Foraging ecology and learning

Adaptive behavioural strategies and the value of information

Sigrunn Eliassen

Dissertation for the degree doctor scientiarum (dr.scient.)

at the University of Bergen

September 2006

Scientific environment

The study was carried out at the Department of Biology, University of Bergen, with financial support from the Research Council of Norway, Division of Science and Technology, through the program BeMatA (Computational mathematics in applications).

Acknowledgements

Writing this thesis would not have been possible without the help of a number of people. In particular, I would like to acknowledge my supervisor Jarl Giske for believing he could turn a field ornithologist into a marine modeller. You did not quite succeed, partially because you have given me the freedom to explore my interest in general ecological questions. Your ideas and enthusiasm have kept me going and I appreciate that you have always found time to discuss and comment on my work.

I am grateful to my co-supervisor Marc Mangel. The few months in your dynamic lab group at University of California, Santa Cruz, were most enjoyable. Your sharp thinking and insightful comments have inspired and focused my own work.

A special thank to Christian Jørgensen for paying such great interest in the progress of my thesis. I have really appreciated our numerous discussions, your genuine enthusiasm and generosity. Your creative thinking and clever comments have improved the work a lot.

I am grateful to my other co-authors Øyvind Fiksen and Josefin Titelman for introducing me to the challenges of the marine ecosystem. I would also like to thank Øyvind for valuable comments on the synthesis, for encouragement and support and for always fixing my bike. The synthesis chapter also benefited from valuable and constructive input from Øystein Varpe. To the rest of the modelling group: thanks for providing such a stimulating environment for discussions and work.

To Magnus, Iver and Hans, you are my joy! Thanks for being so patient and for always taking my mind off modelling trouble and putting things in perspective. Now, less constrained by thesis work, I look forward to spending a lot more time with you all. I would like to thank my parents for years of encouragement and help, and the rest of my family and friends for invaluable support.

Finally, I would like to express my gratitude to Lars for giving me the opportunity to explore my interests and for supporting me throughout. I appreciate your hard work and enduring love, and look forward to our next project!

Bergen, 29 September 2006

Sigrunn Eliassen

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*

Contents

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*"). Fourty 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 recourses (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.
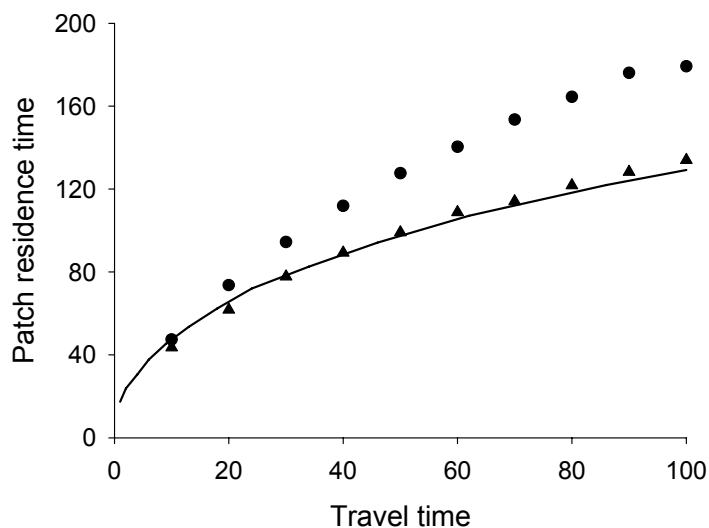
Figure 2: The Marginal Value Theorem (MVT) predicts that time spent on a patch should increase with travel time between patches (solid line). In a stable environment, foragers may arrive at a similar patch time allocation using a proximate patch-leaving strategy based on a simple giving-up time rule (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.
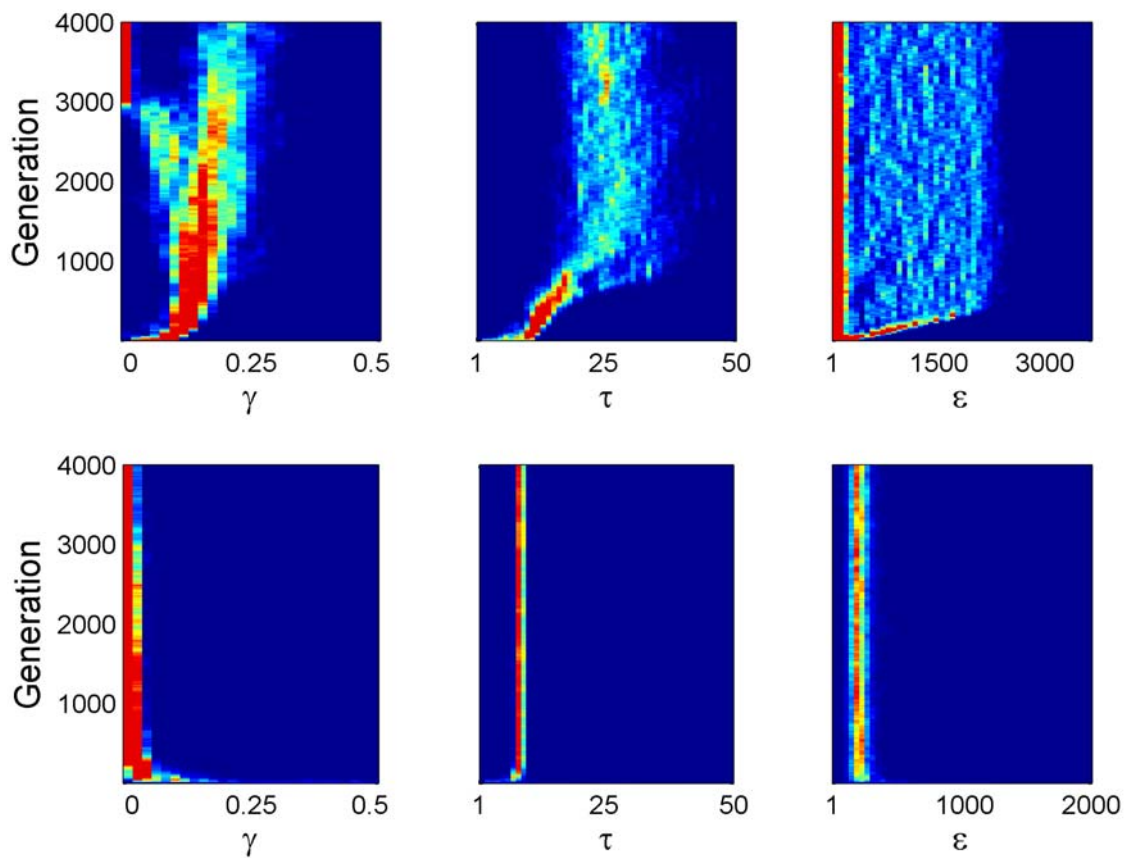
Figure B1. Artificial evolution of foraging traits: Typical trajectories of learning factors γ, initial giving-up thresholds τ and hatching times ε.

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_0s 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 $\gamma \sim$ 0.0-0.1, $\tau \sim$ 1-10, $\varepsilon \sim$ 1-375). 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)
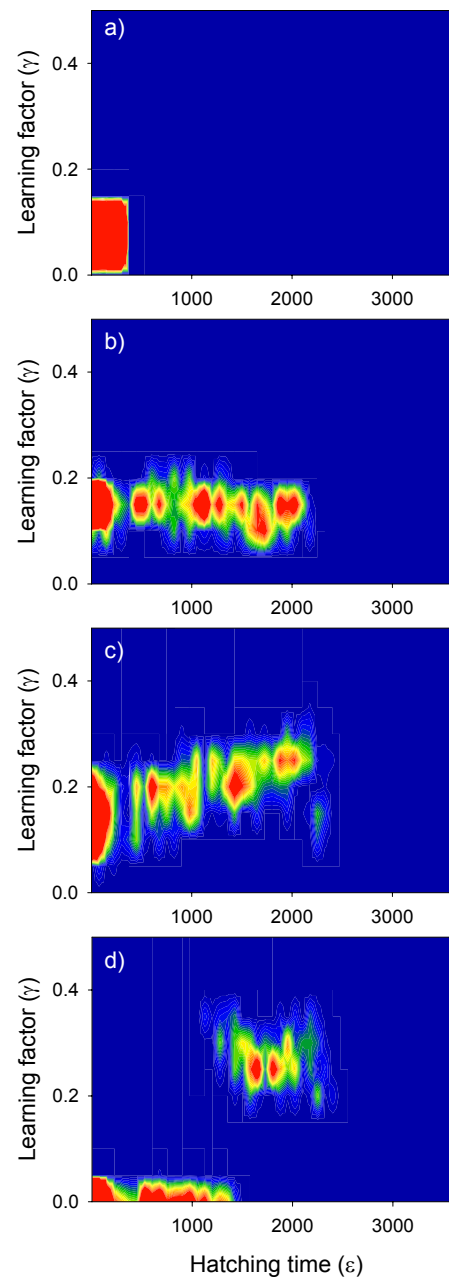
Different foraging strategies proliferate during various parts of the season and facilitate coexistence of several patch allocation strategies (Fig. B2 & B3). As illustrated in **Paper 3** and **Paper 4**, strategies with fixed giving-up thresholds will prosper in periods with relatively stable population- 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).
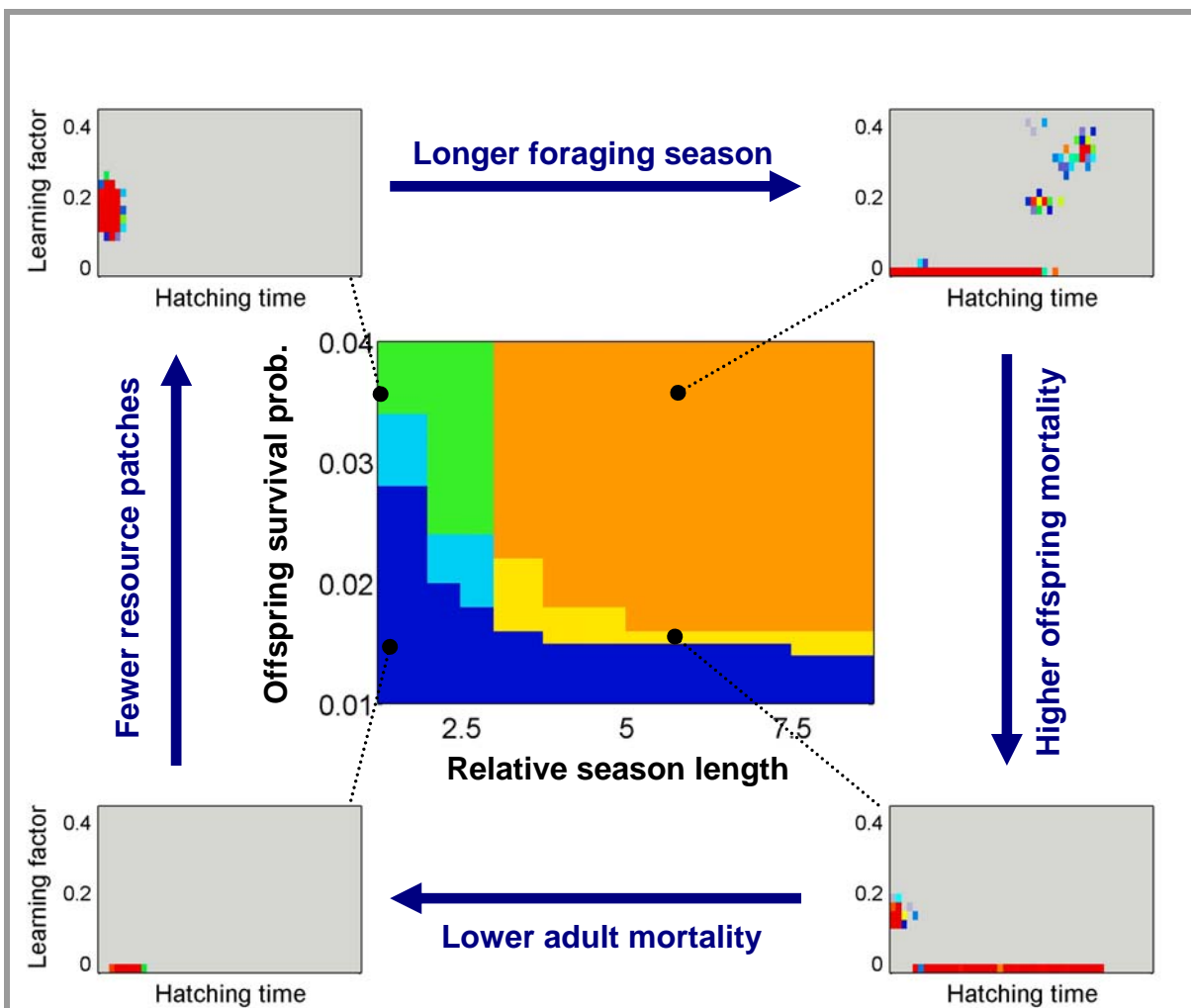
Figure B4. Coexistence and ecological trade-offs. The potential for coexistence between different foraging strategies as a function of the probability of offspring survival and relative season length (expected life-time of foragers relative to the length of season). Coexistence between learners and non-learners 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).

References

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

Abrams, P.A. (1984) Foraging time optimization and interactions in food webs. *Am Nat*, **124**, 80-96.

Ackley, D. & Littman, M. (1991) Interactions between learning and evolution. In *Artificial Life II* (eds C. Langton, C. Taylor, J. Farmer & S. Rasmussen), pp. 487-509. Addison-Wesley, Reading, MA.

Anderson, J.R. & Schooler, L.J. (1991) Reflections of the environment in memory. *Psychological Science*, **2**, 396-408.

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

Arditi, R. & Dacorogna, B. (1988) Optimal foraging on arbitrary food distributions and the definition of habitat patches. *Am Nat*, **131**, 837-846.

Aviles, L., Abbot, P., & Cutter, A.D. (2002) Population ecology, nonlinear dynamics, and social evolution. I. Associations among nonrelatives. *Am Nat*, **159**, 115-127.

Aviles, L., Fletcher, J.A., & Cutter, A.D. (2004) The kin composition of social groups: Trading group size for degree of altruism. *Am Nat*, **164**, 132-144.

Baldwin, J.M. (1896) A new factor in evolution. *Am Nat*, **30**, 441-451.

Beauchamp, G., Belisle, M., & Giraldeau, L.A. (1997) Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. *J Anim Ecol*, **66**, 671-682.

Bernstein, C., Kacelnik, A., & Krebs, J.R. (1988) Individual decisions and the distribution of predators in a patchy environment. *J Anim Ecol*, **57**, 1007-1026.

Bernstein, C., Kacelnik, A., & Krebs, J.R. (1991) Individual decisions and the distribution of predators in a patchy environment 2. The influence of travel costs and structure of the environment. *J Anim Ecol*, **60**, 205-225.

Bizo, L.A. & White, K.G. (1997) Timing with controlled reinforcer density: Implications for models of timing. *Journal of Experimental Psychology-Animal Behavior Processes*, **23**, 44-55.

Bonsall, M. (2004) Life-history trade-offs and ecological dynamics in the evolution of longevity. *Proc R Soc Lond B Biol Sci*, **271**, 1143-1150.

Bonsall, M.B., Hassell, M.P., & Asefa, G. (2002) Ecological trade-offs, resources partitioning, and coexistence in a host-parasitoid assemblage. *Ecology*, **83**, 925-934.

Burtsev, M. & Turchin, P. (2006) Evolution of cooperative strategies from first principles. *Nature*, **440**, 1041-1044.

Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theor Popul Biol*, **9**, 129-136.

Collins, E.J., Houston, A.I., & Lang, A. (2002) The ideal free distribution: an analysis of the perceptual limit model. *Evol Ecol Res*, **4**, 471-493.

Cuthill, I.C., Haccou, P., & Kacelnik, A. (1994) Starlings (*Sturnus vulgaris*) exploiting patches: response to long-term changes in travel-time. *Behav Ecol*, **5**, 81-90.

Cuthill, I.C., Kacelnik, A., Krebs, J.R., Haccou, P., & Iwasa, Y. (1990) Starlings exploiting patches - the effect of recent experience on foraging decisions. *Anim Behav*, **40**, 625-640.

Dall, S.R.X. (2005) Defining the concept of public information. *Science*, **308**, 353-354.

Dall, S.R.X. & Cuthill, I.C. (1997) The information costs of generalism. *Oikos*, **80**, 197-202.

Dall, S.R.X., Giraldeau, L.A., Olsson, O., McNamara, J.M., & Stephens, D.W. (2005) Information and its use by animals in evolutionary ecology. *Trends Ecol Evol*, **20**, 187-193.

Dall, S.R.X., Houston, A.I., & McNamara, J.M. (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol Lett*, **7**, 734-739.

Danchin, E., Giraldeau, L.A., Valone, T.J., & Wagner, R.H. (2004) Public information: from noisy neighbours to cultural evolution. *Science*, **305**, 487-491.

Darwin, C. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.* J. Murray, London.

Dieckmann, U. & Doebeli, M. (1999) On the origin of species by sympatric speciation. *Nature*, **400**, 354-357.

Dieckmann, U. & Ferrière, R. (2004) Adaptive dynamics and evolving biodiversity. In *Evolutionary conservation biology* (eds R. Ferrière, U. Dieckmann & D. Couvet), pp. 188-224. Cambridge Univerity Press, Cambridge, UK.

Dieckmann, U. & Law, R. (1996) The dynamical theory of coevolution: A derivation from stochastic ecological processes. *Journal of Mathematical Biology*, **34**, 579-612.

Doebeli, M. & Dieckmann, U. (2000) Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *Am Nat*, **156**, S77-S101.

Doebeli, M. & Dieckmann, U. (2003) Speciation along environmental gradients. *Nature*, **421**, 259-264.

Driessen, G. & Bernstein, C. (1999) Patch departure mechanisms and optimal host exploitation in an insect parasitoid. *J Anim Ecol*, **68**, 445-459.

Dukas, R., ed. (1998) *Cognitive ecology: the evolutionary ecology of information processing and decision making*. The University of Chicago Press, Chicago, MI.

Dukas, R. (2002) Behavioural and ecological consequences of limited attention. *Philos Trans R Soc Lond B Biol Sci*, **357**, 1539-1547.

Egas, M. (2004) Evolution restricts the coexistence of specialists and generalists: The role of trade-off structure. *Am Nat*, **163**, 518-531.

Eliassen, S. & Wegge, P. (in press) Ranging behaviour of male capercaillie (*Tetrao urogallus*) outside the lekking ground in spring *J Avian Biol*.

Emlen, J.M. (1966) Role of time and energy in food preference. *Am Nat*, **100**, 611-617.

Finne, M.H., Wegge, P., Eliassen, S., & Odden, M. (2000) Daytime roosting and habitat preference of capercaillie *Tetrao urogallus* males in spring - the importance of forest structure in relation to anti-predator behaviour. *Wildlife Biology*, **6**, 241-249.

Fortin, D. (2003) Searching behavior and use of sampling information by free-ranging bison (*Bos bison*). *Behav Ecol Sociobiol*, **54**, 194-203.

Fretwell, S.D. & Lucas, H.L.J. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor*, **19**, 16-36.

Fryxell, J.M. & Lundberg, P. (1997) *Individual behavior and community dynamics* Chapman & Hall, New York.

Giraldeau, L.-A. (1997) The ecology of information use. In *Behavioural Ecology - An evolutionary approach (4nd edn)* (eds J.R. Krebs & N.B. Davis), pp. 42-68. Blackwell, Cambridge, UK.

Giraldeau, L.-A. & Caraco, T. (2000) *Social Foraging Theory* Princeton University Press, Princeton, NJ.

Giske, J., Mangel, M., Jakobsen, P., Huse, G., Wilcox, C., & Strand, E. (2003) Explicit trade-off rules in proximate adaptive agents. *Evol Ecol Res*, **5**, 835-865.

Gould, J.P. (1974) Risk, stochastic preference, and the value of information. *J. Econ. Theory*, **8**, 64-84.

Grafen, A. (1984) Natural selection, kin selection and group selection. In *Behavioural Ecology: An Evolutionary Approach (2nd edn)* (ed J.R. Krebs, N.B. Davies), pp. 62–84. Blackwell Scientific Press, Cambridge, UK.

Green, R.F. (1984) Stopping rules for optimal foragers. *Am Nat*, **123**, 30-43.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Vincent Ginot, Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., Huth, A., Jepsen, J.U.,

Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Pioub, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., & DeAngelis, D.L. (2006) A standard protocol for describing individual-based and agent-based models. *Ecol Model*, **198**, 115-126.

Grimm, V. & Railsback, S.F. (2005) *Individual-based Modeling and Ecology* Princeton University Press, Princeton and Oxford.

Hancock, P.A. & Milner-Gulland, E.J. (2006) Optimal movement strategies for social foragers in unpredictable environments. *Ecology*, **87**, 2094-2102.

Hills, T.T. & Adler, F.R. (2002) Time's crooked arrow: optimal foraging and rate-biased time perception. *Anim Behav*, **64**, 589-597.

Hinton, G.E. & Nowland, S.J. (1987) How learning can guide evolution. *Complex Systems*, **1**, 495-502.

Hirvonen, H., Ranta, E., Rita, H., & Peuhkuri, N. (1999) Significance of memory properties in prey choice decisions. *Ecol Model*, **115**, 177-189.

Holland, J.H. (1992) *Adaptation in natural and artificial systems: An introductory analysis with applications to biology, control, and artificial intelligence.* MIT Press, Cambridge, MA.

Huse, G., Strand, E., & Giske, J. (1999) Implementing behaviour in individual-based models using neural networks and genetic algorithms. *Evol Ecol*, **13**, 469-483.

Hutchinson, J.M.C. & Gigerenzer, G. (2005) Simple heuristics and rules of thumb: Where psychologists and behavioural biologists might meet. *Behav Process*, **69**, 97-124.

Ives, A.R. & Dobson, A.P. (1987) Antipredator behavior and the population-dynamics of simple predator-prey systems. *Am Nat*, **130**, 431-447.

Iwasa, Y., Higashi, M., & Yamamura, N. (1981) Prey distribution as a factor determining the choice of optimal foraging strategy. *Am Nat*, **117**, 710-723.

Kacelnik, A. & Bateson, M. (1996) Risky theories - The effects of variance on foraging decisions. *Am Zool*, **36**, 402-434.

Kacelnik, A., Krebs, J.R., & Bernstein, C. (1992) The Ideal Free Distribution and predator-prey populations. *Trends Ecol Evol*, **7**, 50-55.

Krebs, J.R. & Inman, A.J. (1992) Learning and foraging: Individuals, groups, and populations. *Am Nat*, **140**, S63-S84.

Lima, S.L. (2002) Putting predators back into behavioral predator-prey interactions. *Trends Ecol Evol*, **17**, 70-75.

Lotka, A.J. (1925) *Elements of physical biology.* Williams and Wilkins Company, Baltimore.

Luttbeg, B. & Schmitz, O.J. (2000) Predator and prey models with flexible individual behavior and imperfect information. *Am Nat*, **155**, 669-683.

MacArthur, R.H. & Levins, R. (1967) Limiting similarity convergence and divergence of coexisting species. *Am Nat*, **101**, 377-&.

MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *Am Nat*, **100**, 603-&.

Malthus, T.R. (1798) *An essay on the principle of population as it affects the future improvement of society.* Johnson, London, UK.

McNamara, J.M. (1982) Optimal patch use in a stochastic environment. *Theor Popul Biol*, **21**, 269-288.

McNamara, J.M., Green, R.F., & Olsson, O. (2006) Bayes' theorem and its applications in animal behaviour. *Oikos*, **112**, 243-251.

McNamara, J.M. & Houston, A.I. (1985) Optimal foraging and learning. *J Theor Biol*, **117**, 231-249.

McNamara, J.M. & Houston, A.I. (1987) Memory and the efficient use of information. *J Theor Biol*, **125**, 385-395.

McNamara, J.M. & Houston, A.I. (1992) Risk-sensitive foraging: a review of the theory. *Bulletin of Mathematical Biology*, **54**, 355-378.

Meszéna, G., Kisdi, É., Dieckmann, U., Geritz, S.A.H., & Metz, J.A.J. (2001) Evolutionary optimisation models and matrix games in the unified perspective of adaptive dynamics. *Selection*, **2**, 193-210.

Nishimura, K. (1999) Exploration of optimal giving-up time in uncertain environment: a sit-and-wait forager. *J Theor Biol*, **199**, 321-327.

Nolfi, S. (1999) How learning and evolution interact: The case of a learning task which differs from the evolutionary task. *Adapt Behav*, **7**, 231-236.

Nolfi, S. & Floreano, D. (1999) Learning and evolution. *Autonomous Robots*, **7**, 89-113.

Nolfi, S. & Parisi, D. (1996) Learning to adapt to changing environments in evolving neural networks. *Adapt Behav*, **5**, 75-98.

Nolfi, S., Parisi, D., & Elman, J.L. (1994) Learning and Evolution in Neural Networks. *Adapt Behav*, **3**, 5-28.

Nonacs, P. (2001) State dependent behavior and the Marginal Value Theorem. *Behav Ecol*, **12**, 71-83.

Nowak, M.A. & Sigmund, K. (2004) Evolutionary dynamics of biological games. *Science*, **303**, 793-799.

Oaten, A. (1977) Optimal foraging in patches: A case for stochasticity. *Theor Popul Biol*, **12**, 263-285.

Odden, M., Wegge, P., Eliassen, S., & Finne, M.H. (2003) The influence of sexual size dimorphism on the dietary shifts of Capercaillie *Tetrao urogallus* during spring. *Ornis Fenn*, **80**, 130-136.

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

Outreman, Y., Le Ralec, A., Wajnberg, E., & Pierre, J.S. (2005) Effects of within- and among-patch experiences on the patch-leaving decision rules in an insect parasitoid. *Behav Ecol Sociobiol*, **58**, 208-217.

Owens, I.P.F. (2006) Where is behavioural ecology going? *Trends Ecol Evol*, **21**, 356-361.

Parker, G.A. & Smith, J.M. (1990) Optimality theory in evolutionary biology. *Nature*, **348**, 27-33.

Peck, S.L. (2004) Simulation as experiment: a philosophical reassessment for biological modeling. *Trends Ecol*, **19**, 530-534.

Ranta, E., Lundberg, P., & Kaitala, V. (1999) Resource matching with limited knowledge. *Oikos*, **86**, 383-385.

Real, L.A. (1994) How to think about behavior: an introduction. In *Behavioral mechanisms on evolutionary ecology* (ed L.A. Real), pp. 1-8. The University of Chicago Press, Chicago, MI.

Rosenzweig, M.L. (1981) A theory of habitat selection. *Ecology*, **62**, 327-335.

Schacter, D.L. (1999) The seven sins of memory - Insights from psychology and cognitive neuroscience. *American Psychologist*, **54**, 182-203.

Schilman, P.E. & Roces, F. (2003) Assessment of nectar flow rate and memory for patch quality in the ant *Camponotus rufipes*. *Anim Behav*, **66**, 687-693.

Schoener, T.W. (1987). A brief history of optimal foraging theory. In *Foraging behaviour* (eds A.C. Kamil, J.R. Krebs & H.R. Pulliam), pp. 5-67. Plenum Press, New York, NY.

Shettleworth, S.J. (1998) *Cognition, evolution and behavior* Oxford University Press, Oxford, UK.

Shettleworth, S.J., Krebs, J.R., Stepehens, D.W., & Gibbons, J. (1988) Tracking a fluctuating environment: a study of sampling. *Anim Behav*, **36**, 87-105.

Sih, A., Bell, A.M., Johnson, J.C., & Ziemba, R.E. (2004) Behavioral syndromes: An integrative overview. *Q Rev Biol*, **79**, 241-277.

Stephens, D.W. (1989) Variance and the value of information. *Am Nat*, **134**, 128-140.

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

Stephens, D.W. (2002) Discrimination, discounting and impulsivity: a role for an informational constraint. *Philos Trans R Soc Lond B Biol Sci*, **357**, 1527-1537.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging theory.* Princeton University Press, Princeton, NJ.

Strand, E., Huse, G., & Giske, J. (2002) Artificial evolution of life history and behavior. *Am Nat*, **159**, 624-644.

Sumida, B.H., Houston, A.I., McNamara, J.M., & Hamilton, W.D. (1990) Genetic algorithms and evolution. *J Theor Biol*, **147**, 59-84.

Sutton, R.S. & Barto, A.G. (1998) *Reinforcement learning: an introduction*. MIT Press, Cambridge, MA.

Tentelier, C., Desouhant, E., & Fauvergue, X. (2006) Habitat assessment by parasitoids: mechanisms for patch use behavior. *Behav Ecol*, **17**, 515-521.

Thiel, A. & Hoffmeister, T.S. (2006) Selective information use in parasitoid wasps. *Anim Biol*, **56**, 233-245.

Tinbergen, N. (1963) On aims and methods of ethology. *Z Tierpsycol*, **20**, 410-433.

Todd, I.A. & Kacelnik, A. (1993) Psychological mechanisms and the Marginal Value Theorem: dynamics of scalar memory for travel time. *Anim Behav*, **46**, 765-775.

Todd, P.M. (1996) The causes and effects of evolutionary simulation in behavioral sciences. In *Adaptive individuals in evolving populations: models and algorithms* (eds R.K. Belew & M. Mitchell), pp. 211-224. Addison-Wesley Publishing Company Inc.

Tregenza, T. (1995) Building on the Ideal Free Distribution. *Adv Ecol Res*, **26**, 253-307.

Valone, T.J. (1989) Group foraging, public information, and patch estimation. *Oikos*, **56**, 357-363.

Valone, T.J. & Brown, J.S. (1989) Measuring patch assessment abilities of desert granivores. *Ecology*, **70**, 1800-1810.

van Alphen, J.J.M., Bernstein, C., & Driessen, G. (2003) Information acquisition and time allocation in insect parasitoids. *Trends Ecol Evol*, **18**, 81-87.

Volterra, V. (1926) Variations and fluctuations of the numbers of individuals in animal species living together. (Reprinted 1931). In *Animal Ecology* (ed R.N. Chapman). McGraw Hill, New York, NY.

Waddington, C.H. (1953) Genetic assimilation of an acquired character. *Evolution*, **7**, 118-126.

Wajnberg, E., Bernhard, P., Hamelin, F., & Boivin, G. (2006) Optimal patch time allocation for time-limited foragers. *Behav Ecol Sociobiol*, **60**, 1-10.

Wajnberg, E., Gonsard, P.A., Tabone, E., Curty, C., Lezcano, N., & Colazza, S. (2003) A comparative analysis of patch-leaving decision rules in a parasitoid family. *J Anim Ecol*, **72**, 618-626.

Ward, J.F., Austin, R.M., & MacDonald, D.W. (2000) A simulation model of foraging behaviour and the effect of predation risk. *J Anim Ecol*, **69**, 16-30.

Wegge, P., Eliassen, S., Finne, M.H., & Odden, M. (2005) Social interactions among capercaillie *Tetrao urogallus* males outside the lek during spring. *Ornis Fenn*, **82**, 147-154.

Wildhaber, M.L., Green, R.F., & Crowder, L.B. (1994) Bluegills continuously update patch giving-up times based on foraging experience. *Anim Behav*, **47**, 501-513.

Wilson, W.G., Osenberg, C.W., Schmitt, R.J., & Nisbet, R.M. (1999) Complementary foraging behaviors allow coexistence of two consumers. *Ecology*, **80**, 2358-2372.

Wilson, W.G. & Richards, S.A. (2000) Evolutionarily stable strategies for consuming a structured resource. *Am Nat*, **155**, 83-100.

Yamamura, N. & Tsuji, N. (1987) Optimal patch time under exploitative competition. *Am Nat*, **129**, 553-567.

Yodzis, P. (1989) *An introduction to theoretical ecology.* Harper & Row, New York, NY.

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 consepts

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 inhered traits that evolve under the selective forces of the model environment. Individual foragers differ only in the values of the following three strategy traits:

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
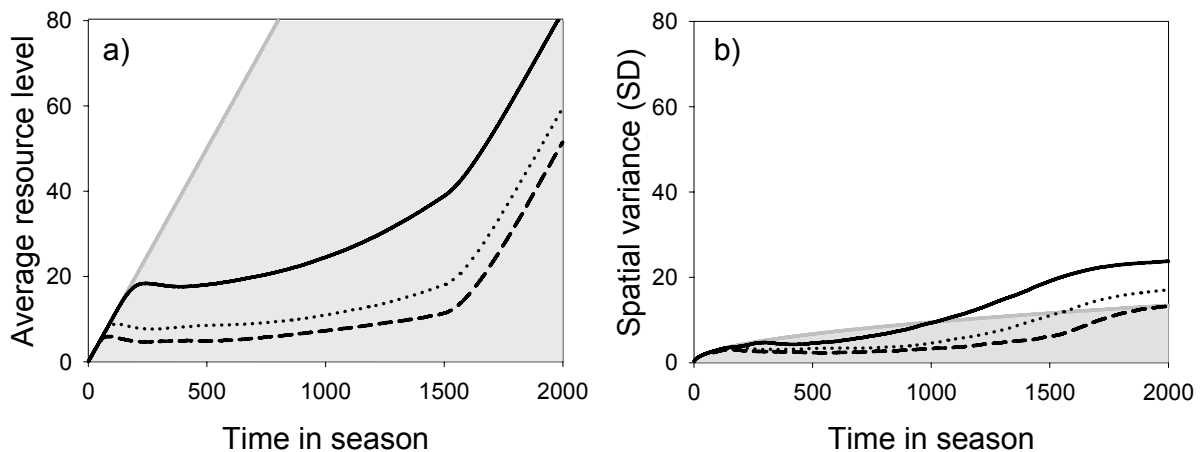

Figure A1. Resource dynamics at different population densities. a) Average resource level in patches as a function of time in season. b) Spatial variability among patches at different times in season, given as the standard deviation in resource levels. The temporal change in resource conditions varies 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 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)
Parameters		
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)
Individual genome		
τ_0	Innate giving-up threshold	1-T
γ	Learning factor	0.0-1.0
ε	Hatching time	1-T
Variables		
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	