect; (Baldwin, 1896; Waddington, 1953; Hinton & Nowland, 1987) may depend on genetic constraints (mutation rates and genetic correlations among traits) as well as the relative costs of learning (sampling costs and learning rates). The interactions between evolutionary and learning processes have been studied in the field of artificial intelligence, using a combination of artificial evolutionary techniques (e.g. genetic algorithms) and learning routines (e.g. neural networks) (Ackley & Littman, 1991; Nolfi *et al.*, 1994; Nolfi & Parisi, 1996; Nolfi & Floreano, 1999). These techniques offer *avenues* for exploring evolutionary dynamics in biological systems, which may replace ancient paths.

Behavioural strategies and perceptual constraints

The second path starts at the crossroad between evolutionary ecology and cognitive psychology, i.e. between behavioural strategies and perceptual constraints. Cognitive aspects of information acquisition have traditionally been the domain of psychologists (Dukas, 1998), but behavioural ecology offers an ultimate, evolutionary understanding of animal learning. In this perspective sensory capacities, attention, and the ability to integrate information can be understood as adaptations to the natural environment of an organism (Anderson & Schooler, 1991; Dukas, 1998 667; Schacter, 1999; Dukas, 2002; van Alphen *et al.*, 2003; McNamara *et al.*, 2006). On the other hand, evolutionary models also need the proximate perspective (Shettleworth, 1998; Hutchinson & Gigerenzer, 2005). To understand the relationships between current environment and a behavioural response, the biases and constraints that affect perception and manipulation of information need to be incorporated (Todd & Kacelnik, 1993; Bizo & White, 1997; Shettleworth, 1998; Hills & Adler, 2002; Stephens, 2002).

Simple questions or simple answers?

In natural settings, not only average resource intake, but also the variance in amount and time between food encounters may influence a forager's decision (risk-sensitive foraging; reviewed in McNamara & Houston, 1992; Kacelnik & Bateson, 1996). Besides, individuals do not devote all their time to food search instead, patch time allocation and habitat selection may represent a trade-off between several conflicting demands. Mating activities and the need to hide from predators can change the motivation for food search and affect energy acquisition and movement behaviours, as illustrated in my field studies on lekking birds (Finne *et al.*, 2000; Odden *et al.*, 2003; Wegge *et al.*, 2005; Eliassen & Wegge, in press). Interference and dominance relations may also influence the spatial organisation of individuals and restrict access to resource locations (Fretwell & Lucas, 1970; Fryxell & Lundberg, 1997; Giraldeau & Caraco, 2000; Wegge *et al.*, 2005).

Information acquisition may also be multifaceted. Sampling information on food distributions often yields knowledge of other environmental properties, such as refuges and distribution of predators or mates. Foragers with poor information on predation risk may reduce conspicuous movements, and simultaneously limit their ability to acquire other types of information. Individuals may hence show consistent response patterns on different behavioural tasks (Dall *et al.*, 2004 ; Sih *et al.*, 2004), which highlights the importance of considering several information problems in concert.

Emlen's (1966) assumption that natural selection would favour foraging preferences, subject to scrutiny as a time- and energy-optimization, has been powerful. Early conceptual models produced elegant analytical solutions that, although unrealistic in their assumptions, created a conceptual framework in which to interpret animal behaviours. Looking back on the same questions considering individual decision rules and information acquisition may, however, yield quite different predictions of adaptive behaviour, as illustrated in **Papers 2-4** and **Box 1**. Complex behavioural trade-offs and composite information problems may benefit from other

methodologies, such as individual-based modelling, genetic algorithms, and neural networks. These approaches, however, introduce new parameters with new uncertainty, and there are seldom simple solutions to complex problems. On the other hand, the methods of Individual Based Ecology (*sensu* Grimm & Railsback 2005) are transparent, realistic and easily combined with experimental ecology, cognitive science, and physiology.

Combining adaptive processes and forces at different scales (Todd, 1996), more realism in individual differences, and environmental complexity may reveal other trade-offs in behaviour and life history: Including variation in individual cooperative investment alters predictions of group sizes in social systems - with feedbacks to population dynamics and carrying capacities (Aviles *et al.*, 2002; Aviles *et al.*, 2004). Letting individual strategies emerge from basic assumptions of sensory abilities and behavioural responses reveals underlying *mechanisms* facilitating phenomena such as cooperation (Burtsev & Turchin, 2006). In stead of being satisfied with perfect answers to simple questions, evolutionary ecologists can now address far more fundamental questions, albeit with less clear-cut answers (Peck, 2004).

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Appendix 1: Model description (Box 1)

Overview

The main purpose of this model is to study information use and individual patch-leaving strategies in a population where foragers interact and compete for resources. I consider adaptive processes both within the lifetime of an organism (learning) and between generations (artificial evolution). Frequency- and density-dependent processes influence the profitability of individual foraging strategies. The value of learning depends on the temporal change in resource conditions, which is mainly driven by the resource consumption of the competing foragers.

The model was inspired by the relationship between insect parasitoids and their host species. In host-parasitoid systems there is a relatively simple link between host attacks and parasitoid recruitment, which makes the system convenient as a model for studying predator-prey interactions. Female parasitoids search for hosts in which to lay their eggs, and the host (often an insect larva) represents a food source for their offspring. The number of offspring a female produces is therefore tightly linked to the number of hosts she locates during a lifetime. The model approach may also apply to predator-prey systems in which there is a restricted season of interaction between species and non-overlapping generations.

I consider a population of foragers that compete for resources in a patchy habitat. All foragers may potentially differ in their patch-time allocation strategies. The behavioural strategies are based on inherited traits that can be altered through experience and learning. The inherited components are coded as genetic strings with three strategy traits: the initial giving-up threshold τ_0 ; the learning factor γ ; and the hatching time ε . The traits evolve under the selective forces of the model environment (see detailed description in *Submodels* below).

At the onset of a new foraging season, the number of resources in all patches starts to grow. There is a fixed probability g that a new resource will emerge in a patch at a

given time step t . Individual foragers enter the resource habitat at a time in season determined by their hatching time gene ε . Foragers allocate their time between searching for resources within a patch, handling captured resources, and moving between patches. The probability of encountering a resource depends on the local resource level within a patch.

Resource dynamics of each patch is modelled explicitly as a function of resource renewal and forager consumption. Competition among foragers within a patch is a consequence of exploitation of limited resources. Life time expectancy declines with delayed time of hatching. This may select for an earlier time of emergence into the foraging habitat, intensifying resource competition early in season. The trade-off between resource competition and longevity may alter the temporal spread of the population and hence feed back on resource dynamics.

Foragers continuously reproduce in proportion to their accumulated resources. At the end of the foraging season all foraging activities cease, and with a given probability offspring will survive to enter the foraging habitat next season.

Design concepts

In this section I introduce several properties characterising the individual-based model. For detailed description of the design concepts, see Grimm & Railsback (2005) and Grimm *et al.* (2006).

Emergence: The patch-leaving behaviour is modelled explicitly as a result of the inherited foraging strategy and the experiences of individual foragers. Distribution of both resources and foragers hence emerges, with patterns changing both within and between foraging seasons. The size of the forager population is proportional to the reproductive output in the previous generation, which is linked to foraging efficiency and survival. Resource levels change within a season as a function of resource consumption, but the probability that a resource will be added to a patch does not vary within or between seasons.

The seasonality is imposed and restricts the life-time expectancy of individuals. The frequency- and density-dependent selection on the hatching time trait ε may cause different foraging strategies to emerge that vary in the way they trade life-time expectancy against level of resource competition.

Adaptation: Foragers assess local patch quality and adjust their patch-time allocation accordingly. Upon entering a new patch, a forager may integrate past experience and new information to obtain a new estimate of the giving-up threshold. The patch-time allocation of an individual may therefore change both as a result of local resource levels and with changes in average resource conditions within the environment.

Fitness: Genetically inherited traits determine the learning factor γ , the initial expectation of the habitat τ_0 , and the time of hatching ε . These traits determine a forager's patch-time allocation strategy and are adapted to the prevailing ecological conditions by a genetic algorithm. The patch allocation strategy and the time of emergence within the foraging season determine the amount of resource accumulated during a lifetime, and consequently a forager's reproductive output (see *Submodels*).

Interaction: There is no direct interference among foragers, but individuals compete for common limiting resources. Several foragers may exploit a patch, but individuals move solitarily between patches. The spatial dimension of the landscape is not considered explicitly, there is an equal probability that a forager will reach any patch in the habitat.

Submodels

Individual variation

The behavioural strategy of an individual forager is determined by its genetically inherited traits and the forager's experiences during its lifetime. The model does not intend to represent the actual genetics of individuals, but considers genetically inherited traits that evolve under the selective forces of the model environment. Individual foragers differ only in the values of the following three strategy traits:

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1. The learning factor (γ) is an individual's tendency to change its giving-up threshold from its inherited value, in accordance with experiences on a patch. The learning factor can take any value between 0 and 1. As the learning factor approaches one, more weight is given to recent experiences as opposed to past information. When γ equals zero, the forager will not update its information and behaves according to a fixed innate giving-up threshold.
 2. The initial giving-up threshold (τ_0) determines the time from last resource encounter until the individual gives up resource search and leaves the first patch. Learners update their giving-up thresholds based on experience and I use the symbol (τ_p) for the modified value of the giving-up threshold used by a learner in patch p .
 3. The hatching time (ε) is the time within a season at which the forager will enter the foraging habitat. It may be the birth date, the day the organism moults to the parasitic or predatory stage, or the day the organism is left alone by its parents.

Foraging events

The forager is expected to maximise its resource intake. The lifetime of a forager is divided into discrete time steps, and for mathematical simplicity I let one time step equal the time needed to handle one resource. All foragers have equal search efficiency (a). The probability that a forager encounters one resource during a time step depends on the number of resources left in the patch (r_t):

$$P_{enc} = 1 - e^{-ar_t}$$

Foragers compete for resources, and their collective consumption will result in a depletion of the patch.

Every time step the forager may choose to stay in the patch or leave and search for another. The patch leaving decision is modelled as a stochastic event based on its

inherited trait as well as its experiences of resource encounters. When time since last resource encounter (t_s) increases, the probability that a forager leaves the patch changes according to:

$$P_{leave}(t_s) = \frac{1}{1 + e^{\alpha(\tau_p - t_s)}}$$

where τ_p is the individual's patch leaving threshold in patch p . The parameter α determines the slope of the response curve, which may for instance be affected by the accuracy by which a forager assesses the length of time intervals.

Memory and learning

The inherited patch leaving threshold τ may be altered during the lifetime of an organism through experience and learning. Foragers may acquire information about resource level on several scales. Inside a patch, individuals may record the time between successive resource encounters and use this estimate to determine the quality of the current patch. Upon leaving a patch this resource estimate is treated as a sample of the overall quality of the habitat at a given time within a season.

The new estimate (τ_{p+1}) is a weighted average of the previous estimate (τ_p) and the average time between encounters in the last patch, including the fixed travel time v :

$$\tau_{p+1} = (1 - \gamma)\tau_p + \gamma \frac{n + v}{k}$$

The weight given to new information is specified by the inherited learning factor γ . The forager has encountered k resource items in the patch during n time steps of search, and v is the travel time between patches.

Resource dynamics

The environment contains a fixed number of resource patches. At the start of a foraging season, food items start to emerge within these patches. For each patch the

emergence of a new resource item is a stochastic event which occurs with a constant probability g for each time step in the foraging season.

Local resource levels depend on resource renewal rate and the number of items consumed by each forager visiting the patch. Fluctuations in resource levels will hence be affected by foraging behaviour and densities at different times in the season (Fig. A1a). Foraging strategies also affect the spatial variance as depletion of patches in the habitat depends on movement patterns and patch-leaving strategies (Fig. A1b). With a low forager density (low offspring survival), the underlying resource dynamics result in a constantly improving resource environment. In high density populations, resource levels are to a large extent regulated by forager consumption. Temporal change hence reflects the number of competitors at a given time in season.

The rate of resource gain (g) is constant between years, implying that the consumption of resources within one generation does not affect the resource conditions the following year. As a consequence, all generations of foragers

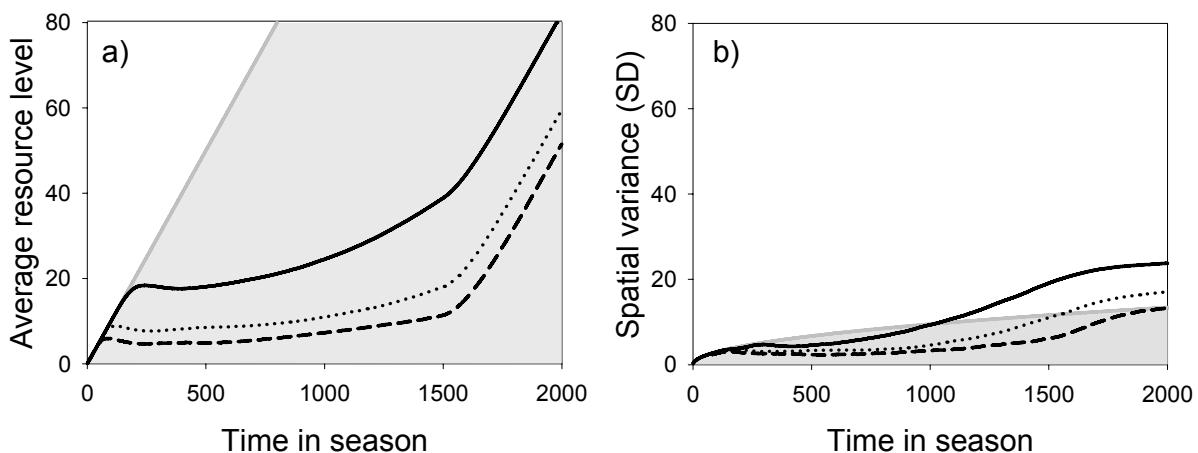


Figure A1. Resource dynamics at different population densities. a) Average resource level in patches as a function of time in season. b) Spatial variability among patches at different times in season, given as the standard deviation in resource levels. The temporal change in resource conditions varies with the number of foragers in the population. At low population densities (solid line, $s = 0.01$) resource levels are generally higher than for intermediate (dotted line; $s = 0.02$) and high (hatched line; $s = 0.03$) population densities. The grey lines indicate resource conditions given no forager consumption.

experience the same underlying resource dynamics, but the actual dynamics may vary depending on the temporal and spatial distribution of foragers.

Evolving strategies

I use a genetic algorithm (Sumida *et al.*, 1990; Holland, 1992) to search for adaptive solutions to the patch leaving problem. At the start of a simulation all values of the individually inherited traits are assigned random values within a given parameter range (Table A1). The initial population therefore comprises N combinations of the different trait variables, each representing a random strategy. Individuals enter the model environment at time ε specified in their individual genome. They are assigned a random patch and start to search for resources. Depending on their initial giving-up threshold τ_0 and encounter history, a forager will leave the current patch and move to a new location.

There is a constant probability that a forager will survive to the next time step, and mortality is modelled as a stochastic process. A foraging season corresponds to the maximum number of time steps T for which conditions are suitable for the forager. In natural systems, T could be linked to host development or prey migrations, changing weather conditions or other seasonal factors. I assume a fixed time horizon, but simulations with gradual increase in rate of mortality late in season give similar results.

At the end of a season, a new population of foragers is generated by replicating the parent strategies in proportion to their reproductive output. The patch-time allocation strategy and the probability of survival determine the total number of resources that a forager accumulates during a lifetime, E_{tot} . This relates to an individual's reproductive output (V_i) according to:

$$V_i = b(E_{tot} - mt_{tot} - l)$$

The amount of resources needed to produce one offspring equals b (for a parasitoid laying one egg in every host, b equals 1). Energetic cost of maintenance m (on the

scale of resources per time step) reduces the reproductive output depending on the total lifetime of an organism (t_{tot}). For learners, there is an energetic cost of developing and maintaining a memory record l . I assume that foragers are constantly laying eggs, which is the case for parasitoid oviposition in a host.

The new generation of genetic solutions undergoes mutation and recombination: A mutation will hit a specific position on the genetic string with a probability F_M and change its initial value by some random fraction F_S (0.5-10 % of the gene value). Individual strings are recombined with a probability F_R per generation. This involves swapping a subset of the strategy vector with a randomly chosen partner. Since I am interested in studying the potential for coexistence between different foraging strategies, the rate of recombination is set very low ($F_R \sim 0.005$) to allow associations between genetic traits to establish in the population. The genetic string in this model is haploid, but diploid strings may also be used where an offspring's trait is the average of the parents' values. The cycle of selection, reproduction, recombination, and mutation is repeated, and the gene pool of the population is evolved for a number of generations Y .

I expect survival from egg stage to adult forager to have a constant probability s . Offspring production varies depending on resource encounters and survival of individuals, hence population size may vary between years. The total amount of resource within the environment will, however, restrict reproductive output. Consequently, population size tends to fluctuate within the range of 10 000-14 000 individuals between years.

It is possible to alter population densities by changing the offspring survival probability s between simulations. This will change the number of individuals surviving to the next season and influence the strength of resource competition.

Table A1: Variable and parameter definitions. Values for the standard model scenario are given along with the range of parameter values for which the sensitivity of the model was tested.

Symbol	Description	Standard value (range)
<i>Parameters</i>		
N_0	Initial number of foragers in population	10000
P	Number of patches in environment	5000 (2000-10000)
T	Number of time steps in a season	1250-10 000
Y	Number of generations in a simulation run	5000 (3000-15 000)
g	Gain rate of resource in patch per time step	0.1 (0.05-0.2)
a	Search efficiency of forager	0.01 (0.005-0.02)
m	Mortality rate	0.001 (0.0005-0.003)
s	Survival probability from egg to adult	0.005-0.04
b	Resources needed to produce one offspring	1.0
l	Resources needed to develop/maintain a memory record	0.3-3.0 (1% of average V)
F_M	Mutation rate in reproduction routine	0.01
F_S	Mutation step length	0.5-10%
F_R	Recombination rate	0.005 (0.0-0.5)
α	Responsiveness in patch-leaving decision	0.1
v	Time to travel between patches	10 (2-50)
<i>Individual genome</i>		
τ_0	Innate giving-up threshold	1- T
γ	Learning factor	0.0-1.0
ε	Hatching time	1- T
<i>Variables</i>		
P_{enc}	Probability of resource encounter (per time step)	
P_{leave}	Probability of leaving a patch	
t	Time in season	
t_S	Search time since last encounter	
r_t	Number of resources in a patch at time t	
V_i	Reproductive output of individual i	
t_S	Time since last resource encounter	
t_{tot}	Total lifetime of an individual	

Paper 1

Øyvind Fiksen, Sigrunn Eliassen & Josefin Titelman. (2005) Multiple predators in the pelagic: modelling behavioural cascades. – *Journal of Animal Ecology* **74**: 423-42

Multiple predators in the pelagic: modelling behavioural cascades

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Summary

1. The behaviour of predators is rarely considered in models of predator–prey interactions, nor is it common to include multiple predators in models of animal behaviour.
2. We introduce a model of optimal diel vertical migration in zooplankton prey facing predation from two functionally different predators, fish and other zooplankton. Zooplankton predators are themselves subject to predation from larger zooplankton, and all zooplankton face the classical trade-off between increasing growth rate and predation risk from fish towards the surface. Prey are most vulnerable to zooplankton predators at small sizes, but become more visible to fish as they grow. However, by habitat selection prey continuously manage their exposure to different sources of risk.
3. We analyse situations with cascading behavioural interactions of size-structured predator–prey interactions in the pelagic. In particular, we explore how vertical gradients in growth rates and relative abundance of fish and zooplankton predators affect optimal distribution patterns, growth and mortality schedules.
4. A major model prediction is that prey susceptibility to one functional predator type depends on the abundance of the other predator. Higher abundance of zooplankton predators leads to risk enhancement from fish, minor increases in predation rate from zooplankton and unchanged prey growth rates. Increasing abundance of fish does not alter the risk from zooplankton predators, but reduces growth and development rates. Such asymmetric emergent effects may be common when prey and predators share the same spatial refuge from a common top predator.

Key-words: DVM, dynamic programming, emergent effects, multiple predators, zooplankton.

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Introduction

Predator and prey theory is biased towards one-predator-one-prey interactions (Sih, Englund & Wooster 1998). However, most prey are exposed to and responsive towards several predators, and may balance their antipredator behaviours with the relative predator abundance. It is usually not obvious how the presence of several predators affect behaviour, growth and predation risk of prey. Prey may benefit from the presence of multiple predators if these interfere with each other. Also, behavioural defence of prey to one predator may enhance the exposure to other predators. Presence of

several predators thus may increase predation rates more than the additive expectation from the predators in isolation. Recently, the need to include multiple and behaviourally responsive predators in models of animal behaviour has been emphasized (Holt & Polis 1997; Sih *et al.* 1998; Alonso 2002; Lima 2002; Lima, Mitchell & Roth 2003).

In size-structured pelagic food webs the classification of organisms as predator or prey is determined largely by relative size. Behaviour in one size category may therefore structure the behaviour of smaller size-groups, because predators often induce behavioural or strategic changes in their prey. If these prey are important predators to smaller organisms they may in turn cause further behavioural changes, or ‘behavioural cascades’ (Romare & Hansson 2003), where the abundance of a predator at a higher trophic level leads to behavioural changes of organisms over several lower

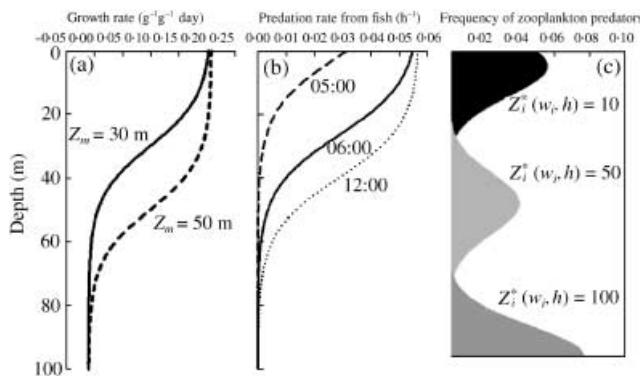


Fig. 1. Vertical profiles of growth and predation rate. (a) Growth rates with two different mixed layer depths Z_m (30 and 50 m). (b) Predation rate (from fish only) for a 5 mm prey at three different times of the day (05, 06 and 12), with $B_F = 1 \text{ g m}^{-2}$ and light extinction at 0.12 m^{-1} . (c) The concentration of zooplankton predators $N_i(z,w,h)$ in depth z , size class w_i at time h is defined by the total zooplankton abundance (in biomass B_P or numbers I_i ; Table 1) and a normal distribution with mean $z_i^*(w_i,h)$ and standard deviation 7.5 m. The graph shows the depth distribution of size-classes with three different optimal depths (10, 50 and 100 m).

trophic levels. An example is when planktivorous fish induce normal (up at night, down during the day) diel vertical migration (DVM) in large predatory copepods and chaetognaths, which in turn leads to inverse DVM in their smaller copepod prey (Ohman 1990). Such observations indicate that the optimal DVM strategy depends on the presence and relative abundance of two functionally different predators.

Situations where prey responses dominate and predation rates or distribution patterns change considerably in the presence of several predators are called ‘emergent effects of multiple predators’ (Sih *et al.* 1998). In the absence of fish, large zooplankton predators may remain in the preferred habitats of their prey. In the presence of fish, large zooplankton are forced out of the illuminated habitats during the day, which reduces spatial and temporal overlap with smaller zooplankton prey. The best response of small zooplankton may then be to remain near the surface during the daytime, despite the cost of higher predation from fish. In this case, it is not obvious if prey experience risk enhancement or reduction. Behavioural interactions between predators could lead to deviations from simple additive or linear effects from the two predator types. Also, prey themselves may adjust their habitat selection in response to relative densities or efficiencies of predators, and exhibit considerable ontogenetic changes in behaviour (Titelman & Fiksen 2004).

DVM is a classic example of the trade-off between growth and predation risk (Pearre 2003). Despite the wide range of models on DVM strategies in both fish and plankton (Clark & Levy 1988; Fiksen 1997; Eiane & Parisi 2001), none of them consider behavioural cascades. However, modelling behavioural interactions in size-structured predator–prey systems with functionally different predators is challenging. In particular, if both predators and prey respond readily to the movements of each other, a game-theoretical approach is required (Iwasa 1982; Gabriel & Thomas 1988). If prey has a safe refuge or predators do not tend to follow their prey, then an optimality approach is appropriate.

Using an optimality approach, we predicted successfully ontogenetic habitat switches of different copepod species in a Swedish fjord system (Titelman & Fiksen 2004). Here, we develop a general model of DVM patterns and predation rates under multiple predators, assuming that prey behave optimally. The model predicts interaction strength between prey and its two predator types to change abruptly with their relative abundance.

Model

The model is formulated mainly with the pelagic oceanic community in mind, where large omnivorous or predatory euphausids, copepods and chaetognaths and smaller zooplankton grazing on microzooplankton, phytoplankton and detritus are core components. We focus on a zooplankter resembling a large copepod or euphausiid. It increases in body length from 0.5 mm at birth to 20 mm at maturity (196 discrete size-groups in 0.1 mm intervals), after which they allocate all surplus energy to reproduction. The specific growth rate $g(z)$ varies over depth reflecting a typical situation with a well-mixed layer of warm or food-rich water above the thermocline and deeper, colder or food-deprived water where growth becomes slightly negative (Fig. 1a). We assume that all zooplankton, including both prey and predators, have a fixed habitat-specific growth rate. Larger stages act as predators (‘zooplankton predators’) on smaller stages. The planktivorous fish predator is represented as a size-structured (0.02–0.3 m) population, with equal biomass in each size category (smaller fish more abundant). Fish are inert to prey movements, and distributed homogeneously across all depths. The fish population is therefore described fully by its abundance (Table 1). Fish are cruising predators, with clearance rates determined by ambient light, prey size and search-and-capture efficiency, as described by Titelman & Fiksen 2004). The predation rate $\mu_F(z, w_p, h)$ from fish on prey with body mass w_p in depth z at time h is a function of clearance rate β_F , density N_F and capture

Table 1. A description of variables, parameters, their dimensions and values. The subscripts F , P and i denote fish, zooplankton prey and zooplankton predators, respectively

Symbol	Description	Value (range)	Unit
z	Depth	1 (0–100)	m
h	Time	0·5 (0–48)	hour
d	Day number	1 (1–150)	day
l_p, l_i	Zooplankton length class	10^{-4} (0·5– 20×10^{-3})	m
l_F	Fish length class	10^{-2} (2 – 30×10^{-2})	m
w_F	Fish weight ¹	—	g
w_p, w_i	Zooplankton weight ²	—	g
B_F	Total fish abundance (biomass)	(0–1)	g m^{-2}
B_P	Total zooplankton abundance (biomass)	(0–25)	g m^{-2}
I_F	Number of fish in length class ³	—	ind m^{-2}
I_p, I_i	Number of zooplankton in length class ³	—	ind m^{-2}
J_F	Number of fish length classes	29	—
J_p	Number of zooplankton length classes	196	—
N_F	Concentration of fish in length class ⁴	—	ind m^{-3}
N_p, N_i	Concentration of zooplankton predator at any depth, length and time ⁵	—	ind m^{-3}
μ_F	Fish predation rate ⁶	—	h^{-1}
μ_P	Zooplankton predation rate ⁷	—	h^{-1}
P_F	Capture success of fish predator ⁸	—	ND
P_i	Capture success of zooplankton predator ⁹	—	ND
β_F	Clearance rate of fish predator ⁸	—	$\text{m}^3 \text{ h}^{-1} \text{ ind}^{-1}$
β_i	Clearance rate of zooplankton predator ⁹	—	$\text{m}^3 \text{ h}^{-1} \text{ ind}^{-1}$
Φ	Zooplankton fitness ¹⁰	—	Eggs
m	Maximum movement range per time ¹⁰	—	m
z^*, z_p	Optimal depth	(0–100)	m
Z_m	Mixed layer depth	30, 50	m
g	Zooplankton growth rate ¹¹	(−0·01–0·2)	$\text{g g}^{-1} \text{ day}^{-1}$
b	Zooplankton reproduction ¹²	—	Eggs day ^{−1}
k	Growth-to-egg conversion efficiency ¹²	0·1	Eggs g ^{−1}

¹ $w_F = l_F^3 \times 10^4$; ² length-weight relation as for *Calanus finmarchicus* in Mauchline (1998); ³ $I = B/wJ$; ⁴ $N_F(l_F) = I_F/100$ (abundance/number of depth cells); ⁵ $N_i(z, w_p, h) = I_i \eta(z, \sigma) / \int_z \eta(z, \sigma) dz$, where η is a normal distribution with mean $z^*(w_p, h)$ and standard deviation σ equal 7·5 m (see Fig. 1c); ⁶ eqn 1; ⁷ eqn 2; ⁸ Titelman & Fiksen (2004); ⁹ Svensen & Kiørboe (2000); ¹⁰ eqn 3; ¹¹ $g(z) = 0·21/(1 + e^{0·125(z - Z_m)}) - 0·01$, plotted in Fig. 1; ¹² $b(w_p, z) = g(z)w_p k$.

success P_F summed over all fish size categories (Table 1, Fig. 1b):

$$\mu_F(z, w_p, h) = \sum_{l_F=002}^{l_F=03} \beta_F(z, w_p, l_F, h) N_F(l_F) P_F(w_p, l_F) \quad \text{eqn 1}$$

Similarly, we have included an explicit model of the zooplankton predation rate $\mu_P(z, w_p, h)$, where clearance rate β_i is taken from Svensen & Kiørboe (2000) and capture success P_i depends on predator-prey size ratio (Titelman & Fiksen 2004). The total mortality rate is the sum from all potential predators (length l_i) larger than the focal prey of length l_p and body mass w_p :

$$\mu_P(z, w_p, h) = \sum_{l_i=l_p+00001}^{l_i=002} \beta_i(w_i, w_p) N_i(z, w_i, h) P_i(w_i, w_p) \quad \text{eqn 2}$$

The largest zooplankton are not susceptible to predation from other zooplankton. For smaller prey, which are themselves prey of larger zooplankton, the picture is more complex, as they must balance risk from different predators against growth. To smooth the predator field, the concentration N_i of each size class of zooplankton predators is distributed normally around the optimal habitat, constrained by surface and bottom

(Fig. 1c, Table 1). The predation risk from both fish and zooplankton is highly size-dependent (clearance rate, capture success, numerical abundance of size class; see Table 1). Figure 2 shows an example of size-dependent predation rates when both prey and predators are restricted to the surface layer. Prey outgrow their zooplankton predators, but can always be consumed by at least some fish.

The optimal habitat is defined as the depth that maximizes expected future egg production, and is found by dynamic programming (Houston & McNamara 1999; Clark & Mangel 2000). Habitat selection is restricted to depths that can be reached by constant, directional swimming (assuming a swimming velocity of one body length s^{−1}) during one time step (i.e. $z^* \pm m$). The general dynamic programming equation is:

$$\Phi(w_p, z^*, h, d) = \max_{z^*-m \leq z \leq z^*+m} \left[b(w_p, z) + e^{-\mu_F(z, w_p, h) - \mu_P(z, w_p, h)} \times \Phi(w_p + w_p g(z), z, h + 1, d) \right] \quad \text{eqn 3}$$

This equation maximizes expected lifetime reproductive output by choosing the best sequence of habitats from the present time (hour h , day d) until the end of the season ($d = 150$). The diel cycle is divided into 48

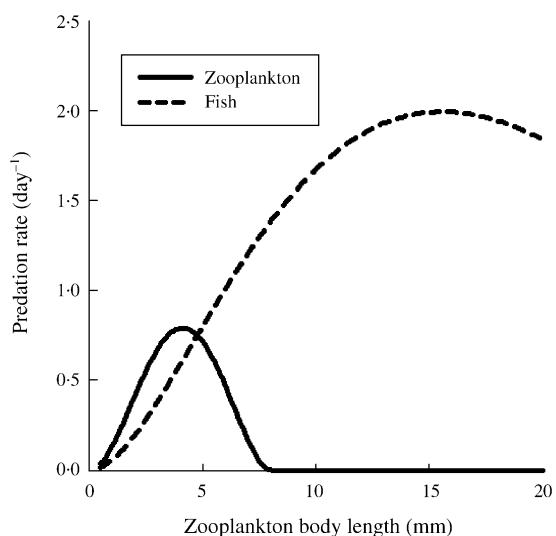


Fig. 2. The predation rate from fish and zooplankton predators when the model has no spatial resolution (only the surface layer) and there is no behaviour. The predation rate is low for small individuals as they are less conspicuous to both fish and zooplankton. At some size, prey outgrow their predators capture abilities. Here, B_p was reduced to 1 g m^{-2} and B_F to 0.01 g m^{-2} .

discrete time intervals. The terminal fitness value $\Phi(w_p, z^*, 48, 150)$ equals zero, meaning that all individuals die in the end. As time to horizon decreases, animals become more risk-prone to produce as many offspring as possible before the end of the season. We therefore ran the model for more than 100 days to avoid these terminal effects. Reproduction $b(w_p, z)$ is restricted to mature stages and is proportional to specific growth rate $g(z)$ (Fig. 1a, Table 1). Predation from fish μ_F and zooplankton μ_p varies in space and time. In addition, μ_p is formed by the habitat selections of larger zooplankton. The convergent optimal DVM strategy $z_p^*(w_p, h, d = 150)$ is stored for analysis and presentation.

Results

WITH FISH PREDATORS ONLY: THE EFFECT OF GROWTH GRADIENTS

There are striking differences in the optimal strategy $z_p^*(w_p, h)$ as the mixed layer depth increases from 30 to 50 m (Fig. 3). The deeper growth profile alters the balance between risk and growth to the point where it becomes profitable also for larger zooplankton to remain within the mixed layer during the day (Fig. 3, lower panel).

The optimal diel trajectories of different size classes are not obvious, even with only one predator type. Some intermediate size classes descend in the water column at dusk and dawn (Fig. 3). The profitability of this behaviour emerges from the diel changes in predation risk (Fig. 1b). In the early morning the risk decreases exponentially with depth. At midday, the profile is sigmoid due to light satiation in the functional response of the fish. Zooplankton must leave the mixed layer completely

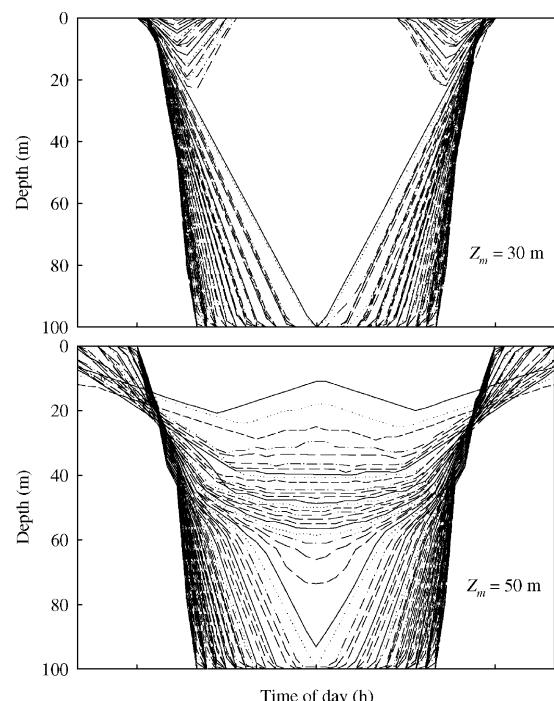


Fig. 3. Modelled optimal habitats over one diel cycle for all size groups (0.5–20 mm) of zooplankton when fish is the only predator ($B_F = 0.1 \text{ g m}^{-2}$). Lines represent one size group structured from small to large from surface to bottom during midday. The simulations differ in their inflection point Z_m (Table 1) of the growth function (mixed layer depth), which is 30 m in the upper and 50 m in the lower panel. The vertical growth profiles are as in Fig. 1a.

to significantly reduce predation risk at high levels of irradiance, whereas in the morning and evening they benefit from simply moving deeper into the mixed layer.

OPTIMAL BEHAVIOUR WITH TWO PREDATORS

The picture becomes more complicated when zooplankton predators are included. In Fig. 4, we present optimal DVM strategies for four size classes at combinations of 0.1 and 1 g m^{-2} of fish B_F and 10 and 25 (wet weight) g m^{-2} of zooplankton B_p . These concentrations (Table 1) are scaled to fit with those seen typically in oceanic areas. Now, the behaviour, abundance and distribution of larger zooplankton predators also affect the emerging spatial distributions. The effects of B_F and B_p on zooplankton distribution vary with size, and there are threshold predator levels that trigger behavioural shifts that cascade down the food chain.

The largest zooplankton predators ($> 10 \text{ mm}$) are vulnerable to fish, but safe from other zooplankton predators. They are efficient swimmers, and migrate between the habitat with the highest growth during the night and the safest habitat during the day. Similarly, the 5 mm prey are susceptible to visual predators, but can also be eaten by the largest zooplankton predators. Consequently, 5 mm prey migrate out of the mixed layer during the day, but avoid the deepest habitats to reduce overlap with the largest zooplankton. For the

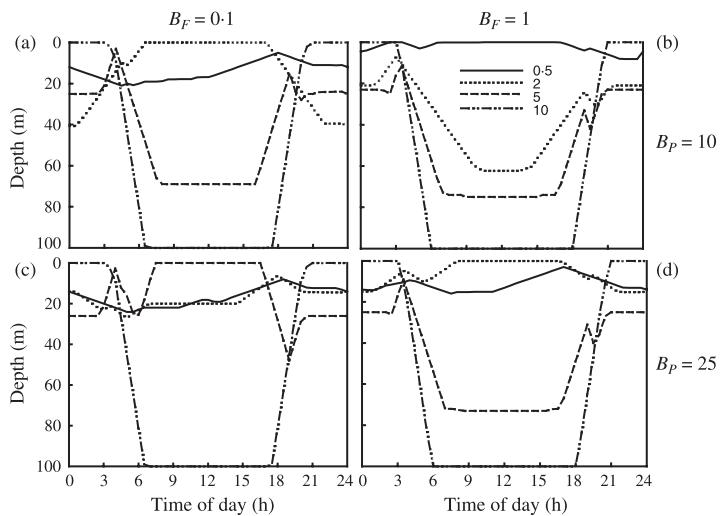


Fig. 4. Predicted optimal habitats over the diel cycle for selected size-classes of prey (0.5, 2, 5 and 10 mm) under four different predator regimes: (a) low fish–low zooplankton; (b) high–low; (c) low–high and (d) high fish–high zooplankton abundance.

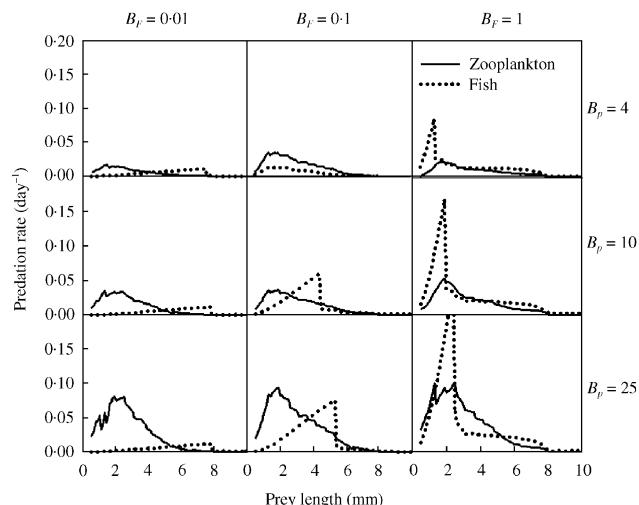


Fig. 5. Average diel rate of predation under various combinations of predator abundance. The abundance of fish B_F is 0.01 (left panels), 0.1 (middle panels) and 1 g m⁻² (right panels) and B_p is 4, 10 and 25 g m⁻² from top to bottom. Predation rates are low and constant for prey > 10 mm, and are omitted from the graphs.

same reason, they avoid the maximum growth habitats near the surface at night. This pattern changes with low B_F and high B_p (Fig. 4c). The enhanced risk in deeper layers during the day, including descent and ascent, and reduced risk in the surface shift the balance towards an inverse DVM strategy. The optimal behaviour includes strategic movements to reduce temporal overlap with large zooplankton at dusk and dawn.

Smaller zooplankton (< 2 mm) are more difficult to assess, as they have numerous predators behaving in different ways. The optimal strategy for these varies with predator regime (Fig. 4). The 2 mm prey do inverse DVM in the low B_F – low B_p case (Fig. 4a), but normal DVM for the high B_F – low B_p case (Fig. 4b). Under high B_p (Fig. 4c,d), this response is reversed. Migratory activity is low in both cases. The smallest prey (0.5 mm) have limited mobility (1.8 m h⁻¹), and migrate typically asymmetrically over the diel cycle as a response to the ascending and descending zooplankton predators. In summary, inverse, normal and no DVM

may be optimal depending on the relative abundance of predators and prevailing environmental conditions.

REALIZED PREDATION RATES UNDER VARIOUS PREDATOR REGIMES

Predator-induced behavioural changes typically modify both magnitudes of risk and exposure and vulnerability to other predators (Fig. 5). At low B_F (0.01 g m⁻²), an increase in B_p from 4 to 25 g m⁻² increases the predation rate proportionally, without changing fish predation rate. However, at $B_F \geq 0.1$ g m⁻² emergent effects appear. In fact, an isolated increase (4–10 g m⁻²) in B_p yields only minor increases in predation from these predators. Simultaneously, predation from fish increases considerably.

The exposure to fish changes markedly as zooplankton grows in size. Initiation of strong normal DVM is reflected in a conspicuous drop in fish predation (Fig. 5). This behavioural shift is delayed as B_p increases, mainly

Table 2. Number of days required for a 0.5 mm prey to reach the size of 1, 10 and 20 mm under various combinations of predator abundance

Size (mm)	$B_F = 0.1 \text{ (g m}^{-2}\text{)}$			$B_F = 1 \text{ (g m}^{-2}\text{)}$		
	$B_P \text{ (g m}^{-2}\text{)}$					
	4	10	25	4	10	25
1	10.3	10.9	11.8	9.7	9.9	10.3
10	75.1	70.0	70.0	102.0	98.1	95.0
20	102.0	96.9	98.1	132.0	129.9	127.0

as a result of increased danger in deeper layers during the day and the increased benefit of growing rapidly through the small and vulnerable size classes.

The emergent effect of multiple predators appears to be one-way in the case outlined here (Fig. 5). While higher B_P strongly affects the allocation of risk between predators, a corresponding increase in B_F at a given level of B_P does not affect the predation rate from zooplankton (Fig. 5).

Managing risk from several predators comes at the cost of slower growth and higher age at maturation (Table 2). More fish generate longer development times than do higher abundance of zooplankton. This is because the behavioural response to visual predators is associated more directly with growth – more normal DVM implies less time in the best habitats for growth. At higher levels of B_P , the surface is a better alternative at times when larger zooplankton predators are located below the mixed layer.

Discussion

The model suggests that predation rates are sometimes, but usually not, proportional to the density of predators (Fig. 5), nor do they resemble the predation rate expected under the assumption of no antipredator behaviour (Fig. 2). Increasing fish abundance will lead partly to reduced rates of growth and development of their prey (Table 2) and partly to higher, but not proportionally higher, rates of mortality. The presence of two size-structured predator populations led to marked switches in the spatial distribution of size-classes as the abundance of the predators changed (Fig. 4). With only fish as predators, we demonstrated that mixed-layer depth is surprisingly important for DVM strategies of zooplankton (Fig. 3).

All animals are normally at risk of predation from several predators. In the pelagic oceanic community, most mesozooplankton may be eaten by several species with different foraging strategies: schooling fish appearing randomly at any depth or mesopelagic fishes forming ‘deep scattering layers’ in the daytime and migrating to the surface at night (Kaartvedt 2000). Other animals in the deep scattering layers are omnivores such as krill and predatory invertebrates with

considerable migration activity. Zooplankton are flexible in their migration behaviour, depending on the abundance of fish (Bollens & Frost 1989) or invertebrates (Ohman, Frost & Cohen 1983; Irigoien, Convay & Harris 2004). Our model includes many of these features: intraguild predation, flexible prey and strong spatial gradients of growth and risk. In Titelman & Fiksen (2004), we demonstrated that this approach successfully predicted ontogenetic habitat shifts in numerous marine zooplankton species.

Behavioural cascades may be important in structuring aquatic ecosystems. Wissel, Boeing & Ramcharan (2003) conducted an enclosure experiment with combinations of fish, invertebrate predators (*Chaoborus*) and various herbivorous zooplankton in high and low turbidity water. As expected, larger zooplankton did best in turbid treatments, where the predation from fish was reduced. However, small herbivorous zooplankton dominated over larger *Daphnia* in clear water treatments with *Chaoborus* but no fish. Wissel *et al.* (2003) related this to the altered distribution pattern in clear water, where the smaller herbivores concentrated nearer the surface, the larger herbivores deeper down and the invertebrate predators more evenly in the water column. Thus, the increased light may have generated a perceived feeling of risk that increased the spatial overlap between large herbivores and invertebrate predators. This behavioural response had a strong effect on the structure of the food web (Wissel *et al.* 2003). Similarly, Romare & Hansson (2003) added caged piscivores to an enclosure with planktivores (roach) and herbivores (*Daphnia*). The presence of piscivores caused planktivores to spend more time in the safer (vegetated) habitats, and this triggered large *Daphnia* to increase time spent in open waters. In this behavioural cascade herbivores had only one predator, and the planktivore had reduced efficiency in the safe habitat shared with the herbivores.

Asymmetry in predator effects should occur in any system where predator 1 consumes predator 2 and prey, and the best response to increasing threats from predator 1 for both predator 2 and prey is to hide in the same habitat. This tends to increase the spatial overlap between predator 2 and prey, and at some point it may become profitable for the prey to move back to the habitat where it is exposed to predator 1.

The prey exposure to fish predators varied with B_F ; at lower fish abundance the model predicted that zooplankton should be larger before the onset of strong DVM (Fig. 5). Therefore smaller zooplankton remain vulnerable to fish at larger sizes at low fish abundance. On the other hand, a higher abundance of zooplankton may lead to major changes in predation from fish due to the behavioural responses of prey. Such shifts in exposure between predators represent a major challenge to models, including organisms with flexible behaviour, in systems where behavioural cascades are prominent. In these systems, major changes in abundance or distribution of predators will induce behavioural changes

in their prey and transfer of energy between trophic levels will be altered.

A wide range of explanations of diel rhythms of zooplankton migration has been suggested (reviewed in Pearre 2003), and only a limited number has been addressed here. Our model suggests that the optimal positioning of zooplankton in a water column is sensitive to environmental gradients, abundance and distribution of predators. The model predicted DVM patterns to depend on mixed layer depth and the relative shapes of growth and mortality rates. When growth can be achieved at lower risk, as with a deeper mixed layer depth, the value of daytime migration decreases.

The optimality framework that we have applied here has two main limitations. First, it is difficult to incorporate a behavioural response in the predator to the defensive strategy of its prey. This implies that the model does not fully 'put predators back into behavioural predator-prey interactions' in the game-theoretical meaning of Lima (2002). Secondly, the model does not allow for environmental feedback mechanisms to operate. Thus, the consequences of behaviour of either predators or prey on population dynamics or food web structure cannot be modelled realistically (Persson & De Roos 2003). To include such processes, simulations with individual-based models including explicit genetic structure governing behavioural responses (Eiane & Parisi 2001; Strand, Huse & Giske 2002; Giske *et al.* 2003) or models with rule-based individual behaviour (Persson & De Roos 2003) may be more suitable. However, our model allows explicit solutions, and is valid when prey has safe refuges or prey responses dominates.

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Paper 2

Sigrunn Eliassen, Christian Jørgensen & Jarl Giske. (2006) Co-existence of learners and stayers maintains the advantage of social foraging. – *Evolutionary Ecology Research* **8**: 1311-1324

Co-existence of learners and stayers maintains the advantage of social foraging

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ABSTRACT

Question: To what extent can learning facilitate group formation in a social forager?

Model features: An individual-based simulation model is used to explore frequency- and density-dependent interactions between mobile learners and non-selective stayers that forage in a patchy resource environment.

Key assumption: Foraging efficiency peaks at intermediate group sizes.

Conclusions: Frequency-dependent interplay between mobile learners and sedentary stayers represents a general mechanism of group formation that maintains the advantage of social foraging. When rare or at moderate frequencies, learners redistribute and aggregate in groups of optimal size. This enhances the foraging performance of both learners and stayers. When the learning strategy dominates in the population, group size dynamics become unstable, resource intake for learners drops, and stayers do best. The strategies mutually benefit from each other and may potentially co-exist.

Keywords: frequency dependence, group formation, group size, individual-based model, learning, optimal foraging theory, social foraging.

INTRODUCTION

Animals that live in groups interact with conspecifics through competition and cooperation. Social foragers experience both costs and benefits of being in a group: increased foraging rates may result from improved search and attack efficiency or sharing of information among group members, whereas vigilance or dilution effects may reduce predation risk (reviewed in Giraldeau and Caraco, 2000; Krause and Ruxton, 2002). Competition and interference will eventually reduce the benefits of increasing group size, and as a consequence resource intake rates of social foragers often peak at intermediate group sizes.

The group size that maximizes individual food intake may, however, be evolutionarily unstable (Sibly, 1983; Clark and Mangel, 1984). Solitary foragers may benefit from joining a group as long as the intake rates of group members are higher than those for solitary foragers (see Fig. 1). Group size will then increase above the optimum, and eventually reach an equilibrium size at which group foraging has no advantages. This has been referred to as the

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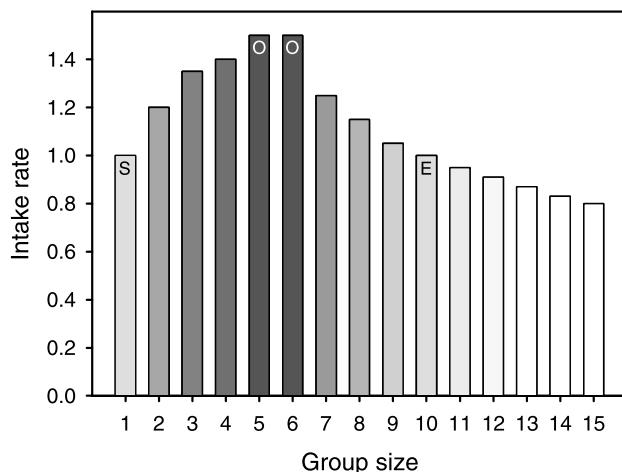


Fig. 1. The relationship between group size and individual resource intake per time step (adapted from Beauchamp and Fernández-Juricic, 2005). The letters denote resource intake rate of individuals foraging solitarily (S), in a group of optimal size (O), and in a group at the equilibrium size (E). The intensity of the grey shade is proportional to the intake rate of foragers in a group of that particular size; the shading corresponds to that used in Figs. 2 and 3.

paradox of social foraging, and the argument relies on the assumptions that (1) solitary foragers are free to enter a group at no cost (Giraldeau and Caraco, 2000), (2) foragers know the profitability of joining a group versus foraging alone, (3) individuals act sequentially and move solitarily between patches (Kramer, 1985), (4) group members are not genetically related (Giraldeau and Caraco, 1993; Higashi and Yamamura, 1993), and (5) resources are divided equally among group members (Hamilton, 2000). In this study, we address the first two of these assumptions.

For solitary foragers, the benefits of joining a foraging group must be outweighed by the costs of acquiring group membership. Individuals that move between groups experience reduced foraging time. Travelling may also elevate energy expenditure and increase exposure to predators. Foragers commonly experience trade-offs where high performance on one ecological function (e.g. dispersal) reduces performance on another task (e.g. foraging efficiency). Foragers may therefore differ in their mode of exploiting resource patches. Co-existence between explorative and sedentary foraging strategies has been reported in several systems, including rodents (Kotler and Brown, 1988; Benus *et al.*, 1991) and marine and freshwater snails (Wilson *et al.*, 1999; Chase *et al.*, 2001). In *Drosophila melanogaster*, ‘rover’ larvae travel long distances and often abandon food patches, whereas ‘sitters’ move to the nearest patch and feed there (Sokolowski, 1980; Sokolowski *et al.*, 1997). In the nematode *Chaenorhabditis elegans*, a similar co-existence exists between social foragers that aggregate in areas where food is most abundant and solitary feeders that distribute more randomly (de Bono and Bargmann, 1998; de Bono, 2003).

The mechanism by which an individual assesses the potential benefits of foraging in groups has seldom been considered in social foraging theory. Part of the problem concerning the ‘paradox of group foraging’ is the lack of a general theory explaining how groups form and split. In a recent contribution, Beauchamp and Fernández-Juricic (2005) proposed that if foragers were able to learn the quality of a patchily distributed resource, they could abandon under- and over-crowded patches and keep group sizes close to an optimal value. They argued that such a learning mechanism would solve the apparent paradox of group

foraging. However, they did not analyse the performance of their learning rule to determine whether the individual behavioural strategy was adaptive and evolutionarily stable.

The aim of this study is to establish whether learning may facilitate group formation in social foragers. Learners have to estimate environmental resources from experience and spend time travelling between foraging groups (replacing assumptions 1 and 2 above with more ecological realism). The cost of information (sampling and movements) and the benefits of using information (ending up in a better group) determine the profitability of the strategy; these are emergent properties of the interaction between foragers and the environment in our model. By studying the frequency- and density-dependent dynamics of mixed populations of mobile learners and sedentary foragers, we illustrate how co-existence between these two strategies may be evolutionarily stable. Learning is thus one mechanism that may explain group formation and thereby maintain the advantage of social foraging.

METHODS

We use an individual-based simulation model to explore group size dynamics in a population of social foragers. The environment consists of discrete identical food patches with renewable resources. Intake rate is a dome-shaped function of group size, where foragers in a group of intermediate size experience the highest intake rate [Fig. 1 (modified from Beauchamp and Fernández-Juricic, 2005)].

Foraging strategies

We distinguish between two types of foraging strategies: *stayers* are non-selective and remain within the first foraging patch they encounter; *learners*, on the other hand, may travel between foraging patches and search for groups of preferred size. These mobile foragers need to sample their environment to estimate its quality. The two strategies are analogous to the learning and non-learning foragers in Beauchamp and Fernández-Juricic (2005), with modifications in the learning algorithm, search behaviour, and the patch-leaving rule. Briefly, learning foragers know their current intake rate and use experiences from visited patches to estimate the global average intake rate in the environment. This global intake rate is then compared with their current intake rate to determine when to stay and when to leave a patch (detailed description below).

Resource intake and learning

All resources are found in patches, which are renewed every time step. Time is discretized in the model, and the duration of a time step is short compared with the period over which behaviour is studied. In each time step, the forager locates and consumes food if it is not travelling. Individual resource intake rate during time step t is denoted $i(t)$ and is determined exclusively by the numbers of foragers in the patch (Fig. 1). Average resource intake rate in patch P for a forager that enters at time step t_1 and leaves again at time t_2 is:

$$\bar{i}_P = \frac{1}{t_2 - t_1} \sum_{t=t_1}^{t_2-1} i(t)$$

Learning foragers update their expectation of the average resource intake rate in the habitat according to their experiences in patch P using a linear operator rule (Mangel, 1990):

$$E_P(i) = (1 - \alpha) E_{P-1}(i) + \alpha \bar{i}_P$$

The expected intake rate in the environment $E_P(i)$ is hence a weighted average of experiences from previously visited patches, $E_{P-1}(i)$, and the average intake per time step in the current patch, \bar{i}_P . At the beginning of the season, all learners have the same naive expectation of the average intake rate in the environment $E_0(i)$. The learning factor α represents an exponentially decaying memory, and its value determines the relative emphasis put on recent information. The model's sensitivity to learning rule parameters was tested for $E_0(i)$ in the range 0.8–2.0 and for α between 0.05 and 0.5. Foragers with high $E_0(i)$ are initially 'choosy' and may search for a long time before they settle in a patch, whereas non-selective foragers have $E_0(i)$ close to 1.0 and behave similar to stayers. The rate of learning increases with α , and a higher α is needed to trace a more rapidly changing environment. However, high learning factors also introduce more variability in the environmental estimates (see McNamara and Houston, 1987; Hirvonen *et al.*, 1999). The learning rule performed well and was relatively unaffected by changes in α between 0.1 and 0.2 as long as $E_0(i)$ remained within the range 1.1–1.4. We therefore used $\alpha = 0.1$ and $E_0(i) = 1.3$ throughout.

Patch-departure rule

We employ a patch-leaving rule inspired by the marginal value theorem (Charnov, 1976). Mobile foragers compare their expectations of future resource intake in the current patch to the expected profitability of searching for another resource location. Learners leave a patch if:

$$i(t)[T - t] < E_P(i)[T - t - t_s]$$

A forager that remains in a patch expects to receive the current resource intake rate $i(t)$ until the end of the season T . A forager that leaves a patch at time t will travel for a fixed time t_s before encountering a new patch with expected intake rate $E_P(i)$. Foragers are predicted to become increasingly reluctant to leave a patch when the end of season approaches. All foragers move solitarily between patches, and have an equal probability of ending up in any resource patch within the habitat. We present results from model scenarios with $t_s = 25$ time steps, but the model was tested for travel times ranging from 2 to 50 time steps. The cost of information acquisition increases with travel time, which thereby affects the foraging performance of learners. Dynamics of the interaction between the foraging strategies were, however, persistent to changes in travel time within this range.

Initialization and model observations

At the start of a foraging season, half the individuals in the population were randomly distributed among the 200 resource patches, while the other half were allowed to search for a patch with random travelling times ($\leq t_s$) remaining. A foraging season lasted 3000 time steps, and to prevent artificial patterns from synchronous updating (see Ward *et al.*, 2000), individuals made their patch-leaving decisions in a new random sequence every time step.

Group size distributions and intake rates were averaged over the whole foraging season and not only after reaching equilibrium distributions. In this way, we include the emergent

costs of sampling that learners accumulate during foraging periods of finite length. Forager distributions and average resource intake rates were averaged over 100 replicates, each having the same constant population size and frequency of learners. The relative frequencies of the two foraging strategies were altered from pure stayer populations, increasing the frequency of learners in steps of 2%, to monomorphic learner populations. We ran each simulation set (all learner frequencies and 100 replicates) for population densities ranging from 50 to 2000 individuals. This corresponds to an average density of 0.25 to 10 foragers per available resource patch in the environment. We present the results from the model scenarios with a constant population size of 500 individuals (population density 2.5), unless otherwise stated explicitly.

We call the frequency of learners at which the mean intake rate of stayers equals that of mobile learners the *equilibrium* frequency of the mixed strategy population. At a given population density this represents a Nash equilibrium, since the intake rate of each strategy drops as its relative proportion increases (see below).

RESULTS AND DISCUSSION

Learners move between foraging locations, alter group size distributions, and affect intake rates of other foragers within the habitat. The overall effects depend strongly on the prevalence of learners within the forager population. In the following, we (1) focus on the ecological dynamics and group size distributions as the frequency of learners changes, (2) analyse the performance of each strategy and its evolutionary implications, and (3) investigate how the performance of each strategy depends on population density.

Ecological dynamics and group size distributions

The distribution of group sizes depends on the relative frequency of movers and stayers within the population (Fig. 2). When alone, stayers distribute randomly because they settle in the first patch they encounter (left-hand side of Fig. 2a, b). When learners are introduced, they aggregate in foraging groups (from left to right in Fig. 2a, c) and consequently the number of occupied foraging patches decreases (Fig. 2a). In populations of learners only, foragers use only one-third of the available resource patches (right-hand side of Fig. 2a).

Mobile learners experience different group size distributions than stayers (Fig. 2b, c). At low densities, learners are able to explore the spatial distribution pattern produced by stayers and thereby locate more profitable patches. This increases the number of groups of preferred size (Fig. 2c), and the population quickly reaches a stable pattern of group sizes (Fig. 3a). At higher frequencies of learners, aggregation results in over-crowded groups. The fraction of learners that moves between patches increases: (1) because the number of occupied patches drops, and learners therefore need to visit several patches before they locate a foraging group; and (2) as groups grow larger than optimal, newcomers reduce the intake rate of other group members and thereby trigger patch-leaving events (Fig. 2a, c). As a consequence, it takes longer for the population to reach stable group size distributions (Fig. 3b) and learners are more often found in groups that are larger than optimal (Fig. 2c).

The perspective is slightly different from the stayers' point of view (Fig. 2b). Their resource intake is directly influenced by the rearrangement of groups caused by the movement of learners. Stayers tend to become solitary when learners abandon under-crowded patches (Fig. 2b). At the same time, stayers often function as crystallization seeds,

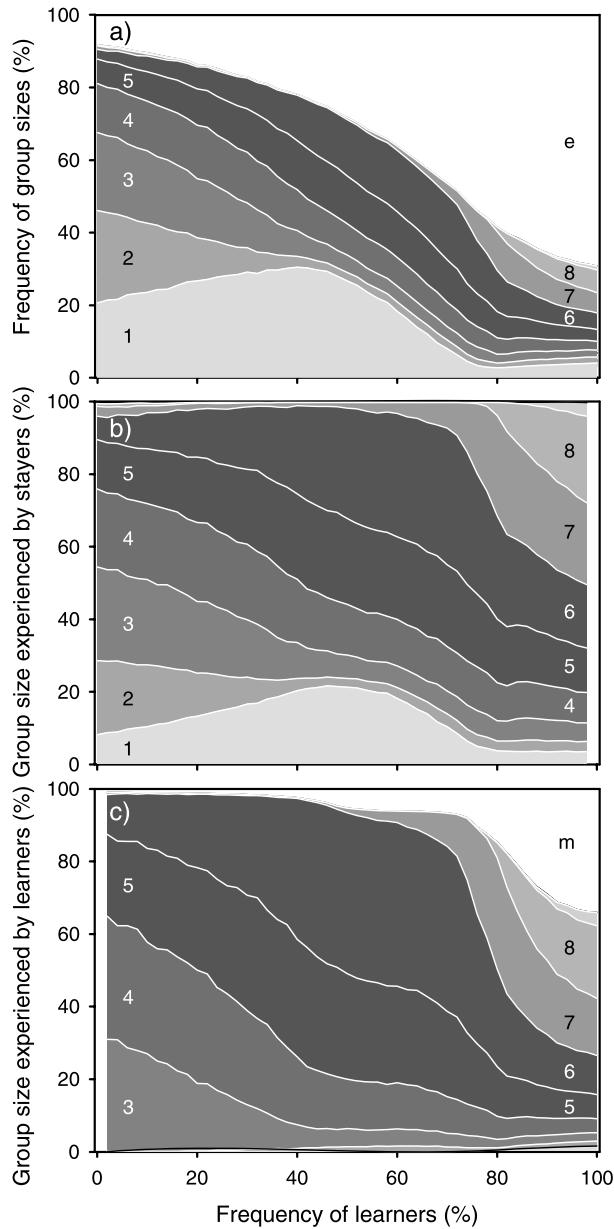


Fig. 2. The distribution of group sizes as a function of the frequency of learners in the population. (a) The frequency of *patches* with different group size. The proportion of patches that are empty is indicated by ‘e’. (b) The group size experienced by *stayers*. (c) The experienced group size for mobile *learners*. Individuals on the move between patches are indicated by ‘m’. The intensity of the grey shade is proportional to the intake rate of foragers. Distributions were averaged over 100 simulations for each of 50 populations varying in frequency of learners.

and stayers that reside in patches where learners aggregate benefit as learners bring group sizes closer to optimal.

Performance and evolutionary considerations

The average long-term intake rate gives a measure of each strategy’s foraging performance (Fig. 4a). First, note the advantage of being rare: at low frequencies, both learners and

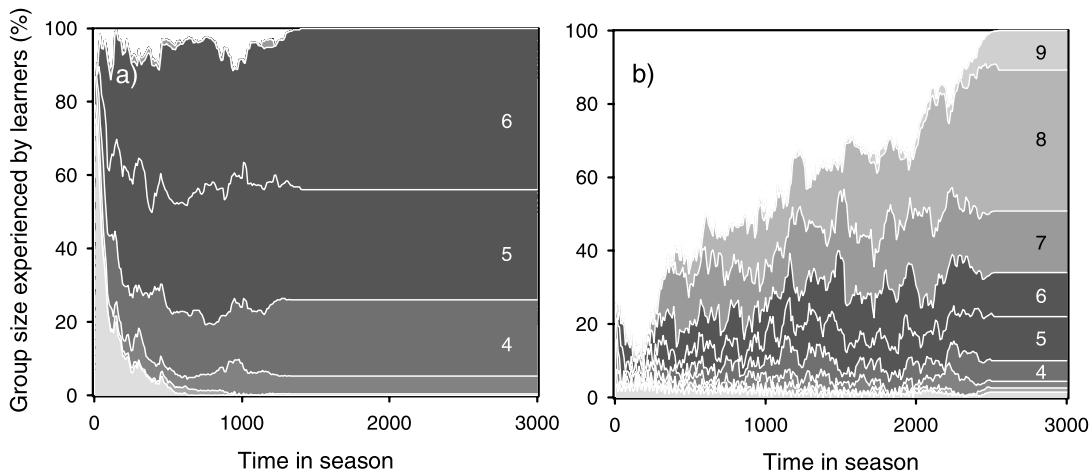


Fig. 3. The group size distributions experienced by learners in a population of (a) 40% and (b) 100% learners as a function of time in season. The intensity of the grey shade is proportional to the intake rate of foragers. The distribution of 500 individuals among 200 patches was calculated every time step.

stayers have a higher long-term intake rate than the more abundant strategy. The redistribution of learners enhances performance of both foraging strategies at low to intermediate frequencies of learners. The variation in long-term intake rate among stayers is larger, however, since learners are able to actively aggregate in groups of preferred size (Fig. 4b). The performance of learners peaks at intermediate frequencies, while stayers continue to benefit as learners become more prevalent. At the equilibrium proportion of 62% learners, the long-term intake rate of learners equals that of stayers. At high frequencies, learners experience a dramatic reduction in foraging performance (Fig. 4a).

The frequency-dependent foraging performance arises because learners and stayers alter the spatial and temporal variability in intake rates within the environment. At low frequencies, learners do well because they exploit the spatially heterogeneous but temporally stable distribution of stayers (Fig. 4c). Such populations quickly attain stable distributions of profitable group sizes (Fig. 3a). Learners aggregate in larger groups, hence the spatial variance in intake rate continues to increase until the two strategies are equally represented in the population. The spatial variation in intake rate decreases when mobile learners become even more abundant, since the number of solitary stayers declines (Fig. 4c).

Mobile learners not only influence the spatial variability, but also alter the temporal stability of groups (Fig. 4c). At high frequencies of learners, the temporal variability *within* a patch approaches the spatial variation among groups and the performance of the learning strategy declines dramatically. At this point, good patches are ephemeral. Foragers have almost the same probability of experiencing profitable group sizes by staying in the same patch as they would by searching for a new one. In such circumstances, stayers prosper because they need not pay the cost of travelling. When the learning strategy dominates, group size distributions stabilize late in the season and with relatively many groups being larger than optimal (Fig. 3b).

Effects of population density

So far, we have considered model scenarios where the number of resource patches is sufficiently high to allow foragers to choose between solitary and group foraging. We now

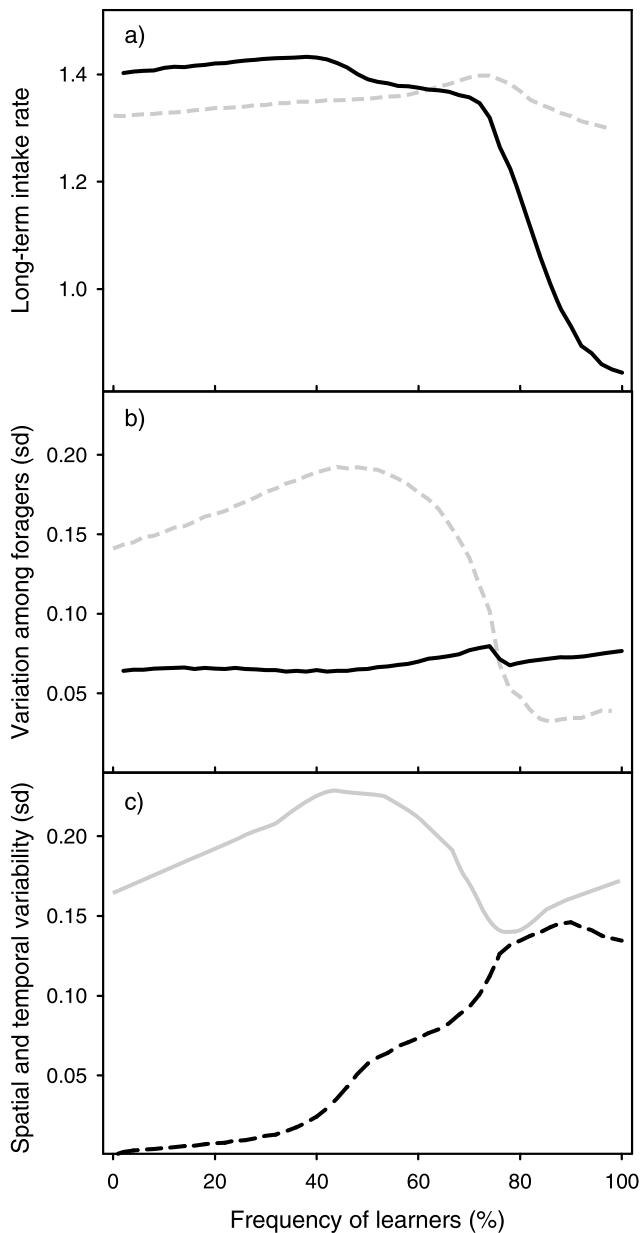


Fig. 4. Average foraging performance, individual variation, and spatial and temporal variability among groups as a function of frequency of learners in the population. (a) Average long-term intake rate of learners (black solid line) and stayers (grey dotted line), (b) variation in long-term intake rate among learners (black solid line) and stayers (grey dotted line), and (c) the temporal variability *within* each occupied patch (black dotted line) and the average spatial variation *among* occupied patches (grey solid line) (standard deviation of intake rates; sd).

consider how population density affects intake rates and the dynamics between the two strategies. Intake rates of learners are always lower than for sedentary foragers in populations consisting of one strategy only (Fig. 5a). When both foraging strategies are present at equilibrium proportions, foragers have a higher mean intake rate than they would have in pure populations of each of the two strategies. This means that there is a potential for stable co-existence between the two strategies at all population densities tested.

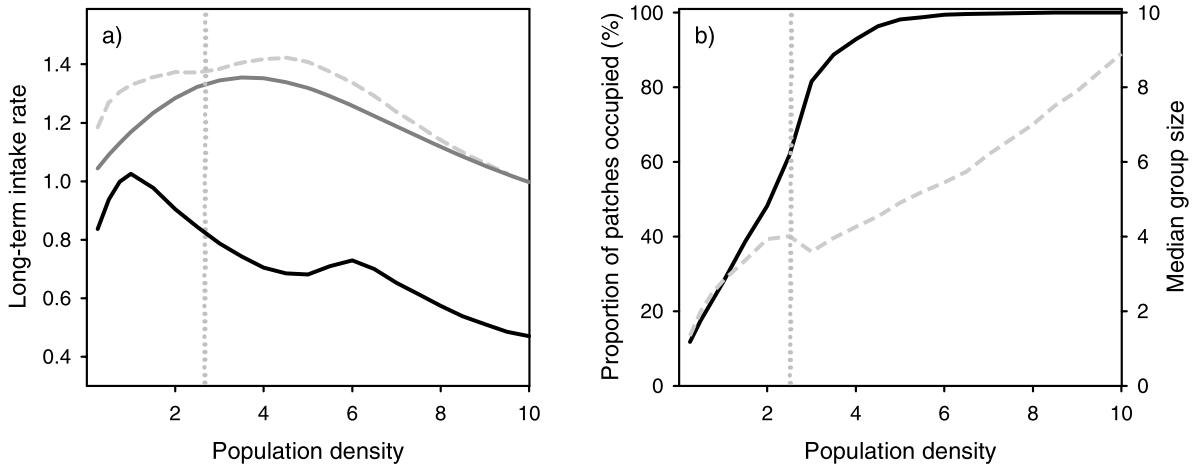


Fig. 5. (a) Average long-term intake rate of foragers as a function of population density (the x-axis gives the average number of foragers in the environment per resource patch available). The average performance of foragers in the mixed-strategy populations at the equilibrium proportion of learners (grey dotted line) is higher than for monomorphic learner populations (black solid line) and stayer populations (grey solid line). (b) The proportion of patches occupied by foragers (black solid line) and the median group size (grey dotted line) in mixed-strategy populations at the equilibrium frequency of learners. The vertical dotted line gives the population density for the model scenarios used in Figs. 2–4.

Overall, the highest intake rates are attained in a mixed population where the density of foragers is close to the optimal group size of 5–6 individuals per patch (Fig. 5a). At this point there are foraging groups distributed among all resource patches and median group size lies at the optimum (Fig. 5b). Sedentary foragers distribute randomly and are therefore better off at slightly lower population densities (Fig. 5a), since the reduction in intake rate is more severe in over-crowded than in under-crowded patches (cf. Fig. 1). In general, pure populations of learners do best at low population densities, since patches seldom become over-crowded (Fig. 5a). The intermediate peaks in long-term intake rate result in part from how parameters of the learning rule ($E_0(i)$ and α) interact with the intake rate function.

The frequency of learners in the equilibrium population also varies with population density and peaks at low to intermediate densities (Fig. 6). This population size covers the transition region between two separate challenges: in dilute populations the challenge is to locate other foragers to form groups of optimal size, while in dense populations the challenge lies in over-crowding and dealing with a limited number of resource patches. As patches become over-crowded, learners quickly suffer from frequent movements and the equilibrium frequency drops. At high densities, the distribution of foragers is Pareto optimal in the sense that individual foragers cannot increase their resource intake by joining a new group without simultaneously decreasing the intake rate of resident group members (Clark and Mangel, 1986). In such circumstances, it may be more advantageous for resident group members to defend the limiting resource and restrict the access of solitary joiners. When resources are not restricted to a limited number of patches, social foragers seek to aggregate in groups of appropriate size. In such systems, we expect the interplay between mobile and sedentary strategies to be most important.

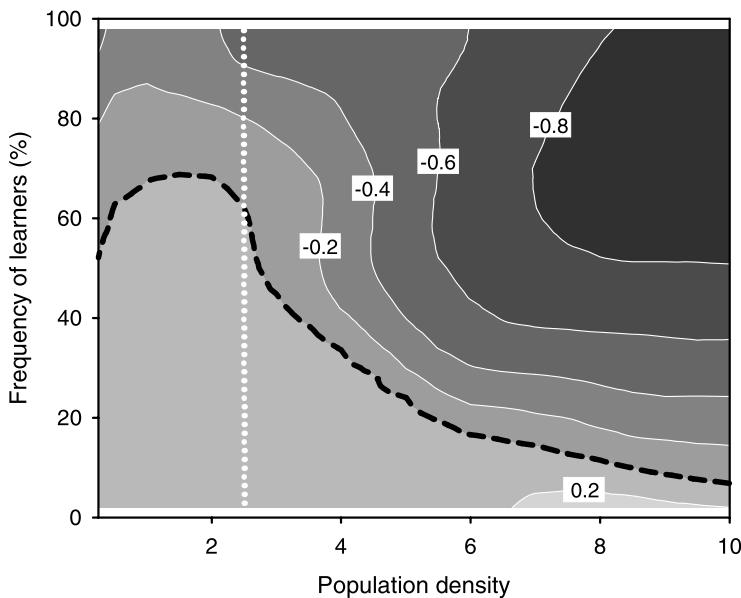


Fig. 6. Difference in average food intake of learners compared with stayers as a function of forager density and frequency of learners in the populations. Population density is given as the average number of foragers in the environment per resource patch available. The dashed line gives the equilibrium frequency of learners in the mixed populations. Below this line, average intake rate is higher for learners than for sedentary foragers. Above the line, the intensity in the grey shade gives the relative decrease in intake rate of learners compared with stayers. The vertical dotted line corresponds to the population density of the model scenario used in Figs. 2–4.

GENERAL DISCUSSION

Learners are able to aggregate in groups of more optimal size and may improve foraging performance in populations of social foragers that benefit from being in groups of intermediate size. The learning strategy will, however, not out-compete non-selective sedentary strategies. As learners become abundant, group size dynamics turns inherently unstable and the performance of the learning strategy drops dramatically. In this way, learners alter the environmental heterogeneity and interact with the environment in intricate ways. The frequency-dependent perspective of our analysis reveals how learners and stayers may mutually benefit from the presence of each other and thus potentially co-exist. In the following, we will (1) discuss how the profitability of mobile strategies depends on spatial heterogeneity and temporal stability, (2) investigate how frequency dependence arises from feedbacks between the strategies and the environment, (3) highlight the relevance for social foraging theory, and (4) briefly discuss some consequences for the potential co-existence of foraging strategies.

Mobile strategies require persistent cues to explore spatial heterogeneity

Habitats are seldom uniform; hence mobile foragers may exploit spatial heterogeneities by searching for better than average locations. This requires an estimate of patch quality and a measure of the general resource conditions within the environment. Environmental

information could be incorporated in behavioural rules of thumb (inherited mechanisms adapted to prevailing environmental conditions), or acquired through learning from individual experiences within a lifetime (McNamara *et al.*, 2006). Although the underlying behavioural mechanisms of learning are more complex than a fixed patch-leaving strategy, the assumptions one has to make about information flow are simpler. Foragers gather information as they search the resource habitat; hence the quality of information is an emergent property of the feeding and movement behaviour. Learning is generally favoured when there is some structure or persistence in the information stimulus and some variability within or between generations to favour flexible behavioural responses (Stephens, 1991, 1993). The ability of learners to explore the spatial heterogeneities hence relies on some temporal inertia in the group size distributions. In our model, current resource intake is a good estimate of future gain when foragers have strong site fidelity, but the persistence in this signal fades as mobile learners increase in numbers.

Feedback between learners and the environment causes frequency dependence

Foraging theory has commonly focused on how behavioural strategies are adapted to different environmental conditions (Stephens and Krebs, 1986). This perspective neglects that adaptations may also shape the environment to which they respond (Dieckmann and Ferrière, 2004; Nowak and Sigmund, 2004). Frequent movements to sample foraging options inevitably alter the surroundings, as illustrated in our model. This potentially makes the task of learning more challenging, and may reflect a fundamental property of explorative strategies.

The fitness of a strategy often depends on its prevalence within the population. Dynamics of social foragers have therefore commonly been analysed using game-theoretic approaches (reviewed in Giraldeau and Caraco, 2000). In foraging groups, behavioural strategies that actively search for resources (producers) may co-exist with individuals that exploit the foraging opportunities created by others (scroungers). Parasitic scroungers reduce the average resource intake rate in populations of producers (Vickery *et al.*, 1991; Barta *et al.*, 1997). This contrasts the mutual benefit that learners and stayers experience in our model, where mixed equilibrium populations achieve higher intake rates than monomorphic populations. It is the resource dynamics mediated by the strategies themselves that creates the potential for co-existence.

Learners benefit from the presence of other learners at low frequencies because they facilitate aggregation. An increased frequency of learners has a detrimental effect, as it causes over-crowding and unstable patch-leaving dynamics. These emergent frequency-dependent interactions illustrate how difficult it is to simply parameterize the costs and benefits of such dynamic relationships. As opposed to traditional game-theoretic approaches, individual-based models handle temporal dynamics and constantly changing competitive relationships between strategies. Our results suggest that the performance of even the simplest strategies strongly depends on the biotic environment, and that the dynamic interactions between foraging strategies and their resource environment may be more important than hitherto reflected in foraging models.

Relevance for social foraging theory

The paradox of group foraging (Sibly, 1983; Clark and Mangel, 1984), namely that solitary foragers would continue to join groups until there is no benefit of social foraging, relies on the

assumption that foragers are free to move between groups at no cost. Whenever foragers need to spend time locating a group, the benefits of joining more optimal groups must be traded off against the direct and indirect costs of moving. This has several implications for social foraging models. First, that learning foragers may keep group sizes close to the optimal value (Beauchamp and Fernández-Juricic, 2005) does not guarantee that the behavioural mechanism is advantageous or evolutionarily stable. Learners have to pay costs related to habitat exploration, hence the long-term intake rate of the strategy needs to be evaluated (Beauchamp and Ruxton, 2005). Second, the foraging efficiency of monomorphic populations may give an erroneous picture of the overall performance of a behavioural strategy. In our model, learners did quite well when rare but never performed better than stayers in pure-strategy populations. Third, in our model the benefits of mobility – that is, the increased average intake rates achieved by abandoning over- and under-crowded patches – depend on the temporal stability of the system. This emphasizes the need to consider dynamic movement patterns of all foragers in a population, and not only sequential choices made by solitary foragers.

We consider a system where resources constantly renew, which allows us to focus on the density-dependent part of the food intake function. In many natural systems, resources show only partial recovery or foragers experience diminishing returns due to reduced search or handling efficiency. In such circumstances, groups deplete patches more quickly than solitary foragers, and will spend more time travelling between patches (Beauchamp and Ruxton, 2005). This reduces the potential benefit of foraging in large groups compared with completely renewing environments (Beauchamp and Ruxton, 2005). In such situations, patch-leaving decisions are influenced both by group size and patch longevity. Foragers are thus faced with a dual problem: when to leave a patch and when to leave a group. If group members were able to synchronize their movements between patches, learners could compare their average performance within one group (both feeding and searching) to the profitability of joining differently sized groups. Foragers with strong group fidelity (analogous to stayers) and learners that select between groups could then potentially co-exist whenever group search is time-consuming or involves additional costs such as increased risk of predation. Learning and the logic of patch-leaving behaviour may thus apply to several hierarchical levels, which motivates further studies on how individual rules and mechanisms scale up to collective decisions and group cohesion (Sumpter, 2006).

Co-existence between social foraging strategies: an evolutionary outcome?

When rare, both learners and stayers performed better than the more abundant strategy. The strategies are therefore mutually invadable, meaning that they may spread from low frequencies (and thus potentially arise from single mutations). The strong frequency dependence between learners and stayers suggests two evolutionary outcomes. First, the benefit that each strategy gains from the presence of the other may facilitate stable co-existence. Alternatively, the poor performance of the learning strategy when present at high frequencies may select for more robust behavioural mechanisms. This includes foraging strategies that more actively search for foraging groups, sub-group formation with synchronized movements, and individual recognition. Learners could potentially assess group size dynamics using more environmental cues and thereby adjust to temporal instability. The problem of mobile strategies may, however, be more fundamental, as the temporal fluctuations within a patch and the reduced spatial variance among patches would

eventually decrease the efficiency of any mobile strategy. One option could be foraging strategies that switch between mobile and sedentary modes. Such strategies may be less efficient than obligate learners, however, since lower sampling frequencies introduce more uncertainty in environmental estimates. Such behavioural trade-offs in information acquisition may be interpreted in a specialist–generalist context (Dall and Cuthill, 1997).

Individuals or strategies that differ in movement behaviour will most likely differ in the way they gather information and put it to use (Sokolowski, 1998). Such strategies will not necessarily differ in overall performance, but will probably show differences in the trade-off between exploration and exploitation, or variable responsiveness to local environmental conditions. Our results highlight that information exists in an ecological context and is acquired through sampling behaviour, which in turn affects information patterns. Models including full dynamic feedback between the population, the strategies, and the environment facilitate the study of emergent costs and benefits of behavioural strategies and raise interesting questions regarding the underlying behavioural mechanisms of social organization in natural systems.

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Paper 3

Sigrunn Eliassen, Christian Jørgensen & Jarl Giske. Exploration or exploitation: life expectancy changes the value of learning in foraging strategies. – *Manuscript conditionally accepted in Oikos*

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

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Abstract

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 trade-off 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.

Introduction

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 resource exploitation or other activities (e.g. Stephens, 1987; Krebs & Inman, 1992). Traditional models of patch use (Charnov, 1976) and forager distributions (Fretwell & 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 & Vásquez, 1997).

When resource conditions vary temporally, new experiences become more valuable than older information, and a foragers should bias its estimate towards recent information (McNamara & Houston, 1985, 1987). However, with more weight given to each sample, estimates becomes more sensitive to natural variability and sampling errors (McNamara & Houston, 1985; Hirvonen *et al.*, 1999). In changing environments, this imposes a trade-off 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 & 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, 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 information and resource harvesting (Clark & Mangel, 1984). This does not necessarily mean that foraging and sampling are mutually exclusive behaviours. Commonly there is an interaction between the two (e.g. 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 & 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.

Behaviours commonly range from those that are unaffected by specific experiences to those that wholly depend on them (Arak & Enquist, 1993; Papaj, 1993; Dukas, 1998). 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 & Mangel, 1986). Hence, to predict the way optimal learning strategies change with environmental characteristics, we need to understand the trade-offs 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 through the forager's lifetime. The acquisition of information is treated as an integral part of the patch-leaving behaviour, which emphasizes the trade-off between investment in

exploration (information harvesting) and exploitation (immediate foraging reward). We study how learning strategies reflect the trade-off between the rate of information updating and the resulting uncertainty in estimates. Costs and benefits of learning are dynamic properties that depend on local patch assessment, the updating mechanism, and characteristics of the resource environment. We aim at evaluating how risk of mortality may alter the trade-off between exploration and exploitation, and thus change patch sampling effort and 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. *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. We use a genetic algorithm to evolve learning factors and initial giving-up thresholds. To track temporal changes in average resource conditions, a learner may 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. We compare behaviour and performance of *Learning Foragers* to:

- 1) *Informed Foragers* that have free access to information about the global resource level. They know the optimal giving-up threshold and how it responds to seasonal changes in resource conditions.

2) *Fixed Foragers* that use a single genetically determined giving-up threshold throughout the foraging season, thereby ignoring information about 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 and to *Informed Foragers* in order to evaluate the costs of uncertainty. 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 a 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 exceeds P_e the forager will hence encounter one resource. A forager can handle no more than one resource 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, a 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 &

Houston, 1987; Mangel, 1990) and like Bayesian updating rules it integrates prior estimates and new data.

Evolving behavioural strategies

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 a forager, but the initial giving-up threshold τ_0 is updated by experience. We find the best combination of learning factors and initial giving-up thresholds using a genetic algorithm (Sumida *et al.*, 1990; Holland, 1992). The learning factor may take any value between 0.0 and 1.0, and initial giving-up thresholds range from 1.0-50.0. Each model run was initiated with a population of 10 000 foragers, having randomly assigned values of τ_0 and γ . We evaluated the performance of the patch-leaving strategies by simulating individual foraging behaviour under different environmental conditions. Mortality is a stochastic process in the model, and all individuals have an equal probability P_s of surviving each time-step until the end of season T when all foraging activity ceases. Mortality rate does not change between years and we only consider within-year variation in resource levels.

In order to produce an offspring, a forager needs to accumulate a certain amount of resources. A constant fraction of the offspring survives and produces a new population of foragers that enter the foraging habitat next season. The fitness of a forager is hence proportional to its offspring production, which in turn depends on the amount of resources accumulated during a lifetime.

The genetic strings are haploid in the model and trait values are coded as continuous numbers. An offspring inherits both the learning factor and the initial giving-up threshold from its parent, unless the genetic traits are recombined with a randomly chosen partner. Recombination occurs with a probability M_r and then the offspring inherits one trait from each parent. There is a probability M_m that mutations may alter a trait and change its initial value by some random fraction M_s . We evolved the learning

rule traits for 3000 generations and used population means of τ_0 and γ when comparing foraging performance between strategies and resource environments.

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 & McNamara, 1999; Clark & 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* *i*) have to decide on a giving-up threshold when they enter a patch, *ii*) within each patch they rely on time between stochastic resource encounters to estimate the local patch quality, and *iii*) they update their giving-up threshold only as they shift between patches. As a consequence, the behavioural mechanisms of *Learning* and *Informed Foragers* 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 for free. As a consequence they spend more time outside foraging patches.
- 2) *Cost of uncertain estimates* 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).

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

Variable or parameter	Description	Standard value(s) (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_t	Resource level in environment (per patch) at time t	5-55 (0-60)
R_0	Initial resource level in patches	5 (0-60)
r_t	Resource level in local patch	0-55 (0-60)
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 <i>Learning Foragers</i>	1.0-50.0
τ_p	Giving-up threshold in patch p for <i>Learning Foragers</i>	
τ_F	Giving-up threshold of <i>Fixed Foragers</i>	1 - 50
$\tau^*(t)$	Optimal giving-up threshold of <i>Informed Foragers</i> at time t	1 - 50
M_m	Mutation rate	0.01
M_s	Mutation step length	0.5-10 %
M_r	Recombination rate	0.1 (0.0-0.5)
f	Reproductive value of one resource encounter	
F	Maximum expected reproductive output using the <i>Informed</i> strategy	
V	Reproductive value for <i>Informed</i> and <i>Fixed Foragers</i>	
$I_{n_i=\tau}$	Patch-leaving indicator function	0 or 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

Learners behave differently from both *Fixed* and *Informed Foragers*. In the following, we will 1) show that different strategies result in behavioural changes throughout the season, 2) illustrate the temporal distribution of costs and benefits of learning, and 3) show that life expectancy may affect the value of information and thus change behaviour and foraging efficiency.

Patch allocation strategies and sampling rates

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 two levels. First, *Learning Foragers* need to reside sufficiently long in a patch to estimate local patch quality. Second, they need to visit several patches to estimate the global resource conditions. As *Learners* harvest both resources and information, time allocated in each patch represents a trade-off 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, differences in resource intake between *Learning* and *Fixed Foragers* represent the value of learning. The relative performance of each strategy changes through 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. As long as the benefits of updating resource estimates outweigh the costs of sampling, there will be a value of acquiring information from patch experiences (Fig. 1c).

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 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

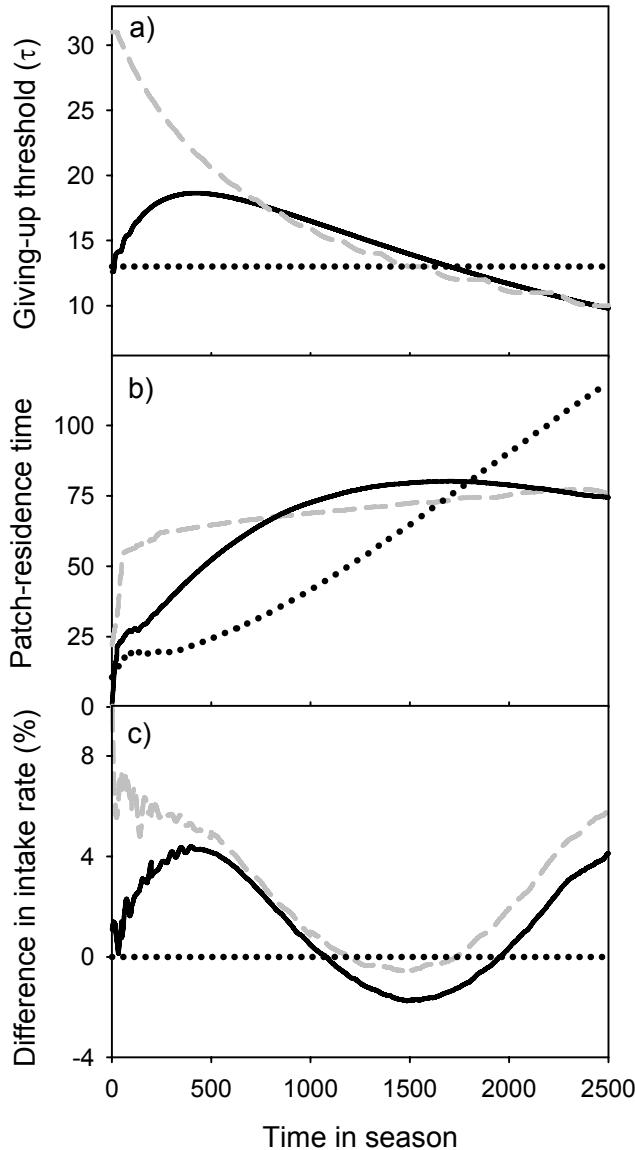


Figure 1. Patch-leaving strategies, patch-allocation behavior and relative foraging performance as a function of time in season. *Fixed Foragers* (black dotted) are restricted to use the same giving-up threshold throughout the season. *Learning Foragers* (black solid) sample the resource environment 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 of *Informed* and *Learning Foragers* relative to *Fixed Foragers* change as resource conditions gradually improve through the season ($g = 0.02$, $R_0 = 5$).

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 free information about changes in average 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* information. First, *Learners* pay a time cost of frequent sampling as they forego foraging opportunities by sampling 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.

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 important 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). As a consequence, learning costs increase later in the season (Fig. 2c).

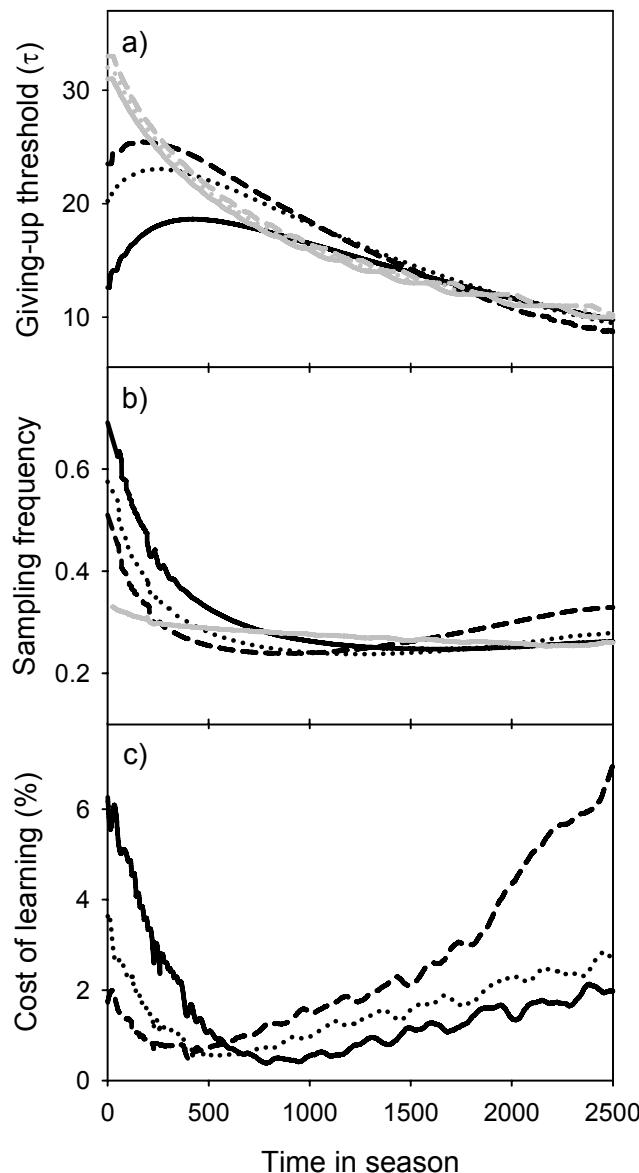


Figure 2. Patch-leaving strategies, sampling frequencies and learning costs as a function of time in season. *Learning* (black lines) and *Informed Foragers* (grey lines) are adapted to high (solid, $m = 0$), intermediate (dotted, $m = 0.001$), and low (hatched, $m = 0.002$) lifetime expectancies. a) 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 uncertain estimates reduce foraging performance later in season. (Standard parameter values as listed in Table 1).

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), foragers evolve fixed strategies with giving-up thresholds similar to the informed strategy. Learning factors generally increase with environmental variation, as has been found also in previous studies (McNamara & Houston, 1985, 1987). The effect is, however, more pronounced in high mortality regimes.

When life-time expectancy decreases, fixed foraging strategies evolve 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 & Visscher, 1994). In environments where

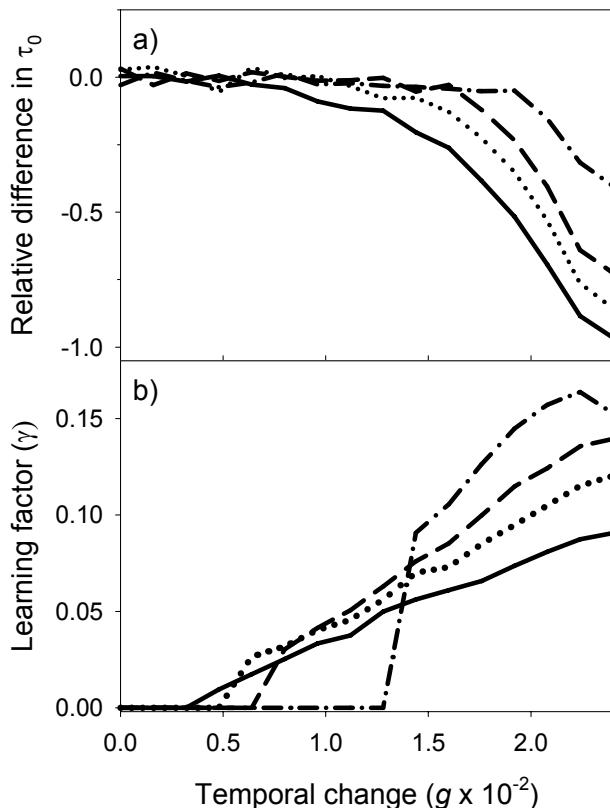


Figure 3. Inherited traits (τ_0 and γ) of *Learning Foragers* adapted to different mortality regimes (solid: $m = 0.000$, dotted: $m = 0.001$, hatched: $m = 0.002$, hatch-dotted: $m = 0.004$). The average resource level equals 30 resources per patch in all environments. Learning rule parameters vary with the rate of temporal change (g) in resource level: a) 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.

resource levels decrease through the season, foragers attain fixed threshold strategies (results not shown). This is because patch sampling then has to take place during the period of prosperous resource conditions early in season, which increases the cost of exploration relative to 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 trade-off 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).

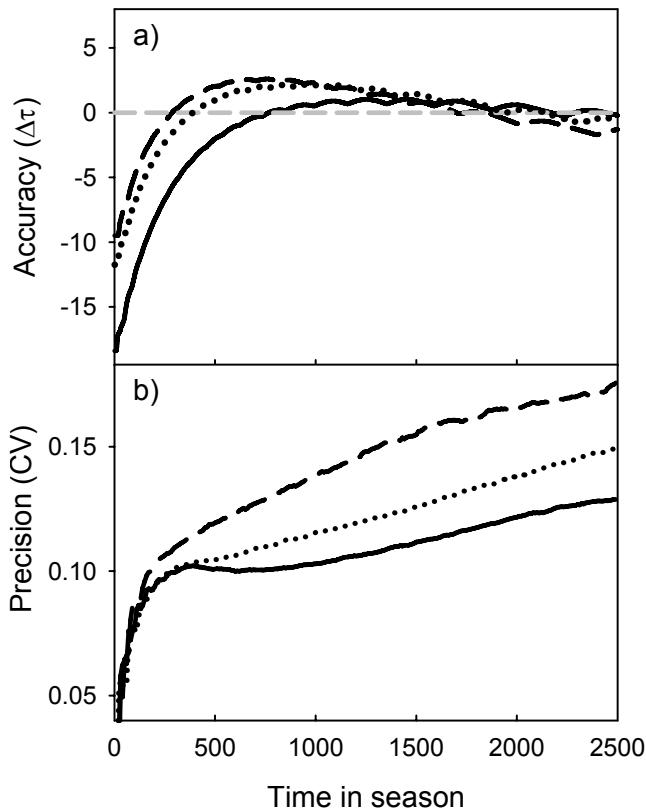


Figure 4. Precision and accuracy in estimates of giving-up thresholds of *Learning Foragers* adapted to different mortality regimes. Solid lines represent foragers adapted to environments with no mortality ($m = 0.000$, $\tau = 12.7$, $\gamma = 0.078$); dotted lines represent intermediate life-time expectancies ($m = 0.001$, $\tau = 18.9$, $\gamma = 0.096$); and dashed lines low survival prospects ($m = 0.002$, $\tau = 23.5$, $\gamma = 0.129$). 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.

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 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* evolve higher initial giving-up thresholds when mortality rate increases, which reflects how they invest in early foraging. As 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. 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. 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 alternatives should be evaluated in immediate food intake rates (Emlen, 1966; MacArthur & 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 behaviour of *Learners* deviate 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 trade-off 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 fitness. An additional aspect not addressed here, is the robustness of a strategy in obtaining basic requirements which become increasingly important in unpredictable and variable environments (Mangel, 1990; Inglis *et al.*, 2001; Dall & Johnstone, 2002; Carmel & Ben-Haim, 2005).

Learners need to integrate past and present information to efficiently track temporal change. The time period that information is retained in memory (Devenport & Devenport, 1994; Devenport *et al.*, 1997; Devenport, 1998; Hughes & Blight, 1999; Devenport *et al.*, 2005) and the way recent patch experience influences behavioural choices vary with characteristics of the natural environment (van Baaren *et al.*, 2005). Neural structures involved in memory storage and learning are metabolically costly, hence energy supply may potentially constrain coding and processing of sensory information (Bernays, 1998; Laughlin *et al.*, 1998; Dukas, 1999; Laughlin, 2001). In *Drosophila melanogaster*, larval competitive ability and adult resistance to desiccation

and starvation are lower in individuals with genetically high learning capacity (Mery & Kawecki, 2003, 2005). This illustrates how formation and maintenance of memory records impose ecologically relevant costs.

In parasitoids, patch-leaving behavior 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). Depending on the spatial distribution of their host, female parasitoids may either adjust their behaviour based on recent patch experiences or use a non-responsive fixed strategy (Vos *et al.*, 1998).

A simple giving-up time rule 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 & Uetz, 1996; van Alphen *et al.*, 2003; Olsson & Brown, 2006). Simple rules of thumb may, however, often work satisfactorily (as Green, 1984 illustrated for the giving-up time rule) and be more biologically realistic as they offer quick responses to environmental cues (Bernays, 1998; Hutchinson & Gigerenzer, 2005). Rules of thumb normally require less computational effort than for instance Bayesian updating rules (Gigerenzer & Todd, 1999). In addition, foragers are generally better at accurately estimating and discriminating between shorter time periods (Shettleworth, 1998; Stephens, 2002).

Under natural conditions, learning abilities are commonly biased towards certain experiences (Arak & 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, learning 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 emphasis 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).

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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. In the same way as *Learners*, *Informed* and *Fixed Foragers* will leave a patch when time since last resource encounter n_i exceeds a giving-up threshold τ . Strategies only differ in the way they obtain their giving-up thresholds.

Informed foragers have free global information 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 enters a patch at a time t in a foraging season of length T :

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

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 when it enters a new foraging patch.

The value of staying in the patch depends on the expected fitness consequences of *i*) encountering a resource in the next time step, and *ii*) 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:

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

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 *i*) 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 *ii*) 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 :

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

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 & 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:

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

As for *Informed Foragers*, 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 Foragers* 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:

$$\max_{\tau_F} \{V_{\tau_F}(0,0,1)\}.$$

Paper 4

Sigrunn Eliassen, Christian Jørgensen & Jarl Giske. When to learn: the ecological basis for learning in a foraging context. - *Manuscript*

When to learn: The ecological basis for learning in a foraging context

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Abstract

The value of acquiring environmental information depends on the benefit of using this information and the cost of collecting it. We model individual foragers that searches a patchy resource environment and use local experiences to track changes in global resource conditions. We study how the value of learning and the rate of updating resource estimates change as environments vary along three ecological dimensions: level of stochasticity in resource intake, spatial heterogeneity among resource patches, and temporal change in resource levels within a season.

The value of learning is highest when low encounter stochasticity results in reliable patch quality estimates, when temporal trends favour strategy changes within a lifetime, and when low spatial variability reduces learning costs. When foragers are able to obtain accurate local information, they rely on recent experiences and quickly adjust to temporal change. High learning factors are, however, susceptible to spatial variation among patches. Learning rules that are updating slowly have on average lower performance, but the strategies are generally more robust to changes in temporal and spatial resource conditions. We discuss memory properties and potential implications for observing learning behaviour in the field and in the lab.

Introduction

Foraging conditions vary in both time and space as a result of fluctuations in physical and biotic factors. Imagine an Arctic fox searching the snow-covered tundra for food in early spring. If lucky, it may encounter a reindeer that has starved to death. There might be periods and areas where reindeer are more likely to die from starvation, but should the fox try to learn such patterns? A reindeer carcass represents a large but rare food package, and to the fox such an encounter may be a highly stochastic event. Contrast this to the situation a few months later, when the same fox feeds on eggs and chicks on a bird cliff. Some parts of the cliff may be easier to hunt, and different seabird species may vary in their anti-predator behaviour. Successful encounters may now be relatively frequent and vary in a more systematic manner between areas. Should the fox try to learn these patterns? And should it adjust its behaviour as more birds populate the cliff in early spring, or when the chicks fledge some months later?

From a forager's perspective, we can distinguish between predictable changes in foraging rates that may result from seasonal trends in a food resource, and unpredictable fluctuations for instance due to stochastic encounter processes influenced by search efficiency and distribution patterns of the resource. The dichotomy between predictable and random events is clearly a simplification; in nature foragers experience the full continuum from nearly deterministic foraging rates (for example an ant feeding on nectar) to highly stochastic resource encounters (such as the fox searching for reindeer carcasses).

Resources are often non-randomly distributed within the environment, and a common model simplification is to assume that food resources are distributed in distinct patches. Models of patch use (e.g. Charnov, 1976) and forager distributions (e.g. Fretwell & Lucas, 1970) expect that foragers are able to assess the spatial heterogeneity and alter their behaviour accordingly. In the classical model of Charnov (1976), a solitary forager moves between distinct resource patches and searches randomly for food within each patch. The forager is predicted to leave the resource

patch when the current intake rate in the patch drops to the environmental average. The Marginal Value Theorem thus tells when a forager should leave a patch, but it does not provide a solution to how the forager can *decide* when to leave, or how it can obtain the information on which to base its decision.

A forager needs information on two hierarchical levels in order to make this decision: First, it needs to assess the current intake on a patch, and second compare this to an estimate of the average intake rate in the habitat as a whole. Under most natural conditions, both local and global assessments are associated with uncertainty, and they pose different but interlinked challenges. Commonly, models and empirical studies of patch allocation behaviour have considered only one of these information problems at a time. Most studies have focused on the way foragers may use their search times and resource encounters to estimate the quality of individual resource patches (Oaten, 1977; Iwasa *et al.*, 1981; McNamara, 1982; Green, 1984; Valone, 1991; Olsson & Holmgren, 1998; van Alphen *et al.*, 2003; Olsson & Brown, 2006). When foragers do not know the average resource intake in the habitat, they may update information on both local resource level and the global conditions (Mangel, 1990; Rodriguez-Gironés & Vásquez, 1997). An additional challenge, which has received less attention, arises when foragers have to assess changes in patch quality through a season due to large-scale temporal changes in resource levels (McNamara & Houston, 1985, 1987; Mangel, 1990; Hirvonen *et al.*, 1999). This was the case for the fox above as seabirds populated the cliff and when fledglings escaped.

Resource heterogeneity may introduce opportunities for specialization or exploitation of predictable patterns. Foragers that explore the environment and sample information can potentially use that knowledge to alter behaviour when resource conditions change (Inglis *et al.*, 2001; Dall & Johnstone, 2002). It therefore becomes important to study the mechanisms that foragers use to assess temporal change and spatial variability. Learning from experience is one such mechanism that allows an individual to adjust its behaviour and update its prior expectations to reflect current environmental conditions. Such an updated world-view is important when inflexible innate strategies are

insufficient, i.e. when the environment changes between generations or within the lifetime of an organism.

The costs of sampling and updating information may vary considerably between environments. Foraging models commonly assume that information is freely available or perceived with some fixed perception error (e.g. Fretwell & Lucas, 1970; Charnov, 1976; Abrahams, 1986; Collins *et al.*, 2002). Learning costs are commonly not considered explicitly, or the models assume fixed costs that are independent of the ecological conditions (e.g. Richards & De Roos, 2001). Another group of models has focused on how learning can minimise uncertainty in an animal's world perception, without considering the utility of that information or the optimal level of uncertainty given sampling costs (McNamara & Houston, 1987; Hirvonen *et al.*, 1999). These studies have mainly been concerned with how foragers most efficiently track changes in average resource conditions and reduce uncertainty in their environmental estimates.

Acquiring information is only valuable as long as environmental knowledge results in behavioural changes that enhance fitness (Gould, 1974; Stephens, 1989; Dall *et al.*, 2005). An important aspect in our model is to consider efficient information use in an ecological perspective, by quantifying the fitness value this information represents to the forager (see also Yoccoz, 1993). The value of environmental knowledge is determined by the way a forager puts it to use. We therefore need to compare the performance of learning strategies to that of foragers with a fixed behavioural strategy that yields the best average performance across different environmental conditions (Gould, 1974; Stephens, 1989).

When costs of learning emerge from active sampling behaviour, and the utility of information results from ecological interactions between individuals and their environment, more fundamental questions that can be asked include: Under what resource conditions should a forager try to learn differences among patches or trends over time? How much emphasis should learners put on recent as opposed to past experiences? And is there an optimal level of uncertainty?

In this paper, we study foragers with a learning strategy that first uses resource encounters within a patch to assess the local patch quality, and then integrates experiences from several patches to estimate changes in the global resource conditions. The learning challenge changes as we vary three important ecological parameters: the level of spatial heterogeneity; the level of stochasticity in resource encounters; and the temporal trend in resource level during a season. We then compare strategies with varying degrees of flexibility and access to free information to investigate the emergent parameters of the learning rule and quantify the potential value of learning in different ecological settings.

Model description

We investigate the value of learning in a foraging context by studying patch-leaving rules that differ in their use of information. The model is individual-based and simulates foragers that are characterized by the strategy they use to obtain information and their experienced foraging history. Our focal strategy is a *Learning* strategy that estimates *local* within-patch resource levels, and integrates this information to track changes in *global* mean resource conditions in the habitat (we also refer to these individuals as *Learners*). These two measures are then compared, and the forager leaves the patch when local search time exceeds a giving-up threshold determined by the global resource estimate.

Resources are distributed in well-defined patches. Time is divided into discrete time steps, in which individuals either search for resources in a patch or move between foraging patches. By harvesting a patch, the forager reduces the local resource levels, thus decreasing the probability that it will encounter further resources in that patch. Individual foragers do not interact, and resource depletion in a patch is unaffected by

other foragers. Foragers travel for a constant travel time v to a randomly selected resource patch, and they experience no metabolic or predation costs.

We evaluate patch leaving *rules* from which *behaviours* such as patch residence times and travel frequencies emerge. Patch allocation behaviour determines the long-term intake rate, and we use the energy gain during a season of constant length as fitness measure. At the start of a season, foragers were assigned to a random patch within the habitat, and for every parameter combination we simulated the behaviour of 2000 individuals over a 4000 time step foraging season.

Patch-time allocation strategies

An ecologically realistic learning strategy has to sample information while foraging. Sampling and foraging normally overlap, but foragers often emphasise information gathering early in the season while applying this information later to enhance foraging performance (Eliassen *et al.*, subm.). To assess the costs and benefits of learning, we constructed a set of strategies that vary in the local and global information that they use (Table 1; details of the strategies are given below). As a baseline for comparison, we use a non-responsive strategy that does not react to individual experiences but instead stay a *Constant Time* within each patch.

We assume a simple *Learning* strategy in the model, but assess the potential for improvement of this strategy by comparing the foraging performance of *Learners* to foragers that have access to free environmental information. There is always a cost of uncertainty associated with environmental assessment, but *Learning* strategies may potentially improve how they estimate both local resource levels and global averages. There may also be interaction effects, for example if better local assessment would benefit the estimation of the global averages. Pair-wise comparisons of strategies that differ in how they obtain information (free vs. sampled) can therefore quantify the fitness potential for improving local or global estimation procedures (Table 2).

The foraging environment

We study foraging in different ecological settings by letting patches vary along three ecological dimensions:

- 1) Temporal change. Patches undergo a linear improvement or impoverishment as time progresses. The linear trend lasts throughout the whole season.
- 2) Spatial heterogeneity. Patches in the habitat differ in resource quality according to a normal distribution.
- 3) Stochasticity in resource encounters. This represents the continuum from deterministic foraging rates to rare and highly valuable stochastic encounters.

In many natural systems, resource conditions change in a consistent manner during a season, for instance as a result of developmental processes in different prey species or variation in food resource growth. We assume that the average resource level changes continuously through the foraging period by a factor g every time step. The resource quality of a randomly selected patch at a time t in the foraging season is hence given

Table 1: Patch leaving strategies that utilize different levels of local and global information. In addition, we used a *Constant Time* foraging strategy that searches each patch for a fixed number of time steps and is insensitive to both local and global information.

		Global information		
		Genetically Fixed	Estimated	Known
Local information	Estimated	Fixed Threshold (FT): Local assessment with fixed giving-up threshold	Learner (L): Local assessment with learning rule for global information	Farsighted (F): Local assessment compared with free global information
	Known	Prescient Fixed (PF): Patch quality known with fixed giving-up threshold	Prescient Learner (PL): Patch quality known with learning rule for global information	Omniscient (O): Forager with full local and global knowledge

by

$$R_t = (R_0 + gt) (1+\varepsilon Z)$$

where R_0 is the mean resource density in patches at the start of a season. The second part introduces the spatial variability assuming a constant coefficient of variance relationship ε . Z is a random variable with normal distribution $Z \sim N(0,1)$.

As the forager consumes resources, the patch is gradually depleted. After a forager has searched the patch for n time steps and encountered k resources of quality q , the local resource quality r_t is:

$$r_t = R_{t-n} + gn - kq .$$

Resource intake and encounter stochasticity

A forager's prey intake may grade from almost constant flow (as assumed by Charnov, 1976) to highly stochastic (Iwasa *et al.*, 1981; Green, 1984). We consider different resource environments along this continuum by letting the resource be distributed from few and large items to many and small. The total amount of energy remains the same in all environments, and in a given habitat all items are of equal quality. For patches with current resource level r_t , the number of resource items y will hence be depend on the energy content per item:

$$y_t = r_t / q , \quad 0 < q \leq 1 .$$

Within a patch, the forager searches randomly for food items. The probability P_e that the forager will encounter a resource depends on the number of items y_t in the patch, the search efficiency a , and the length of the search period Δt :

$$P_e = 1 - e^{-ay_t\Delta t} = 1 - e^{-a(r_t/q)q} = 1 - e^{-ar_t}$$

Note that this equation assumes that the encounter probability stays constant throughout one time step, to retain the numerical approximations of the discrete time model.

We assume handling time to be proportional to energy content q , and that a forager can handle a maximum of $N = 1/q$ food items per time step. Each time step is therefore divided into N independent searches, each of duration Δt . The number of resources encountered during a time step X is binomially distributed and will vary according to:

$$\text{Var}\{X\} = \frac{P_e(1-P_e)}{q} .$$

At a local resource level r , the expected energy intake will, however, be the same in all environments. For a given q , the coefficient of variation in energy intake rate will be:

$$CV\{I|q\} = \frac{q\sqrt{\text{Var}\{X\}}}{E\{I\}} = \sqrt{q} CV\{I|1\}$$

The time to accumulate a certain amount of resources will thus vary more when foragers search for larger and more energy-rich items (q close to 1). Variability in energy intake relative to the scenario with resource quality $q = 1$ will henceforth be termed *encounter stochasticity* and denoted $\sigma = \sqrt{q}$.

Local information: Patch quality assessment

Foragers that adjust their patch residence time to the local resource level need to update their estimate of resource conditions as they gradually deplete a patch. We consider two ways of arriving at this estimate:

- 1) *Assessment* foragers use the time it takes to accumulate one resource unit s as an estimate of patch quality. In environments with large food items of one resource unit, this equals the time between resource encounters and hence corresponds to a giving-up-time rule (e.g. Iwasa *et al.*, 1981; Green, 1984).
- 2) *Prescient* foragers (sensu Valone, 1991) have full and freely available information on the current patch quality, and are hence able to assess the expected resource intake rate.

Global information: Estimating the average conditions in the habitat

To make its patch leaving decision, a forager compares its local estimate with a giving-up threshold. This patch leaving threshold is influenced by the long-term intake rate in the habitat, and we consider three ways in which foragers arrive at this global estimate:

A) Foragers may use a *genetically inherited giving-up threshold* that remains constant throughout the whole foraging season. For every parameter combination, we calculated the fixed τ_F that resulted in the best average performance using dynamic programming (Houston & McNamara, 1999; Clark & Mangel, 2000) (details in Appendix 1).

B) Foragers may *estimate changes in resource conditions based on previous experiences* of resource encounter frequencies. A linear operator rule (Mangel, 1990) determines how past and present information are weighted relative to one another. The new estimate (τ_{p+1}) is a weighted average of the previous estimate (τ_p) and the average time between encounters in the last patch, including travel time v :

$$\tau_{p+1} = (1 - \gamma)\tau_p + \gamma \frac{n + v}{kq}$$

The learning factor γ determines the relative weight given to new experiences, k is the number of food items of quality q that a forager has encountered during n time steps of search on patch p . The initial giving-up threshold τ_0 and the learning factor γ are assumed to be genetically inherited traits, which do not change during an individual's lifetime but are adapted to the prevailing environmental conditions. We determined the parameter combination of τ_0 and γ that maximized lifetime resource intake by numerical simulations. Note that for $\gamma = 0$ the strategy is identical to a fixed threshold strategy with $\tau_F = \tau_0$.

C) *Farsighted* foragers need not estimate the global resource level, but receive *free information* about the best giving-up threshold τ^* when they enter a new patch.

We call them *Farsighted* because they have free long-range information about their environment. The optimal $\tau^*(t)$ that maximizes the expected future resource intake for a forager entering a patch at time t was calculated using dynamic programming (details in Appendix 1).

We investigate strategies that combine one mechanism for local patch assessment with a mechanism for global information. Especially important are the *Learning* strategy, which first performs a local patch assessment (1) and then estimates the global average from experience (B), and the *Omniscient* strategy, which has free information about both the local (2) and global resource levels (C) and thus defines the best possible behaviour for that type of environment. We also consider a *Constant Time* rule that ignores all information and spends the same amount of time in each patch. The optimal amount of time t^* that a forager should spend searching changes with search efficiency and travel time (Olsson & Brown, 2006). Computational details on how to calculate the different strategies are presented in Appendix 1 along with dynamic programming equations.

Strategies with other combinations of local and global information are given in Table 1. Differences in foraging performance between strategies reveal the costs of incomplete information and the benefits of learning. A list of these differences and their interpretations is given in Table 2.

Table 2: Concepts and descriptions.

	Concept	Description
Local information	The value of full local knowledge	$\frac{\Gamma_{PF} - \Gamma_{CT}}{\Gamma_{CT}}$ The value of local knowledge for a <i>Prescient</i> forager relative to a <i>Constant Time</i> forager.
	Performance of local assessment rule	$\frac{\Gamma_{FT} - \Gamma_{PF}}{\Gamma_{PF}}$ The long-term resource intake rate of foragers that assess local resource quality relative to that of <i>Prescient</i> foragers.
	The value of local quality estimates	$\frac{\Gamma_{FT} - \Gamma_{CT}}{\Gamma_{CT}}$ The relative value of updating local estimates based on experiences of resource encounter frequencies as opposed to searching a constant time in each patch.
	Total benefit of full local knowledge	$\Gamma_{PL} - \Gamma_L$ Total value of full local information includes i) the direct benefit of having information on patch quality, and ii) the indirect effect of improving estimates of temporal change through learning.
	Direct benefit of full local knowledge	$\Gamma_O - \Gamma_F$ Difference in long-term intake rate of omniscient foragers and informed foragers represents the benefit of having free local information when foragers have full global knowledge.
Global information	The value of learning	$\frac{\Gamma_L - \Gamma_{FT}}{\Gamma_L}$ The relative value of updating global estimates based on experiences of patch qualities.
	The potential for improving learning rules	$\frac{\Gamma_F - \Gamma_L}{\Gamma_L}$ Loss in long-term intake rate of learners relative to farsighted foragers due to uncertain estimates, time lags, reduced intake rate during patch sampling, and other learning costs.
	The value of full global knowledge	$\Gamma_F - \Gamma_{FT}$ The total value of accurate global information when foragers assess local resource quality from experience.
	Total benefit of free information	$\Gamma_O - \Gamma_{FT}$ Total benefit of having free local and global information.

Results

We will first consider the challenge of assessing local patch quality in a stable resource environment, and investigate how encounter stochasticity and spatial variability affect the performance of the assessment rule. Next, we will include a temporal trend in resource levels and address the patch-leaving problem by also taking global information into account. We will give examples of how *Learning* foragers integrate information, and compare intake rates between strategies that differ in how they obtain local and global information. This reveals the value of learning, the cost of having imperfect knowledge, and thus also the potential for natural selection to improve the mechanisms by which foragers obtain local and global information. We analyse under which ecological conditions *Learning* may evolve and what the parameters of the learning strategy will be.

Local patch assessment

The challenge of assessing local resource levels increases with the level of stochasticity in the encounter process (Fig. 1). A *Prescient* forager knows the remaining resource level and will leave the patch when the resource level falls below the threshold r^* , while a *Constant Time* forager will leave the patch after t^* time steps regardless of the number of encounters. The long-term intake rates of these two strategies are largely unaffected by the level of encounter stochasticity (Fig. 2). In contrast, a forager that estimates patch quality will experience declining intake rates with increasing stochasticity (Fig. 2). At low σ , resource intake approaches a constant flow, encounter frequencies become more predictable, and local information quality increases (Fig. 1). The performance of an *Assessment* forager hence approaches that of a *Prescient* forager (Figs. 2, 3a).

The value of local knowledge increases with the level of spatial variability in resource density among patches (Fig. 3b). Intuitively, foragers are then able to recognise patches that are above or below average quality, and it becomes more advantageous to adjust patch residence times to local resource conditions. In sum, the efficacy of patch

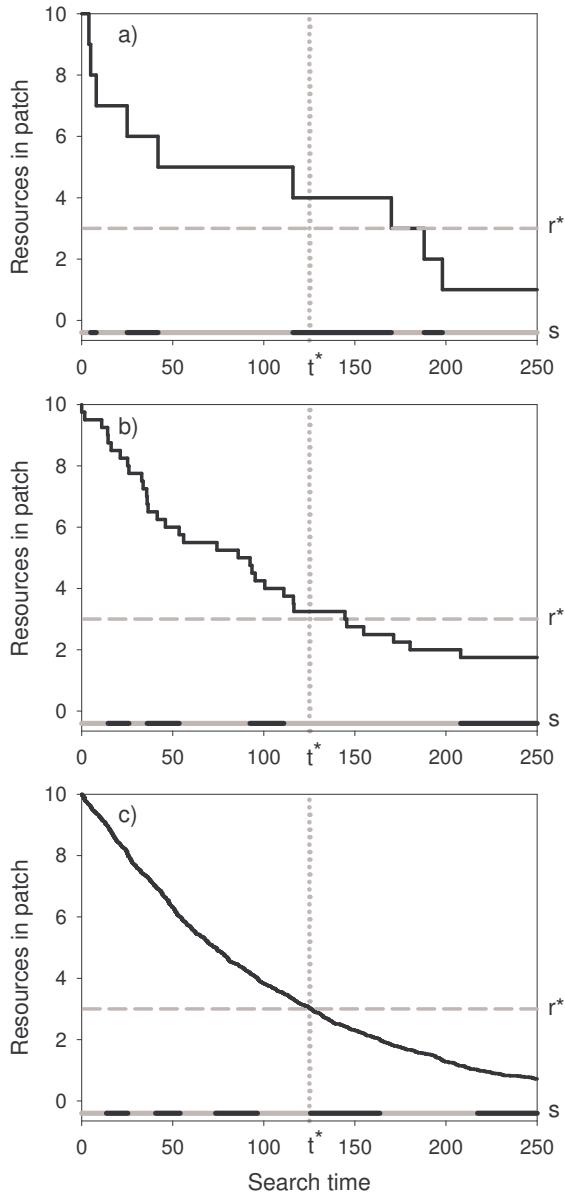


Figure 1: The local patch assessment problem. Local resource level as a function of a forager's search time on a patch, for three environments with different encounter stochasticity a) $\sigma = 1.0$, b) $\sigma = 0.5$, and c) $\sigma = 0.1$. The dashed grey line gives the resource level at which a *Prescient* forager leaves a patch. The grey dotted line gives the search time for which a *Constant Time* forager leaves. An *Assessment* forager will leave the patch whenever the time s to accumulate one resource unit exceeds the giving-up threshold τ .

assessment decreases with encounter stochasticity, whereas the value of knowledge increases with spatial variability. This combines to make patch assessment most profitable under high spatial variability and low encounter stochasticity (Fig. 3c).

In highly stochastic environments, the average performance of *Assessment* foragers may drop below that of *Constant Time* foragers (Figs. 2, 3c). It is not advantageous to make local patch estimates based on a simple giving-up time rule when resources are fairly evenly distributed among patches. This, however, relies on the assumption that

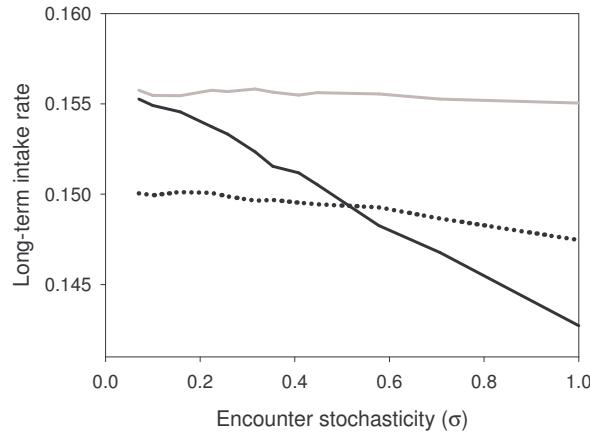


Figure 2: Foraging performance of *Prescient* (grey solid), *Assessment* (black solid), and *Fixed Time* rule (black dotted) foragers in an environment with stable resource level ($\bar{R} = 30$, $\varepsilon = 2.0$). Long-term energy intake rates of *Assessment* foragers decrease with the level of stochasticity in the resource encounter process (σ).

search efficiency and travel time stays constant between foraging seasons, which allows the genetically determined *Constant Time* strategy to be perfectly adapted to the stable environmental conditions.

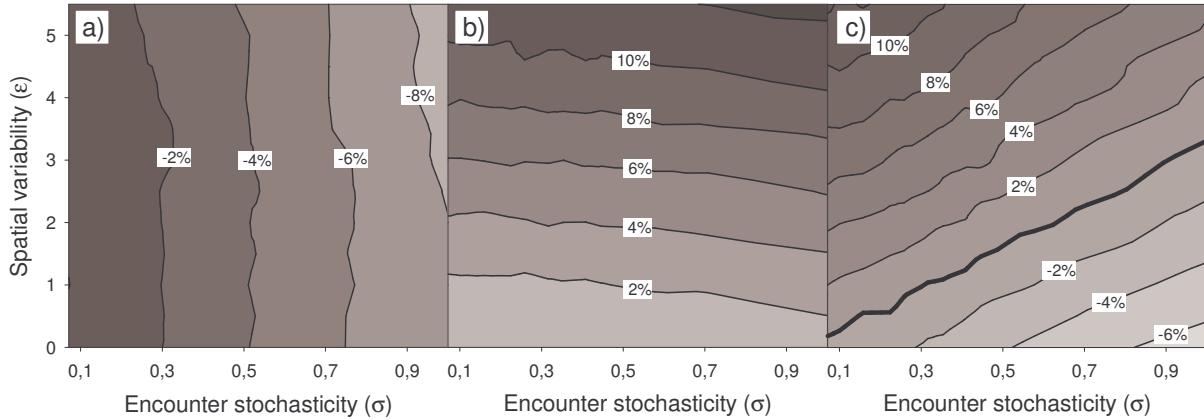


Figure 3: The value of local patch quality assessment in a temporarily stable environment ($\bar{R} = 30$) as a function of encounter stochasticity σ and spatial variance ε . a) The relative performance of a forager using a giving-up time rule compared to a forager that has full local information. b) The value of full local information is the difference in long-term intake rate between *Prescient* and *Constant-time* foragers. c) The value of assessing local patch quality, given as the relative difference in long-term intake rate of *Assessment* foragers compared to *Constant Time* foragers. The local patch assessment rule is beneficial for combinations of encounter stochasticity and spatial variability above the zero isocline (thick line). The contour plots are based on average performance of 2000 individuals tested for 182 parameter combinations of ε and σ for each strategy. For detailed descriptions of strategies and concepts see Tables 1 and 2.

Global resource estimates

We now turn to the second property of the patch-leaving decision: the forager's perception of global resource conditions. We consider environments where resource levels change over time, not only on short time scales as foragers deplete a patch, but also gradually through a season. For illustration, we show foraging strategies in environments where resource levels steadily increase with time (Fig. 4). *Farsighted* foragers that have free and exact information about the global resource level will reduce their giving-up threshold with time (Fig. 4). *Learning* foragers estimate these long-term changes from foraging experiences and update their strategy accordingly; their giving-up thresholds are similar to those of *Farsighted* foragers but deviate notably early in the season when patch sampling is most intense (Eliassen *et al.*, subm.).

With more stochasticity in the resource encounter process the giving-up thresholds for both *Learning* and *Farsighted* foragers shift towards higher values (Fig. 4). When resource intake becomes less predictable, foragers more often experience a period of

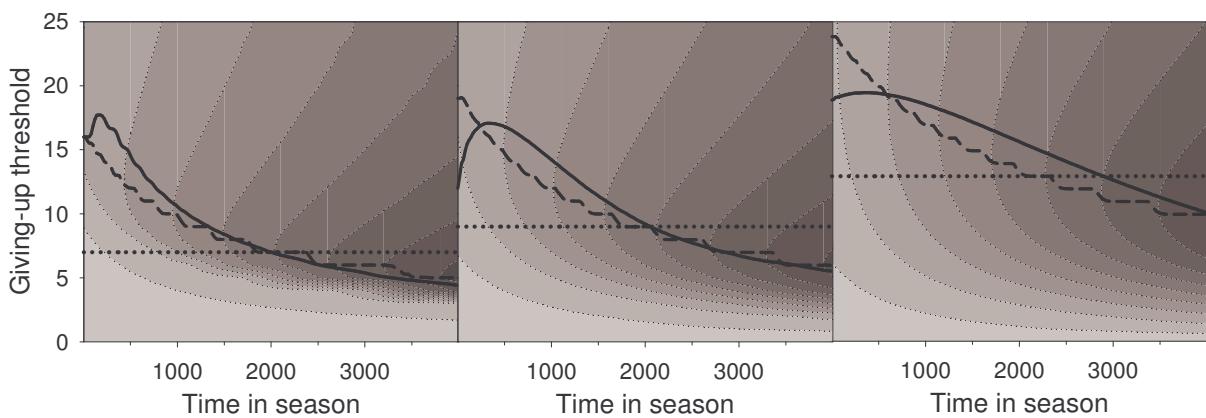


Figure 4: The global estimation problem. Giving-up thresholds of *Learning* (solid line), *Fixed threshold* (dotted line) and *Farsighted* foragers (hatched line) as a function of time in the foraging season. The average resource level in the habitat increases with time ($g = 0.01$, $\varepsilon = 0$, $R_0 = 10.0$, $a = 0.01$, $v = 25$, $T = 4000$). The intensity in the grey shade increases with long-term intake rate of foragers utilizing that giving-up threshold at a given time in season (fitness landscape). Level of stochasticity in the resource encounter process increases towards right ($\sigma = 0.1$, 0.5 and 1.0 , respectively).

‘bad luck’ and hence it becomes more advantageous to wait a bit longer than to leave a potentially good patch early. In environments with low encounter stochasticity, the *Farsighted* foragers experience higher resource intake rates. Performance however, drops quickly off whenever foragers adopt sub-optimal giving-up thresholds. The strategies are hence less robust to change and it becomes potentially more costly to utilize alternative strategies in such environments (Fig. 4).

Learning: Integrating local and global information

The foraging efficiency of learners approaches that of omniscient foragers as the quality of local information increases (Fig. 5). The relative value of learning increases, and is highest for foragers that have good local knowledge and rapidly update global estimates. When resource levels do not vary among patches, the potential for improving local assessment is larger than the potential for refining learning rules (Fig. 5).

In habitats with low encounter stochasticity, local information quality is high and *Learners* with high learning factors can rapidly substitute old estimates with new information (Figs. 6b,d). This is advantageous when resource levels vary little between patches (Fig. 6b). When spatial variability increases, foragers need to sample more patches to obtain a good global estimate, and the *Learning* strategy becomes less

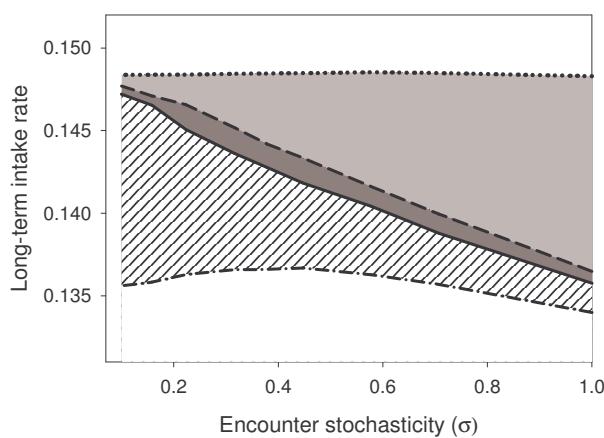


Figure 5: Long-term intake rates of *Omniscient* (dotted line), *Farsighted* (hatched line), *Learning* (solid line) and *Fixed Threshold* (hatched-dotted line) foraging strategies as a function of encounter stochasticity. The value of learning (hatched area) and the potential value of improving local (light grey area) and global information quality (dark grey area) are found as the difference in resource intake between foragers utilizing various levels of environmental information (Table 2). Resource conditions change temporally through the foraging season ($g = 0.01$, $R_0 = 10.0$), but there is no spatial variance among patches ($\varepsilon = 0$).

profitable (Fig. 6a). Foragers decrease their learning factors, and eventually adopt *Fixed Threshold* strategies at high levels of spatial variance (Fig. 6a). To understand why the value of learning decreases so rapidly in spatially heterogeneous environments, we need to consider the fitness landscape around the optimal strategies. Recall (Fig. 4a) that the cost of departing from the optimal patch leaving strategy is relatively high in environments with low encounter stochasticity (the fitness landscape forms a narrow and steep ridge around the optimal strategy). As a consequence, making sampling and estimation errors will impose relatively high costs on *Learners*.

Learning strategies in environments where resource encounters are highly stochastic are qualitatively different because high-quality local information is no longer available. Foragers adopt low learning factors that relatively slowly adjust to global change (Figs. 6b,d). The initial giving-up threshold is lower than for *Informed* foragers, which leads to frequent patch departures and thereby facilitates early sampling behaviour (Eliassen *et al.*, Subm). The slowly updating strategy is more robust to spatial variability among patches than the fast learning rules (Fig. 6b), since such strategies give weight to information from a larger number of patches. In highly stochastic environments, learning factors are not as sensitive to spatial heterogeneity, and it is beneficial to track changes in global resource conditions even when resource levels vary a lot between patches (Fig. 6a, b).

Under stable resource conditions, *Fixed Threshold* strategies perform better than *Learning* rules (Fig. 6c). The value of learning generally increases with the level of temporal change that a forager experiences during its life time (Fig. 6c). The adaptive value of learning is not linked to the rate of change in resource level per se, but rather to the effect that environmental change has on giving-up thresholds (Fig. 4). Whenever altering giving-up thresholds significantly affects resource intake rates, a forager will experience a benefit of having global information. Foragers in environments with low encounter stochasticity adopt the highest learning factors (Fig. 6d), and hence improve the rate at which they respond to temporal change. *Learners* are more prone to make errors when estimates are based on poor local knowledge, hence learning factors drop

with increasing encounter stochasticity. The trade-off between estimation errors and rate of information updating changes as resource conditions increase more rapidly through the season, and we observe a general increase in learning factors (Fig. 6d).

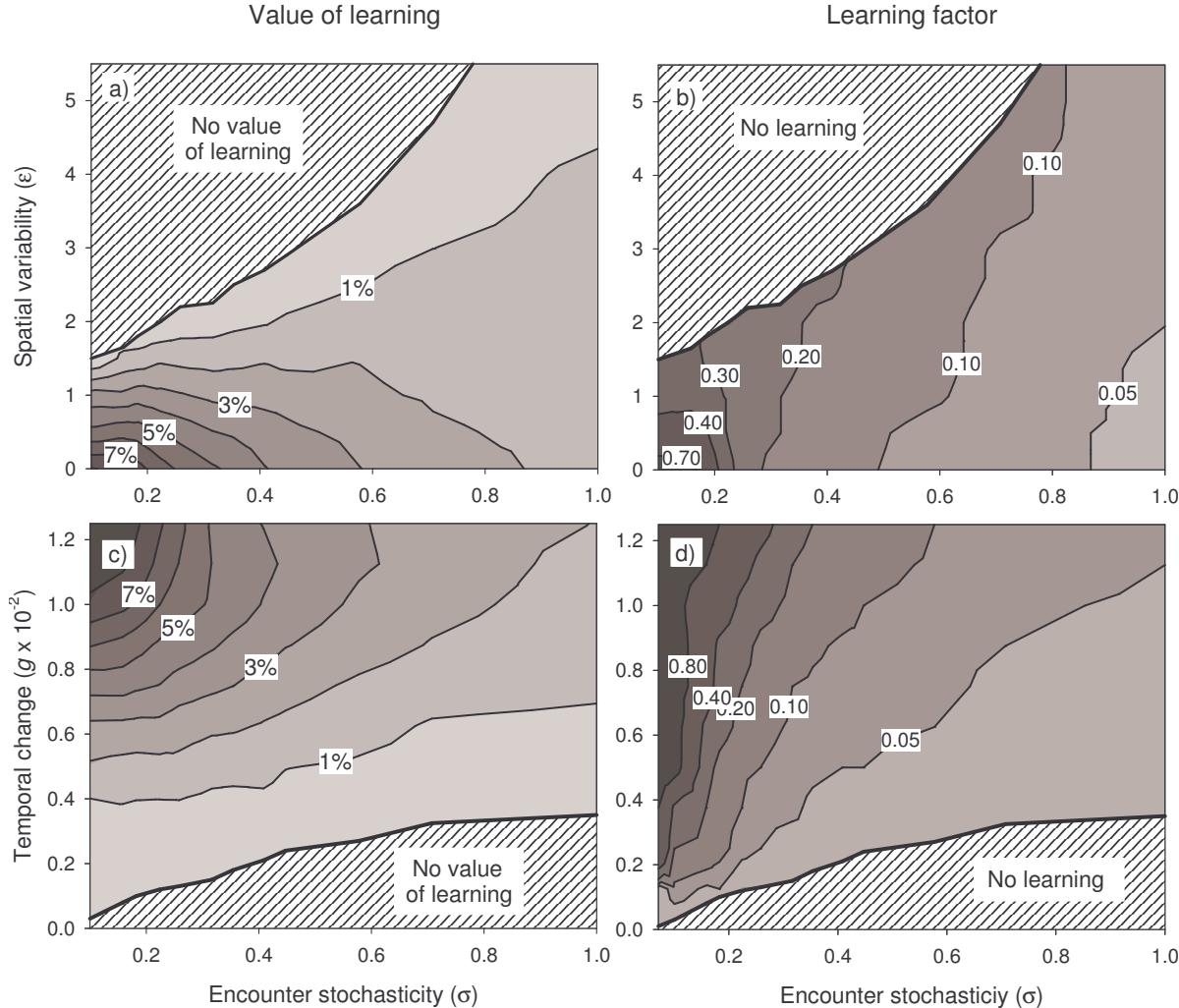


Figure 6: The value of learning (a,c) and the weight given to recent information, i.e. the learning factor γ (b,d) as a function of three ecological variables: *i*) the level of encounter stochasticity (x-axis in a-d), *ii*) the spatial variance ε among resource patches in the habitat (y-axis in a,b) and *iii*) the level of temporal change g through the foraging season (y-axis in c,d). There is no value of learning for combinations of the environmental parameters within the hatched areas, and foragers adopt an innate *Fixed Threshold* strategy. In panel a) and c), the relative difference in long term intake rate between *Learners* and *Fixed threshold* foragers is indicated on the solid lines. The value of information hence increases with the intensity in the grey shade. In b) and d), adaptive learning factors are given, with dark grey corresponding to high learning factors where foragers pay a lot of attention to recent patch quality information. Learning strategies with low learning factors (light grey) slowly updated their estimates of the environment based on experience on several resource patches. ($v = 25$, $a = 0.01$; in a,b; $g = 0.01$ and in c,d; $\varepsilon = 0.0$). The contour plots are based on average performance of 2000 individuals or each strategy tested for 182 parameter combinations.

Discussion

Changes in resource conditions not only influence the quality of information that a forager may obtain, but also the utility of this knowledge. A forager gains information from its activity within the resource environment, and it is within this ecological setting that information takes value. From an ultimate perspective, the utility of environmental information emerges from the benefits an individual obtains from using that information and the costs of collecting it. Conceptual foraging models have traditionally focused on how foragers most efficiently estimate environmental parameters (McNamara & Houston, 1985, 1987; Rodriguez-Gironés & Vásquez, 1997; Hirvonen *et al.*, 1999) or how foraging performance or distributions are affected by limited knowledge (e.g. Green, 1984; Abrahams, 1986; Bernstein *et al.*, 1988; Collins *et al.*, 2002). To combine these two perspectives information quality has to emerge from active sampling behaviour, and the utility of information must result from ecological interactions between individuals and their environment (Dall *et al.*, 2005). In the following, we try to integrate these approaches as we focus on the *Learning* strategy and when and why it evolves.

The multiple challenges of learning in variable environments

Learners rely on some persistency in information gained from different patch samples in order to track changes in resource conditions. Learning incurs lower costs when foragers easily obtain information of high quality, and it has higher value when simple inflexible strategies perform poorly. We have analysed three environmental dimensions along which these properties change.

First, stochasticity in the resource encounter process influences the quality of within-patch information. When foragers search randomly for rare food items, the time it takes to accumulate a given amount of resources may deviate considerably from expectations. Encounter frequencies hence provide inaccurate local information, and this increased noise level necessitates repeated sampling and prolonged learning phases. With more stochasticity, we observed a general increase in giving-up

thresholds of the *Farsighted* strategy, which has freely available global information. Foragers should consequently accept longer waiting times before leaving the patch when time between encounters is more variable. This is consistent with empirical observations in starlings, where giving-up times became more variable and shifted towards higher values as time between food encounters varied more (Brunner *et al.*, 1996). Even though the average time between resource encounters becomes an increasingly biased estimator of the giving-up threshold, it may still pay a forager to respond to this information. The value of utilizing a source of information, does not depend on the reliability of information itself, but rather the relative cost and benefits of responding to this information (Koops, 2004).

Second, temporal change devalues previous experiences and thus adds another learning challenge. At the same time, the potential value of learning increases, as it allows foragers to adjust their strategies to changing conditions. Contrast this to a temporally stable environment, where there is no way of improving foraging performance by acquiring global information. A genetically fixed giving-up threshold may evolve whenever conditions are constant from year to year.

Third, spatial variability increases the cost of learning, as more patches have to be sampled to construct a reliable estimate of the global average conditions. There is hence an interesting interaction between temporal change, which makes recent visits more informative and favour short memory, and spatial heterogeneity, which reduces this temporal correlation and selects for longer memory records (see also McNamara & Houston, 1987; Nishimura, 1994).

The value of global knowledge

Learners estimate and compare local and global information. By contrasting the *Learning* and *Fixed Threshold* strategies, the model reveals how the value of learning is determined by *i*) the potential of utilizing global information to improve foraging behaviour (ultimate utility), and *ii*) the potential of estimating this higher level property from experiences within the environment (ecological constraints on information flow). The global information is constructed by putting together

successive local experiences, hence there is little to gain from better rule for constructing global knowledge if the local information is riddled by noise. This can be illustrated with observations of two closely related parasitoid species that utilise hosts with different spatial distribution patterns. The specialist parasitoid *Cotesia rubecula* and generalist sibling species *C. glomerata* both used a simple non-responsive strategy when feeding on a uniformly distributed host (Vos *et al.*, 1998). On this host, patch quality estimates were hard to obtain, and consequently there was no benefit in updating global information. When the generalist parasitoid was instead foraging on a highly aggregated host species, it adjusted its behaviour based on local host encounters and recent experiences of patch quality. Now local host encounters conveyed higher quality information that could be used both to access local resource levels and to track changes in resource distributions.

Potential for improving patch assessment

There are in principle two ways in which local patch quality estimates can be improved: by using more accurate information; or by integrating the same information using a better or more advanced rule. A simple giving-up time rule may arrive at sub-optimal patch leaving decision in highly stochastic environments (Oaten, 1977; Iwasa *et al.*, 1981; Green, 1984). In such situations, a forager may potentially improve its foraging performance by utilizing information on search times and resource encounters in a more efficient way, for instance by using Bayesian updating rules (Iwasa *et al.*, 1981; McNamara, 1982; Olsson & Holmgren, 1998; Olsson & Brown, 2006). Besides responding to experiences of resource encounters, animals may utilize information from a variety of sensory cues (Persons & Uetz, 1996; van Alphen *et al.*, 2003; Tentelier *et al.*, 2005). These can be both environmental characteristics that are correlated with patch quality, such as habitat features or co-occurring species, or social cues based on the behaviour of con-specific foragers (Valone, 1989; van Alphen *et al.*, 2003). Integrating information from different sources could potentially produce better patch quality estimates, and we would expect additional information to be especially valuable at high levels of encounter stochasticity.

Simple rules of thumb may often work satisfactorily (as Green, 1984 illustrated for the giving-up time rule) and be more biologically realistic as they offer quick responses to environmental cues (Hutchinson & Gigerenzer, 2005). More sophisticated updating rules such as Bayesian learning rules involve more complicated calculations, as prior expectations need to be updated along with the current local estimate whenever resource conditions constantly change within the environment. In such cases, changes in global conditions may be easier to track using linear operator models (Giraldeau, 1997).

The adaptive rate of forgetting

A long-term memory is advantageous in environments where patch quality is relatively stable and predictable (Hirvonen *et al.*, 1999; Fortin, 2002). When the environment is changing rapidly, however, recent information becomes more valuable and this favours shorter memory records. In turn, more emphasis on recent experiences results in decisions based on only a small sample of the available information, which consequently introduces more variance in the global estimate (McNamara & Houston, 1987; Hirvonen *et al.*, 1999).

Memory properties, such as the rate of forgetting, may represent adaptations to characteristics of the natural environment (McNamara & Houston, 1987; Mangel, 1990; Anderson & Schooler, 1991; Hirvonen *et al.*, 1999; Schacter, 1999). Memory suppressor genes, whose products inhibit memory storage, may represent a mechanisms for controlling how memory decays over time (Yin *et al.*, 1994; Yin *et al.*, 1995; Abel *et al.*, 1998; Tully *et al.*, 2003). The genetic and molecular mechanisms underlying memory and learning seem to be remarkably conserved throughout the animal kingdom (Silva *et al.*, 1998; Alberini, 1999; Tully *et al.*, 2003). Evolutionary changes in memory characteristics and learning rates may, however, occur within a few generations in laboratory populations (Mery & Kawecki, 2002). This illustrates the plasticity in learning abilities.

Several empirical studies have illustrated how patch time allocation is influenced by recent experiences of travel time (Cuthill *et al.*, 1990; Kacelnik & Todd, 1992; Todd

& Kacelnik, 1993; Cuthill *et al.*, 1994; Thiel & Hoffmeister, 2004) and patch quality (Wildhaber *et al.*, 1994; Fortin, 2003; Schilman & Roces, 2003; Outreman *et al.*, 2005; van Baaren *et al.*, 2005; Tentelier *et al.*, 2006; Thiel & Hoffmeister, 2006). There is a general bias in the number of experimental studies reporting effects of recent experiences compared to studies of long-term memory and slowly adjusting strategies. Behavioural alterations are more subtle and harder to observe when individuals only slowly adjust to temporal change (Cuthill *et al.*, 1994; Thiel & Hoffmeister, 2006). In such cases, it requires a more intensive study over longer time to achieve the statistical power needed to differentiate slowly updating behavioural trends from fixed strategies. Our model results also indicate that fast updating rules may be more prevalent in nature (see also Shafir & Roughgarden, 1996). Slow learning rules perform best with poor local information or in relatively stable environments, where the value of learning is generally low. In such cases, keeping a long-term memory imposes costs that may outweigh the benefits of learning altogether (Dukas, 1999; Mery & Kawecki, 2003, 2005).

Large scale changes in time and space

One environmental property that this model does not address is autocorrelation structures beyond a gradual and constant temporal trend. Autocorrelations could arise from explicit temporal structure (circadian cyclicity or seasonal trends for perennial or long-lived organisms) or spatial structure (aggregation of patches on a landscape; spatial correlation in patch quality). Real (1991) argued that the short-term memory exhibited by flower-foraging bumblebees is advantageous since nectar rewards are spatially autocorrelated. In much the same way, the impact of recent travel times in starlings (Cuthill *et al.*, 1990; Cuthill *et al.*, 1994) or quality of the previous patch experiences in parasitoids (Outreman *et al.*, 2005) could be adaptations to environments with large temporal correlation in travel distance or patch quality. The spatial structure of resource distributions within a landscape may determine on what scale information should be integrated and how long it should be remembered (Fauchald, 1999). Heavy reliance on recent experience could hence be viewed as an adaptation to a natural environment with strong temporal correlation between similar

foraging events (Jones & Sieck, 2003). In such hierarchically structured environments, memory properties may vary depending on temporal or spatial scale, which potentially requires more sophisticated learning mechanisms.

The value of learning has to be estimated by comparing learning strategies with some parsimonious strategy that does not respond to particular experiences. We have chosen to use strategies with a fixed giving-up threshold that are perfectly adapted to an environment that do not vary between generations. Clearly, there are few such habitats in nature, hence fixed strategies would need to adapt to between-year variation and consequently show suboptimal behaviours in some years. In our model, learning strategies were also initiated with perfectly adapted initial thresholds and learning rates. The flexibility of learning strategies makes them less sensitive to prior expectations however, and especially rapidly updating rules will prosper. Our estimates of the value of learning are hence conservative as our assumptions tend to enhance the performance of the *Fixed Threshold* strategy relative to the *Learning* strategy.

Sensory mechanisms

We have focused on simple behavioural mechanisms and decision rules, addressing constraints and trade-offs in local patch quality assessment and learning. In the model we assumed that foragers were able to assess search time perfectly and discriminate between time intervals of different length. This is an obvious simplification, which may affect the relative profitability of the different patch assessment mechanisms. According to Weber's law, a forager will show larger variance in memorised searching times as time intervals increase (Shettleworth, 1998). This reduces the profitability of strategies that rely on accurate estimates of long time intervals, such as entire patch residence times (e.g., the *Constant time* rule). Mechanisms based on estimates over shorter time periods (giving-up times on prey, time to accumulate a mouthful of grass) may hence represent easier ways of discriminating time differences (Stephens, 2002). An animal's time perception may also be influenced by the resource encounter process

itself (Bizo & White, 1997), potentially causing deviations from optimal behaviour (Hills & Adler, 2002).

Plurality in foraging strategies

As illustrated with the Arctic fox, the optimal strategy may not only differ among species, but also within an organism's lifetime. Animals may adopt general strategies that are applicable in different ecological conditions. Alternatively, they may possess a set of simple strategies appropriate in different environmental conditions. This requires a mechanism for selecting the appropriate strategy in each situation, for instance by way of recognizing prey type or host species. Studies in cognitive psychology illustrate how the rate of information loss may adaptively vary in response to the temporal characteristics of the problem an individual needs to solve (Anderson *et al.*, 1997; Jones & Sieck, 2003). Our analysis illustrates that even though a forager, such as the Arctic fox, is capable of learning, it may not be beneficial to explore all types of resource patterns or learn under all ecological conditions (see also Stephens, 1991, 1993; Nishimura, 1994). Understanding the mechanisms by which information is processed, interpreted and remembered may give further insights to how different behavioural strategies may evolve, and how and when ecologically emerging information is integrated to track and predict environmental change.

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Appendix 1

Farsighted, Fixed and Omniscient patch leaving strategies

Foragers experience no predation or metabolic costs and we expect their reproductive output to be proportional to the amount of resource accumulated during a foraging season. We set the value of a resource unit in terms of reproductive value to f . Foragers have two behavioural options; they may either stay in a patch and search for resources, or leave and travel to a new foraging location.

A **Farsighted forager** has free global information and knows the best giving-up threshold $\tau^*(t)$ to use when it enters a new patch at time t . The forager updates this information only as it shifts between patches, in much the same way a *Learner* updates its estimate of τ_p upon leaving a patch. We seek the giving-up threshold that maximizes expected lifetime reproductive output for a forager that enters a patch at a time t in a foraging season of length T :

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

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

The value of staying in the patch depends on the expected fitness consequences of *i*) encountering resources in the next time step, and *ii*) the value of resource encounters from time $t+1$ until the end of season. The number of resource encounters within a time step is binomially distributed with number of searches equal to $N = 1/q$. In each search, the probability P_e that a forager will encounter a food item depends on the local resource level. The strategy is calculated for environments with no spatial variance. For a resource level r_t , the probability of encountering x food items in a time step is:

$$p(x, N) = \left[\frac{N-x+1}{x} \right] \left[\frac{P_e(r_t)}{1-P_e(r_t)} \right] p(x-1, N), \quad \text{where } p(0, N) = (1 - P_e(r_t))^N$$

At the time horizon T the reproductive output is $F(T) = 0$. Starting at the time horizon T and working backwards, we may calculate the optimal giving-up threshold that maximizes future reproductive value for a forager that *enters* a patch at a given time-step t (Clark & Mangel, 2000):

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

Here, V_{τ} is the value of utilizing strategy τ at a given time t in the season:

$$V_{\tau}(t, r_t, n, b) = F(t+v)I_{n=\tau} + \left[\sum_{x=0}^{N-b-1} p(x, N) \{xqf + V_{\tau}(t+1, r_{t+1}, n+1, b+x)\} + \sum_{x=N-b}^N p(x, N) \{xqf + V_{\tau}(t+1, r_{t+1}-1, 1, b+x-N)\} \right] (1 - I_{n=\tau})$$

The local resource level r_t is updated every time the sum of food encounters accumulated so far (b) and during the current time step (x) exceeds one resource unit. For a given strategy τ , the indicator factor $I_{n=\tau}$ equals 1 if $n_i \geq \tau$ and is 0 otherwise. The first part of the equation represents the value of leaving the patch. The *Farsighted 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 $F(t+v)$. The second part of the equation gives the value of staying, which is the sum of *i*) probabilities where the number of food items accumulated does not exceed one resource unit, multiplied with the expected future reproductive value given that this amount of resource is consumed, and *ii*) the corresponding value if resource accumulation exceeds one resource unit and the time since resource encounter n was reset.

We assume that the forager does not have exact information on when the season ends, and hence calculates the optimal strategy for long time horizons to omit terminal effects.

Fixed Threshold 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:

$$V_\tau(t, r_t, n, b) = V_\tau(t + v, R_t, 1, 0) I_{n=\tau} \\ + \left[\sum_{x=0}^{N-b-1} p(x, N) \{xqf + V_\tau(t + 1, r_{t+1}, n + 1, b + x)\} \right. \\ \left. + \sum_{x=N-b}^N p(x, N) \{xqf + V_\tau(t + 1, r_{t+1} - 1, 1, b + x - N)\} \right] (1 - I_{n=\tau})$$

As for *Farsighted* 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 *Farsighted* foragers that select the optimal giving-up threshold every time they enter a new foraging patch. 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 fixed threshold τ_F that has the best average performance and maximizes lifetime reproductive output over a season, that is: $\max_{\tau_F} \{V_{\tau_F}(0, R_0, 1, 0)\}$.

Omniscient foragers have full information of both local (r_t) and global (R_t) resource levels in the habitat. For a given combination of resource levels we seek the optimal decision whether to leave or stay on the patch:

$$F(R_t, r_t, b) = \max \{V_{leave}, V_{stay}\}$$

The expected future resource intake for a forager that leaves a patch is:

$$V_{leave}(R_t, r_t, b) = F(R_{t+v}, R_{t+v}, 0)$$

This is the value of entering an unexploited patch after travelling for v time steps. Note that this strategy is only calculated for environments without spatial variance.

The value of continued resource search on the patch is given by:

$$\begin{aligned} V_{\text{stay}}(R_t, r_t, b) &= \sum_{x=1}^{N-b-1} p(x, N) \{xqf + F(R_{t+1}, r_{t+1}, b+x)\} \\ &\quad + \sum_{x=N-b}^N p(x, N) \{xqf + F(R_{t+1}, r_{t+1}-1, b+x-N)\} \end{aligned}$$

As for the *Farsighted* forager, the value of staying in the patch is summed over the probabilities of encountering from 0 to N resource items in the current time step, and sums the expected future reproductive value given that this amount of resource is consumed.

The *Omniscient* forager may alter strategy every time step, and will choose to leave a patch if the expected future resource intake when leaving is higher than when staying in the patch, that is if:

$$V_{\text{leave}}(R_t, r_t, b) \geq V_{\text{stay}}(R_t, r_t, b).$$

Starting at the time horizon T , where future reproductive value equals zero, we back-calculated the optimal patch leaving behaviour for all combinations of local and global resource levels.