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Olsson, Ola

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PO Box 117
221 00 Lund
+46 46-222 00 00

Decisions under uncertainty: Bayesian foraging – a meeting held at Lund University in August 2003

In your hands is a collection of 11 papers relating to Bayesian foraging. They explain Bayesian foraging, its history and future, and its uses and applications. They share the delights, excitements and opportunities of studying foraging and other behaviours from a Bayesian perspective.

Simply put, Bayesian foraging is an application of statistical decision theory (reviewed by Dall et al. 2005). Like a Bayesian statistician a Bayesian forager is assumed to have a prior expectation of the state of some aspect of the environment. Using sampling information, it can update its prior expectation into a posterior on which the decisions are based. In this framework we can predict and study how animals make optimal decisions and choices in an uncertain world. Most behavioural studies within a Bayesian framework consider foraging, but there are notable exceptions (e.g. mate choice Luttbegg 1996, reviewed by T. Valone). As pointed out by McNamara et al. the general theory and concepts apply to any decisions that should be optimised. We hope to attract readers from all the disciplines of behavioural and evolutionary ecology, and to inspire more work in the area.

The papers in this volume emerge from a small meeting on Bayesian foraging, held at Lund University in August 2003. The meeting was organized and arranged by Anders Persson, Emma Sernland, Joel Brown, Noël Holmgren, Marika Stenberg, and myself, with financial support from the Hans Kristiansson Foundation and Department of Animal Ecology at Lund University.

These papers cover the full range of studies from broad conceptual, over specific models, to experimental and field tests of predictions and assumptions. As much as the studies here rest firmly on a history of foraging studies, they also point at novel and interesting directions for the future.

In the first paper John McNamara, Richard Green and Ola Olsson provide an overview of how statistical decision theory can be applied to animal behaviour. They review the theoretical history of the field. In particular they discuss how the Bayesian concepts of priors and posteriors fit very well with how we think of animal experience and decision-making.

Next, Thomas Valone reviews the empirical evidence for Bayesian updating. He concludes that all but one of

the studied animals had behaviours consistent with Bayesian theory. Just like McNamara et al. he identifies a need for future work to focus on how animals acquire their prior expectations. In general, Valone's conclusions are encouraging both for the theoretical and empirical studies in this volume.

In the third paper Joel Brown and I reconcile Bayesian foraging with patch use theory. Previously, an optimal Bayesian policy (Green 1980, McNamara 1982, Olsson and Holmgren 1998) seemed incompatible with simpler patch use theory based on constant quitting harvest rates (Charnov 1976, Brown 1988). Olsson and Brown bridge this gap by introducing the concept of the foraging benefit of information.

Bayesian foraging models (Oaten 1977, Green 1980, McNamara 1982, Olsson and Holmgren 1998) can be computationally complex and not so transparent. In the fourth paper, Richard Green presents a simpler model with a more direct computational approach. Like its predecessors this model requires dynamic programming, but the analyses and results yield greater generality and transparency.

The fifth paper provides an application of this general model. I present a model for environments with only two patch types (one rich and one poor). Such systems are commonly used in experimental settings, but all explicit models have considered distributions of patch quality such as binomial, Poisson or negative binomial.

Rodrigo Vásquez presented an experiment from exactly such a setting of two patch qualities. The experiment evaluates how the animals (degus, *Octodon degus*) use and update their prior information (reviewed by McNamara et al. and Valone). Vásquez and his co-workers showed that in a novel environment the degus used an uniformed (fixed time) strategy. As they learned, but were still uncertain, they used a Bayesian strategy, and after long exposure to the constant environment they used a strategy consistent with perfect information.

Chris Fraser presented a model of group foragers that estimated patch content according to a Bayesian strategy. The results of this model were that groups that shared information between members could make a more accurate estimate. They could exploit the environment more efficiently, than groups where members kept their information private.

All patch foraging models, such as many of those considered in this volume, rely on the assumption that animals can identify patches at some relevant scale. Raymond Klaassen presented an experiment with mallards (*Anas platyrhynchos*), and demonstrated clearly that these birds have a foraging scale. Thus, the assumption that animals identify patches, and make their decisions on this scale is supported.

In the ninth paper Marika Stenberg and Anders Persson investigate the foraging of benthic feeding fish at three spatial scales. The fish were unable to respond to differences in prey densities within parts of artificial patches (micro-patches), but between patches their foraging was consistent with a Bayesian strategy. Between lakes, patch departure was related to long-term growth expectations, indicating differences in the prior expectations of the fish.

Finally, Bart Nolet presented two studies on Bewick's swans (*Cygnus bewickii*). The first of these considers the seasonal change in prior expectation of habitat quality. They compared the swans' behaviour with one strategy based on a fixed patch-leaving threshold and one with a flexible, based on a linear operator model. Contrary to expectations for foragers under exploitative competition, the swans behaved mostly in accord with the fixed patch-leaving threshold. That is, they did not seem to modify their prior as much as would be optimal, over the season.

In order to make complete and realistic models of information use other constraints must be incorporated. In the final paper Bart Nolet considers in detail how energetic costs and accessibility of food may, in addition to possible assessment errors, influence the patch departure decision.

In addition to these we had several other contributions, which have either not yet been published, or published elsewhere. Luis Miguel Bautista presented a study on coal tits' (*Parus ater*) information gathering. Sasha Dall gave a talk on how to manage and insure against uncertainty (Dall and Johnstone 2002). Jan van Gils presented a theoretical and empirical study on

incompletely informed knots (*Calidris canutus*, van Gils et al. 2003). Noël Holmgren discussed if information sharing among Bayesian foragers promotes group foraging (Sernland et al. 2003), and Emma Sernland (2005) described a Bayesian foraging PC-game for humans.

Ola Olsson

Department of Animal Ecology, Lund University
Ecology Building, SE-223 62 Lund, Sweden
ola.olsson@zooekol.lu.se

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